Primates are living links to our past: the contribution of comparative studies with wild vervet monkeys to the field of social cognition

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Abstract

By studying the behavior of nonhuman primates, particularly in wild settings, researchers have been able to investigate a range of cognitive abilities, shedding light on the evolution of certain aspects of cognition and revealing potential evolutionary precursors of many capacities considered uniquely human. Vervet monkeys (*Chlorocebus pygerythrus*) have been widely investigated due to their prevalence and their suitability for experimental testing in the wild with an ecologically valid approach that is not possible with many other primates, especially apes. Here we review advances in the understanding of a number of cognitive and behavioral processes that have been gleaned from studies conducted with wild vervet monkeys over the past half century, primarily focusing on social cognitive abilities. We direct our attention to three major areas of study; communication, cooperation and trade, and social learning. We discuss how findings from this species have contributed (and continue to contribute) to our understanding of the evolution of human cognitive capacities and suggest future avenues of research with this species.

Keywords

Vervet monkey, Cooperation, Communication, Social learning, Comparative approach.

1 Introduction

Understanding the human mind is a principal interest in the broad domain of cognitive sciences. To understand the evolution of the human species (*Homo sapiens*) and the origin of our behaviors and abilities, such as sociality and the use of language, researchers have mainly based their studies on our closest living relatives, the nonhuman primates (hereafter simply ‘primates’). From a phylogenetic point of view, nonhuman great apes (hereafter simply ‘apes’) are the closest relatives to humans (Groves, 2001) and therefore many studies have been carried out with chimpanzees (and to a lesser extent with the other apes) to investigate cognitive domains such as language (Tomasello *et al.*, 1997), tool use and physical cognition (Gruber, Clay, & Zuberbühler, 2010), cooperation (Melis, Hare, & Tomasello, 2006), and social learning (Whiten & Boesch, 2001). These studies have proved invaluable, allowing us to better understand the cognitive abilities of our closest relatives and thus form hypotheses about the selection pressures which may have led to the evolution of our own abilities. However, in order to better understand how environmental pressures affect the evolution of certain cognitive abilities (Kappeler & van Schaik, 2002; Liebal, Waller, Slocombe, & Burrows, 2013), it is also beneficial to study a wide range of species under a broad scope of ecological conditions given that challenges imposed by ecological niches differ among species, requiring specific cognitive abilities. Analogous cognitive abilities in more distant species may emerge due to the morphological characteristics of the individuals as well as of their physical and social environments (Liebal *et al.*, 2013). Thus, studying more distant relatives might also provide valuable information on the origin of a wide range of behaviors (communication, Liebal *et al.*, 2013; Meguerditchian & Vauclair, 2008; cooperation, Kappeler & van Schaik, 2006; sociality, Dunbar, 2010; tool use, Sanz, Call, & Boesch, 2013; social learning and social transmission, Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009).

2 Vervet monkeys: a well suited study model.

2.1 Feasibility

From a logistical standpoint, experimental study of wild apes can be problematic due to necessary restrictions upon, for example, provisioning wild populations. Thus studying widespread (Baldellou, 1991; Fedigan & Fedigan, 1988) and currently nonendangered species of monkeys, such as vervet monkeys (*Chlorocebus pygerythrus*), is more ethically and logistically feasible. In addition, vervet populations are found in different environments, including human disturbed areas, and compared with many neophobic primate species, vervet monkeys tend to show strong adaptability (Saj, Sicotte, & Paterson, 1999, 2001).

Vervet monkeys are part of the large genus Chlorocebus (Figure 1a) and are one of the most widespread and abundant species on the African continent (Baldellou, 1991; Fedigan & Fedigan, 1988). Recognizable by their gray pelage and their black face surrounded by a band of white hair (Figure 1b), vervet monkeys show some sexual dimorphism, with males larger and heavier than females (Turner, Anapol, & Jolly, 1997). Individuals can differ notably in facial and body characteristics (pelage color, size and marks left by injury, such as broken tails or fingers). Consequentially, these physical features allow researchers to identify individuals with relative ease and thus allowing close observation of behavior at the individual level. Additionally, the short distances traveled daily (troops territory size can range up to a few square kilometers, depending on the composition and distribution of the vegetation, Struhsaker, 1967a), the ease with which these monkeys can be habituated to human observers and their partially terrestrial nature all make vervet monkeys an optimum candidate for researchers studying primates in the wild.

2.2 Sociality

In addition to purely logistical reasons, vervet monkeys also present a theoretically interesting study species, particularly with regards to their social organization and the study of social cognitive capacities. They are typically organized in multi-male, multi-female stable troops ranging from 2 to 76 individuals (Baldellou, 1991), although group size can vary across study sites (Borgeaud, Sosa, Bshary, Sueur, & van de Waal, 2016; Cheney & Seyfarth, 1982a; McFarland, Barrett, Boner, Freeman, & Henzi, 2014). Females are philopatric and live in female-bonded troops following a matrilineal social organization, while males are the dispersing sex (Cheney & Seyfarth, 1990). During their lifetime, males migrate between different groups at least once after reaching sexual maturity (usually around 4 years old, Baldellou, 1991), which allows them to avoid inbreeding (Cheney & Seyfarth, 1983). The philopatric females display a hierarchy of matrilines, with daughters generally occupying the rank below their mother in reverse birth order (Cheney & Seyfarth, 1990). Males form separate hierarchies which are less stable and rely more on success in conflicts and female support

(Cheney & Seyfarth, 1990; Raleigh & McGuire, 1989). While they preferably eat items off trees (Struhsaker, 1967a; Tournier *et al.*, 2014), they are opportunistic omnivores that adapt their diet depending on food availability, foraging in both trees and on the ground (Fedigan & Fedigan, 1988; Lee & Hauser, 1998) and will often eat human food if available (Struhsaker, 1967a). Thus, vervet monkeys show similarity to humans in terms of this omnivorous diet, compared with fully-arboreal and herbivorous primates.

2.3 Field studies

Compared to chimpanzees, relatively few behavioral and cognitive studies have been conducted with captive vervet monkeys (e.g., Fairbanks, 1980; Raleigh & McGuire, 1989). Experiments in captive and natural environments can provide valuable and complementary evidence regarding animal cognitive capacities. While captive experiments enable a high control of variables, field experiments provide strong ecological validity that might be of importance for some research questions. For instance, captive animals, particularly those in close contact with humans, tend to show an enhancement of certain abilities (such as the 'enculturation effect' in human-reared apes), compared to their wild counterparts (Whiten & van Schaik, 2007) and may show increased levels of curiosity (Damerius, Graber, Willem, & van Schaik, 2017), which is likely to affect their performance and behavior in cognitive testing. This enhancement of abilities has also been observed in vervet monkeys with direct access to human facilities, thus showing the adaptability of these primates in different environments (van de Waal & Bshary, 2010). Additionally, the absence of ecological impacts in captivity may dramatically affect behavior and provide only an incomplete picture to researchers. Thus, in order to gain a greater understanding of primate behavior in a more natural environment, much data has focused on wild populations of this species. In addition to collection of observational data, researchers have also conducted a number of field experiments with wild vervet monkeys (Seyfarth, Cheney, & Marler, 1980; van de Waal, Spinelli, Bshary, Ros, & Noë, 2013a). These experiments allow researchers to introduce an experimental manipulation, whilst still retaining the ecological validity of a field study and are becoming increasingly popular in behavioral and cognitive investigations (Aplin *et al.*, 2015; Pesendorfer *et al.*, 2009).

The studies presented in the current review focus primarily on observational and experimental investigations with wild vervet monkeys. The majority of studies that we discuss here were carried out at four different field sites in Africa: Masai-Amboseli Game Reserve in South-Central Kenya, Amboseli National Park in Southern Kenya, Loskop Dam Nature Reserve in Northern Mpumalanga, South Africa and at the Inkawu Vervet Project in KwaZulu-Natal, South Africa. With this review, we hope to highlight the important contribution that research with vervet monkeys (and primates in general) has made to our understanding of the evolution of human social cognition. We provide an overview of cognitive research on this species across a variety of different domains, but also highlight some gaps in the current knowledge. There are certain areas of research that have been investigated more heavily than others in vervet monkeys owing to their vocal abilities (and in particular for initial research, their alarm calls), their group size and social organization and the interaction between neighbouring groups of a population. Accordingly, this review focuses on three areas of primate research that have taken advantage of these traits to test a number of hypotheses: 1) communication, 2) cooperation and trading, and 3) social learning.

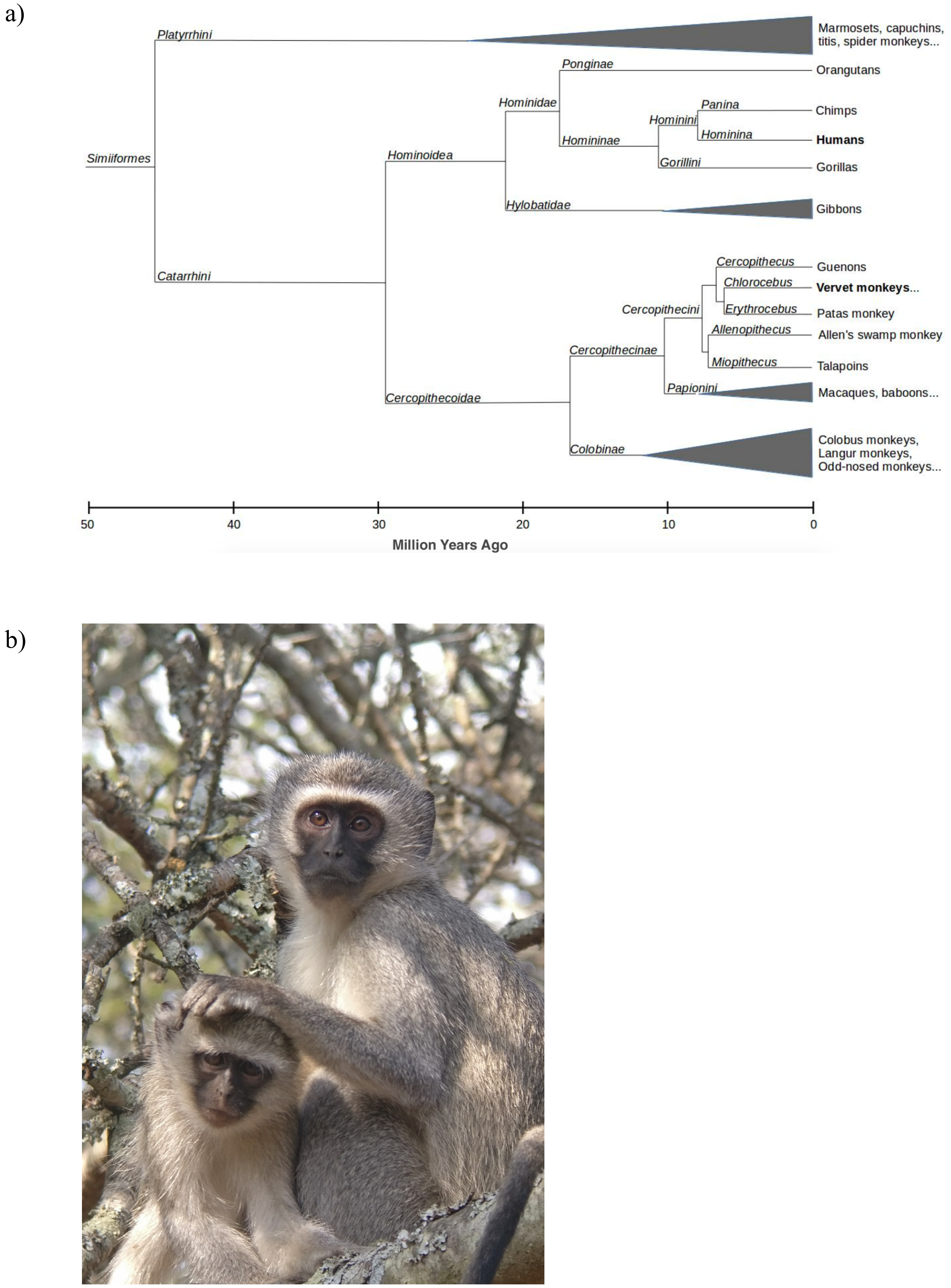

Figure 1: a) Simiiform portion of a time tree (adapted from Springer et al., 2012) to show the phylogenetic relationship between vervets and humans, and their common ancestor (~ 30 Mya);

b) Picture of a female vervet monkey with her baby (< 1 yo).

3 Communication

We begin our review with the research on the evolution of communication; an area in which research with vervet monkeys has contributed significantly. Research on a wide range of animal species has revealed a broad spectrum of communication systems that have evolved, employing different levels of complexity with highly specific olfactory, vocal and/or visual signals. From the perspective of behavioral ecologists, communication is defined as ‘the process in which the actors use specially designed signals or displays to modify the behavior of reactors’ (Krebs & Davies, 2009). Whilst there is some tentative evidence of olfactory communication in both humans (Chen & Haviland-Jones, 2000; de Groot *et al.*, 2015) and vervet monkeys (Freeman, Pasternak, Rubi, Barrett, & Henzi, 2012), we restrict this review to only vocal and gestural communication which have both received more comparative research focus.

Vocal and gestural communication have been widely investigated in primates to understand the origin of the human language. Across their evolutionary history, humans are the only species that have acquired a specific communication mode known as ‘language’. This unique communication system enables us to exchange information intentionally by using referential signals (Tomasello, 2003). Through this system, humans can generate, in an intentional and flexible way, an infinite range of messages from a finite number of discrete units – words – according to language-specific rules (e.g., syntax, semantic; Hauser, Chomsky, & Fitch, 2002).

One of the current biggest challenges in animal communication is to understand why humans possess this complex cognitive ability and how it has evolved. The comparative study of communication systems can help to understand which features were already present in the common ancestor of humans and primates, and which ones emerged later (Hauser *et al.*, 2002). Thus, the aim of this research is to identify which components of human language are present in living primate species (Zuberbühler, Cheney, & Seyfarth, 1999) and to identify potential evolutionary precursors of language. One central debate to this field regards the modality in which language emerged first; gestural or vocal. In this part of the review, we focus on two main hypotheses to understand the origin of human language: (i) the vocal origin of language hypothesis, which proposes that human language evolved from the vocal communicative capacities that were likely present in our last common ancestor (Zuberbühler, 2005), and (ii) the gestural origin of human language hypothesis, which assumes that human's communication system evolved from the gestural communicative abilities that were likely present in our last common ancestor (Hewes *et al.*, 1973). Tomasello (2008) and Meguerditchian and Vauclair (2008) support the theory of a gestural precursor of language based on the observation of a high degree of both individual variability and flexibility in the gestural repertoire, within and among populations. On the other hand, Zuberbühler and colleagues (1999) reported referentiality and semantics of alarm calls as arguments of vocalizations being precursors to human language. Then, we discuss the limits of the unimodal theories and the promising multi-modal theory of human language evolution.

3.1 The hypothesis of vocal communication

Based on the premise that both humans and primates communicate via the vocal modality, and thus present a continuity of the communication mode (Zuberbühler, 2005), some researchers argue that language may have derived from animal vocalizations. Referentiality, the ability to refer to an external object or event, is a key feature of human language. Therefore several studies have investigated this ability in primates and indeed the semantic properties of vervet monkey alarm calls have provided a seminal example of referential ability in nonhumans

(Seyfarth *et al.*, 1980; Struhsaker, 1967b). When vervet monkeys become aware of a predator, three main types of calls, with distinct acoustical features, are produced depending on the predator category: terrestrial predators (referred to as ‘leopard alarm calls’), crawling predators (‘snake alarm calls’) and aerial predators (‘eagle alarm calls’) (Struhsaker, 1967b; Seyfarth *et al.*, 1980; for sound tracks of the three different alarm calls see supplementary materials S1, S2 and S3). Seyfarth and colleagues (1980) conducted a series of field experiments, playing back recordings of each call type to groups of wild vervets in the absence of actual predators. Each type of call elicited a unique response in the recipients which was adapted to the observed predator (even when amplitude was controlled for). These experiments provided evidence that the different call types did not simply reflect different levels of arousal in the monkeys, as had been previously suggested, but conveyed semantic information (Seyfarth *et al.*, 1980). In addition to these alarm calls, vervet monkey grunts also appear to carry specific meanings, referring to external events or objects. Distinct sets of acoustic properties are associated with at least four different social contexts including when a dominant individual approaches, when a subordinate approaches, when another animal moves into an open area and when another group is nearby, such as in between-group encounters (Cheney & Seyfarth, 1982a; Mercier *et al.*, 2017; Struhsaker, 1967c).

Furthermore, Cheney and Seyfarth (1988) have also shown that vervets may have the ability to assess and compare signals based on both the meaning and the reliability of a signaler’s call from one context to another. For example, if a vervet monkey perceives an unreliable leopard alarm call from a specific signaler, he would learn to ignore that signal whilst later he would react to an alarm call for an “eagle danger”, even if the signaler is the one previously ignored (Cheney and Seyfarth, 1988). Thus, the alarm calls could also be processed independently of the identity of the signaler in a different context. In addition, it appears that vervet monkeys pay as much attention to the identity of the caller as to the acoustic features or to the external objects or events that the calls denote (Cheney & Seyfarth, 1990). Mothers can also distinguish their offspring's vocalizations, and more generally, vervet monkeys are able to recognize which individual is producing alarm calls, distress calls, and lost calls (Cheney & Seyfarth, 1980).

However, despite the initial proposal that the vervet monkey alarm calls were symbolic (i.e. the calls were unrelated in form to the predators as words are in human language), researchers later argued that the inflexibility of the alarm calls reflected a 'hard wiring' of these vocalizations and conveyed a link between form and function (Wheeler & Fischer, 2012). For instance, there is evidence that the precision of alarm call meaning is age-dependent and that young vervet monkeys gradually restrict their alarm calls to a small number of genuine predator species within each category (Seyfarth *et al.*, 1980; Seyfarth & Cheney, 1986). Nevertheless, importantly, they do not use the wrong call for the wrong type of predator (e.g., a snake call for a bird) whilst learning and thereby show a lack of flexibility in the use of these alarm calls (Wheeler & Fischer, 2012). Therefore the term 'functionally referential' was adopted to avoid directly implying the level of cognitive sophistication behind the vocalizations (Macedonia & Evans, 1993; Wheeler & Fischer, 2012). However, there is evidence that chimpanzees show voluntary control and repertoire flexibility of vocal behavior (Perlman, 2017) and thus this debate remains open.

More recently some researchers have argued that vocalizations such as grunts, wherein apprehension of context is necessary for full understanding of the vocalization (as in human language), are more useful for examining human language evolution (Wheeler & Fischer, 2012). Additionally, a recent quantitative analysis of these alarm calls, in addition to vocalizations produced in other contexts, has shown both clear distinction in some calls (female 'chirps' given in response to leopards) and some intergradation (calls given in response to snakes and birds were also given during between and within-group aggressions, respectively)

(Price *et al*., 2015). Therefore the authors advocate for looking beyond the concept of functional referential calls and instead towards pragmatics when investigating the evolution of human language. This approach has also been encouraged by Scott-Phillips (2015) who argues that primate vocal communication likely does not share similar foundations with human language, given the differences in apparent underlying socio-cognitive mechanisms between the two. Scott-Phillips (2015) suggests that while primates (especially the apes) show a sophisticated coded communication, they do not exhibit the ostensive communication central to human language. Nevertheless, while adjusting communication to specific situation or individual from previous/present interaction .is indeed common in human language (Bohn, Call, & Tomasello, 2016), comparable cognitive foundations of communicative abilities have also been shown in apes involving socio-cognitive processes (e.g., in chimpanzees, Crockford, Wittig, Mundry, & Zuberbühler, 2012; Crockford, Wittig, & Zuberbühler, 2017). Chimpanzees are aware enough of social partner's knowledge to adapt their alarm calls and visual behavior (e.g., monitoring behavior, gaze alternation) regarding the situation and potential risks. Thus, a chimpanzee will increase his "marking behavior" towards an individual unaware of the risk (i.e. showing the location of the danger by alternating gaze between the receiver and the threat). The meaning appears to be both produced and perceived by individuals since the receiver would change his behavior based on this new given information (e.g., change of trajectory, avoidance behavior). This study therefore highlights the crucial need to deepen the investigation of social-cognitive processes and the development of complex communication system that appear to be shared by at least our closest relatives.

Pursuing this avenue and extending it to other monkeys might help us to clarify the scientific debate of complex communication mechanisms and draw the fundamental basis of language evolution, more than language specific features (e.g., syntax, referentiality).

A recent body of work has also investigated primate communication by using analytical methods from modern (human) linguistics. Schlenker *et al.* (2016) applied formal linguistic approaches to primate calls to conduct comparisons within and across species [cercopithecines: putty-nosed monkeys (*Cercopithecus nictitans martini*), blue monkeys (*Cercopithecus mitis stulmanni*), and campbell's monkeys (*Cercopithecus campbelli*); colobinae: guereza monkeys (*Colobus guereza*) and king colobus monkeys (*Colobus polykomos*); new world monkeys: titi monkeys (*Callicebus nigrifrons*)]. For example, the authors presented some similarities in use and acoustic features in guereza and king colobus monkey calls, suggesting possible preservation of form and function of calls across very distant species (in this case, over 1.6 million years ago). The authors acknowledge that such findings do not predict (at least yet) any convergent evolution between monkeys and human languages, but they suggest that 'comparative approaches to the calls of different monkey species would lay the groundwork for an evolutionary monkey linguistics' (Schlenker *et al.*, 2016, p.62). Therefore, while the vocal theory of language evolution is still very much under debate, the contribution of the observations and field experiments with vervet monkeys to our understanding of language evolution remains significant.

3.2 The hypothesis of gestural communication

As discussed above, one of the prime criticisms of the vocal theory of language evolution is the apparent lack of flexibility shown in vocalization production. According to Corballis (2002), primates use vocalizations more often than gestures in urgent contexts, with very few voluntary controls. For example, the vocal mode is preferentially used in avoidance of predators (Tomasello & Zuberbühler, 2002). On the contrary, gestural communication mainly occurs in less urgent situations, especially in a social context such as playing or grooming (Arbib, Liebal, & Pika, 2008; Tomasello, 2008). Thus, gestures are produced under a lower emotional charge, allowing better voluntary control and flexibility (Tomasello, 2008; Meguerditchian & Vauclair, 2008), which are essential characteristics in the human language

(Corballis, 2002). Gestural precursors are therefore of great interest in understanding the evolution of human language. A gesture can be defined as a form of nonverbal communication which transmits particular messages with visible bodily actions (Kendon, 2004). There have been recent advances in the study of gestural communication in primates, particularly in field observations. These studies have attempted to assess the flexibility and intentional use of gestures, as well as their ontogenetic development (Genty, Breuer, Hobaiter, & Byrne, 2009; Graham, Furuichi, & Byrne, 2017; Hobaiter & Byrne, 2011). This has been primarily conducted with apes (social-cognition flexibility of iconic gestures, Bohn *et al.*, 2016; ontogeny, Fröhlich, Wittig, & Pika, 2019). For example, chimpanzees show markers of intentional communication production affected by the age, social and physical environment (e.g., identity of the dyadic partner, context), and are able to adjust their gestures according to the recipient's attentional state (Fröhlich *et al.*, 2019). Intentional communication has also been assessed in gestural communication in monkeys. Indeed, food-requesting gestures that appear to show intentional communication have been examined in bonnet macaques (*Macaca radiata* in communication to humans, Deshpande, Gupta, & Sinha, 2018) as well as, usage and meaning of nonvocal signals in Old World monkeys (Maestripieri, 1997). An early study described communicative gestures as evolutionary stable signals in contrast to vocal patterns in vervet monkeys (Struhsaker, 1967c); yet a more detailed analysis of vervet monkey gestural communication is required to allow researchers to compare the properties of vervet gestural systems to properties specific to human language (e.g., markers of intentional communication, iconicity, and flexibility). Plus, vervet monkeys' social and physical environment present an advantage to study the impact of these factors, and further studies on the ontogeny of communicative gestures and the cognitive processes involved might bring evidence of its adaptive functions and the emergence of language-specific characteristics. In addition, Armstrong and Wilcox (2007) supported the gestural theory based on evidence from sign languages. The authors highlighted the importance of iconicity: the visual modality of sign languages allows an easier relationship between a symbol and its referent compared to spoken languages. The authors thus used the iconic component of signs as an argument in favor of an earlier emergence of the gestural origin of language compared to its vocal counterpart, in addition to many others (e.g., the evidence of a strong visual acuity in our common ancestor as an arboreal monkey, the presence of co-speech gestures in human language, etc.). In this respect, studying sign languages could shed light on the understanding of the emergence of human language (also see Pfau, Steinbach, & Woll, 2012).

Furthermore, a recent study compared gestures between 1- to 2-year-old human children, and juvenile and adult chimpanzees (Kersken, Gómez, Liszkowski, Soldati, & Hobaiter , 2018) using camera recordings. The authors recorded children's daily lives and annotated their gestural repertoires to compare them to those of wild chimpanzees previously recorded using the same method. The preliminary results showed important overlapping among the repertoires by providing strict comparable data across species, thus opening a new methodology to be applied in many species. In addition with comparisons with our closest ancestors, comparing gestural repertoires between children and more distant relatives as vervet monkeys might increase our knowledge of the role of gestures in the human language.

In summary, field observations and, later, field experiments with wild vervet monkeys have provided us with some important knowledge about communication systems in primates, particularly with regard to the vocal domain. Early work found evidence for semantic communication in vervet monkey alarm calls that prompted similar investigations and findings in wild chimpanzees (*Pan troglodytes schweinfurthii*, Slocombe & Zuberbühler, 2005), western red colobus, western black-and-white colobus, diana monkey, lesser white-nosed monkey, campbell’s guenon and the sooty mangabey (respectively *Colobus babius*, *Cercopithecus diana*, *Cercopithecus petaurista, C. campbelli* and *Cercocebus atys*;

Zuberbühler *et al.*, 1999). More recent analyses have since furthered our understanding of context and variability within these vocalizations.

As in the above examples, most of the studies addressing the origin of human language are based on a unimodal perspective, i.e. on different theoretical and methodological approaches, making the intermodal comparison problematic. The validity of theories based on such comparisons may therefore be questionable and call for integrated multimodal research taking into account the social and physical environment as well as the cognitive processes involved in communication abilities. While both vocal and gestural systems of communication were already present in mammals and evolved to be part of complex communicative skills (Kendon, 2017), theories that advocate a multimodal origin of human spoken language seem to be a promising approach. Moreover, the coupling of gestures and vocalizations is well documented, bearing the question of a potential multimodal origin of human speech where gestures and speech evolved conjointly without one modality taken over another (McNeill, 1992). It has been established that primate and human communication are produced and perceived in a multimodal way accompanied by nonlinguistic and nonverbal signals (gestures, hands, face and body, McNeill, 1992; Liebal *et al.*, 2013). For example, chimpanzees produce and recognize bimodal communication (Parr, Cohen, & de Waal*,* 2005; Fröhlich *et al.*, 2019; Taglialatela *et al.*, 2015; Crockford *et al.*, 2012, 2017) to meet specific communicative ends (e.g., alternation of vocalizations with gaze monitoring).

More important than finding out which modality prevails over the other via unimodal studies, it is interesting to look through a multimodal approach at the emergent properties, such as pragmatism, iconicity or intentionality, coordinated across the multiple modalities, that have evolved from the abilities already present in our common ancestors, as well as the cognitive, social, and environmental parameters that affect them (Slocombe, Waller, & Liebal, 2011; Perlmann, 2017; Kendon, 2017; Fröhlich *et al.*, 2019). In this respect, studying wild vervet monkeys with different group characteristics using a multimodal approach might therefore provide further insight into the linkage between social, ecological and communicative abilities to fulfill our understanding on how human language emerged and evolved.

Whilst there is still considerable debate concerning the extent to which primate communication modes share evolutionary foundations with human language, research with wild primates has, and will likely continue to, provide valuable insight into this debate.

4 Cooperation and exchange of commodities

Another behavior, particularly complex in humans, is the behavioral act of cooperation, defined as the assistance or support of one individual by another wherein it is beneficial for the recipient (van Schaik & Kappeler, 2006). Depending on the action, the cost may vary; a cooperative act is called mutualistic when both individuals involved benefit equally from the interaction, while an altruistic act provides a greater benefit to the receiver than to the actor (van Schaik & Kappeler, 2006). In apparent contrast to other animals, humans show widespread cooperation among non-kin and there are often long time delays before an altruistic act is reciprocated (Clutton-Brock, 2009). Indeed, we display an unusually high level of cooperation, which is apparent in many aspects of life and likely crucial to our success as a species (Melis & Semmann, 2010). It has been suggested that without a means of specifying agreements (i.e. language), other animals are not able to maintain such reciprocity (Clutton-Brock, 2009). However, cooperative behaviors are observed in several animal species, highlighting the importance of investigating these behaviors to understand the evolutionary origins of our own remarkable cooperation (Fehr & Rockenbach, 2004). Several examples of cooperation seen in the animal kingdom are from primate taxa and both observations and field experiments with primates have contributed much to our knowledge of animal cooperation. In particular, the social structure of vervet monkeys, including groups of both kin and non-kin and of both sexes, has allowed us to examine cooperation within and between kin, hierarchy, and sex. Below we detail several studies in wild vervet monkeys that reveal evidence of reciprocity and trading of commodities. We focus our review on the aspects of cooperation which have been most intensively studied in this species, including grooming, infant handling and participation in between-group encounters, and discuss the roles these cooperative behaviors play within the social organization of this species.

4.1 Reciprocal grooming

Allogrooming has been described as the most common form of affiliative behavior in primates (Dunbar, 1991; Seyfarth & Cheney, 1990; Leinfelder, de Vries, Deleu, & Nelissen, 2001). Aside from its apparent health benefits, such as ectoparasite reduction and thermoregulation (Tanaka & Takefushi, 1993; Barrett & Henzi, 2006), grooming has an important social impact. Indeed, allogrooming likely creates and maintains bonds between group members (Carpenter, 1942; Dunbar, 2010; Dunbar & Sharman, 1984; Sade, 1972). Grooming constitutes approximately 15% of female vervet monkeys' time-budget (Fruteau, Lemoine, Hellard, van Damme, & Noë, 2011a) and thus represents a valuable commodity which can potentially been changed for grooming from others, for infant access (Fruteau, van de Waal, van Damme, & Noë, 2011b) or for tolerance and building alliances. There is evidence that vervet monkeys, as well as other primates, are aware of the value of grooming as a commodity and do indeed exchange it in reciprocal grooming; to receive a satisfactory amount of grooming, they modulate the time they invest in grooming a partner, depending on their rank and the rank of their dyadic partner (Fruteau *et al.*, 2011a).

Early observations of vervet monkeys showed that unrelated females preferentially form alliances with those individuals who groom them at the highest rates (Cheney & Seyfarth, 1990) and that most grooming-related interactions are initiated by lower-ranking individuals

(Fruteau *et al.*, 2011a). Indeed observations of vervet monkeys led to one of the first models of commodity exchange in primates (Seyfarth, 1977). This suggested that grooming is also exchanged for cooperation in alliances. In addition to observational work, a series of field experiments have been conducted to examine reciprocity in vervet monkeys. Borgeaud and Bshary (2015) found that during a short period following grooming between a dyad, subordinates monkeys were more tolerated in a foraging context by dominants whom they had groomed. The subordinate grooming partner was also supported during aggressions by a third party in within-group conflicts, although support was selectively given against lower-ranking third parties only (Borgeaud & Bshary, 2015). As these conflicts represent a high-risk activity for vervet monkeys (Cheney & Seyfarth, 1987), this earned support might play an important role for the safety of the groomer. This exchange of services is thus a convincing example of direct reciprocity and highlights the importance of such short-term direct reciprocity among related and unrelated individuals in the same group (Borgeaud & Bshary, 2015). While several studies have investigated reciprocity in apes (e.g., in white-handed gibbons, *Hylobates lar,* Barelli, Reichard, & Mundry, 2011) and various primate species (e.g., in common marmosets, *Callithrix jacchus*, see Lazaro-Perea, de Fátima Arruda, & Snowdon, 2004; in samango monkeys, *C. mitis erythrarchus*, Henzi, Payne, & Lawes, 2003), further studies are still required to assess whether this reciprocity is widespread throughout all primate species or specific to social structures similar to the one of vervet monkeys.

4.2 Food access and infant handling

One limitation of Seyfarth's (1977) model was that agonistic support is not the only commodity which is in demand in primate society and therefore primates may also groom in order to obtain other, monopolizable, resources (Barrett & Henzi, 2006; Sànchez-Amaro & Amici, 2015). Both observational and experimental works have revealed that, in addition to tolerance and support in conflicts, grooming in vervet monkeys can also be traded for food and infant handling. Fruteau and colleagues (2009) provided pieces of apple in a large box accessible by only one specific individual. Results showed that the other members of the group significantly increased their grooming time to the provider, ostensibly allowing them to be more tolerated and gain easier access to the box and thus exchanging grooming for food access. Moreover, the authors showed that introducing a second provider yielded decreased grooming-time of the first provider to enable an increase in grooming time of the second (Fruteau *et al.*, 2009). Replicating it in captive conditions might be of interest as increasing our understanding of the exact value, and also the time frame vervet monkeys use for grooming (Sànchez-Amaro & Amici, 2015). Additionally, there is also evidence that vervet females are able to make strategic social decisions with regard to tolerance. When interacting with a subordinate who had recently groomed them, they choose whether to be tolerant or to reinforce rank relationships depending on the audience attending the interaction (Borgeaud, Schnider, Krützen, & Bshary, 2017).

In addition to food resources, there is also evidence that grooming can be exchanged for access to infants. During the first month following birth, the amount of grooming and other nonaggressive social contact with mothers from other members of primate groups increases (Struhsaker, 1971). Females, and more specifically juvenile females, exhibit a specific interest for newborn infants and try to carry them as often as possible (Struhsaker, 1971). This social mechanism, called allomothering, allows the mother to rest while the allomother practices her own maternal behavior before bearing her own infant (Fairbanks, 1990; Struhsaker, 1967a). However, letting another female handle her own baby carries a high potential cost if the infant is harmed. Whilst some females (particularly more dominant females) will simply grab and steal the babies, others appear to exchange grooming for permission to handle the mother’s infant. Indeed, Fruteau and colleagues (2011b) showed that female vervet monkeys, as well as sooty mangabeys (*C. atys*), have a trading system of grooming and infant-handling; the longer a mother was groomed, the more she tolerated the groomer handling her infant. However, some researchers have suggested that rather than a system of exchange, this grooming instead serves to calm down the mother prior to her allowing her infant to be handled (Sànchez-Amaro & Amici, 2015). Indeed, this particular behavior does not seem to be observed in all primate species. In tufted capuchin monkeys (*Cebus apella nigritus*), for example, no evidence has been found for a grooming-infant handling market (e.g., Tiddi, Aureli, & Schino, 2010), possibly excluding this behavior as a valuable resource from the market. Capuchin and vervet monkeys have different social organization, and have to face different environmental pressures [e.g., tufted capuchin monkeys are arboreal (Robinson & Janson, 1987), while vervet monkeys spend most of their daylife on the ground (Fedigan & Fedigan, 1988)], although it is not clear what specific pressures would lead to differences in grooming-infant handling exchange.

Further investigations are clearly needed to more fully understand such variations in commodity exchange across primate species (Sànchez-Amaro & Amici, 2015). Nevertheless, the apparent commodity exchanges observed in vervet monkeys have been valuable in developing initial models of market trading in primates; since the attempt to gain mutualistic partners in humans might be one evolutionary precursor to reciprocation (Barclay, 2011, 2013), it seems reasonable to suggest comparable reciprocal and trading behaviors in monkeys as being precursory to the evolution of these human behaviors.

4.3 Between-group encounters

Finally, recent experiments with vervet monkeys have also revealed evidence that trading can also occur during between-group conflicts. Vervet monkey territories frequently overlap with other troops of conspecifics which leads to encounters between groups. These encounters can be affiliative, aggressive, or more neutral with groups either ignoring or observing each other, or vocalizing (Cheney, 1981). From observations of these naturally occurring encounters, Arseneau-Robar and colleagues (2016a) showed that during pauses in encounters, females will groom participants and especially males who participated actively during the most recent episode. Interestingly, the authors also found that females will exhibit aggression towards males who did not participate, indicating punishment in a wild primate. Both males who were rewarded and punished participated more in future episodes, thus highlighting the use of grooming as currency in exchange for another valuable commodity, in this case male support in between-group encounters. It also reveals the apparent efficacy of female punishment in this context. Such behaviors as punishment and reward have also been described for humans (Fehr & Rockenbach, 2004; Sefton, Shupp, & Walker, 2007), although the exact relationship between punishment and cooperation in humans remains unclear (Bone & Raihani, 2015; Raihani & Bshary, 2015). A field experiment which simulated between-group encounters via playbacks found that males participated in encounters more often when a female monkey was visibly leading the agonistic encounter. The males' probability of participation did not vary with females' access to food resources, thus suggesting they were not participating to protect females' food sources, but in order to heighten their reputation as a cooperative group member (Arseneau-Robar, Müller, Taucher, van Schaik, & Willems, 2016b).

To summarize, studying biological markets in primates remains a challenge for researchers, and the different investigations in primates grooming behaviors show various discrepancies. Indeed, while the exchange of commodities appears to be a common task in most of the primate species (Barrett & Henzi, 2006), defining the real time frame of the grooming bouts across the various primate species is a complex and sensitive task (for discussion, see Sánchez-Amaro & Amici, 2015). In addition, most studies focus on dyadic interactions (e.g., Chancellor & Isbell, 2009 in gray-cheeked mangabeys, *Lophocebus albigena*) whereas grooming bouts can be reciprocated in groups including several individuals at the same time (Sánchez-Amaro & Amici, 2015). Numerous challenges still remain, including a debate on the number of bouts to consider as part of one unique interaction to test reciprocity (see

Frank and Silk, 2009 in olive baboons, *Papio anubis*), and the length of these bouts over given observed differences between species [e.g., one hour of time frame in vervets (Fruteau *et al.*, 2009) vs two hours in chimpanzees (de Waal, 1997)]. Chimpanzees have also shown the ability to keep track of grooming reciprocity over a period of 15 months (Gomes, Mundry, & Boesch, 2009), a time frame never before observed in primates. These findings, and the cognitive capabilities required to maintain such apparent book-keeping, generate the possibility that the remarkable cooperation seen in humans may share its evolutionary roots with other primates. Indeed it has been suggested that our advanced communicative and social cognitive skills arose as an alternative to this social grooming once group sizes grew too large Dunbar (2004).

Whilst further research in this area is needed to fully understand the mechanisms and rules which govern such cooperation, but also the variations across the different species, these studies have revealed important findings about the nature of cooperative and trading behaviors in primates. However, there is also evidence for seemingly remarkable levels of cooperation in more distantly related species such as fish and eels (Bshary, Hohner, Ait-el-Djoudi, & Fricke, 2006; Bshary & Grutter, 2006). Therefore the complexity of cognition required for cooperation remains unclear, while the ecology of the species is emerging as an important factor in what cooperative specific behaviors might be displayed by a species. Further studies into various kinds of cooperative behaviors, both in primates and in more distantly related taxa would be highly beneficial in shedding more light on the evolution of cooperation. By understanding the mechanisms and limits of cooperation and reciprocity in other animals, we can attempt to understand how and why our uniquely human level of cooperation arose (Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012).

5 Social learning and culture

Primates acquire many of their abilities (e.g., food selection, communication) through asocial learning, i.e. learning without social interaction (Liebal & Call, 2012), and/or social learning, i.e. learning from interactions with conspecifics (Heyes, 1994). During the last few decades, social learning in animals has been widely investigated for a number of reasons. Firstly, it bears light on the origin of human language, given that language needs to be socially learned (Tomasello, 2008). More broadly, social learning provides the basis for culture in animal species (Whiten, 2005) with culture defined as 'group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information' (Hoppitt & Laland, 2013, p.4). Thus, interest in the evolutionary origins of culture has led to a growing interest in the study of primates within this domain (although it should be noted that some of the most convincing examples of nonhuman culture come from outside of the primate taxa, for example in cetaceans, Whitehead & Rendell, 2014). Key areas of research in social learning have investigated both how information is transmitted between individuals, in terms of mechanisms, and under which circumstances information is likely to be transmitted (Whiten & van de Waal, 2018). Here we review a number of recent studies that have examined these questions in vervet monkeys and discuss how they have furthered our knowledge of cultural evolution.

5.1 Social learning mechanisms: transmitting behaviors through imitation and/or emulation

Social learning involves observation of, or direct interaction with, another individual, and encompasses a wide range of mechanisms, from stimulus/local enhancement to more complex forms, such as teaching or imitation (Heyes, 1994; Hoppitt & Laland, 2013). Interest in the mechanisms of social learning emerged because of the striking differences between the cultures exhibited by humans and nonhuman animals. Humans are seemingly uniquely capable of cumulative culture (Dean, Kendal, Schapiro, Thierry, & Laland, 2012), the ability to make behaviors increasingly more efficient or complex through accumulating information from others. Therefore, it is highly plausible that the way in which we transmit information between individuals may be a key factor in this apparently unique capability, and that mechanisms which allow information to be transmitted with higher fidelity, such as imitation, may have allowed cumulative culture to evolve (Whiten *et al.*, 2009; Dean *et al.*, 2012). The processes of imitation (copying another's actions, Whiten & Ham, 1992) and emulation (copying the end-state of the behavior, Tomasello, 1996) are thought to be cognitively more complex than stimulus or local enhancement (wherein an individual's attraction to, or engagement with, a certain stimulus or location is enhanced by the presence of another animal, e.g., Tomasello, 1996; Tennie, Call, & Tomasello, 2009). In the last decade, a growing corpus of studies has been conducted to provide insight into the potential ability of primates to imitate, primarily with captive chimpanzees (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Whiten *et al.*, 2009; Hopper, Lambeth, Schapiro, & Whiten, 2008). However, debate still continues as to whether nonencultured chimpanzees use imitation (Tennie, Call, & Tomasello, 2012; Buttelmann, Carpenter, Call, & Tomasello, , 2013). The vast majority of these studies have been conducted with captive chimpanzees (and to a less extent, other captive species of primates), due to the aforementioned constraints of experimentation with wild primates. Whilst wild observations of apparently cultural behaviors are still confined to a relatively small number of primate species (Whiten *et al.*, 1999; van Schaik *et al.*, 2003; Santorelli *et al.*, 2011; Perry *et al.*, 2003; Hohmann & Fruth, 2003), investigations into social learning processes have been conducted with wild vervet monkeys, revealing evidence for social learning in this species.

In 2012, van de Waal and Whiten investigated bodily imitation in captive vervets using an 'artificial fruit' (first used by Custance, Whiten, Sambrook, & Galdikas, 2001), a foraging device containing food that can be opened in multiple, different ways. When models tried to open the artificial fruit (a canister with a lid and held by ropes on either end), they used three different opening methods: the lid was opened (i) with the mouth, (ii) with hands, or (iii) by grasping the ropes and pulling (Figure 2a). During the demonstration phase, each model then opened the artificial fruit several times in front of its group members. While the mouth-opening method emerged as the most popular method overall, in the group with the hand-using model, the individuals preferred to manually open the box significantly more often than the other groups. The same results were observed with the rope-pulling model in which individuals pulled the ropes at a significantly higher level than in the other groups. These behaviors thus suggested that captive vervet monkeys exhibited bodily imitation in their social learning.

To investigate social learning in wild primates, van de Waal, Claidière and Whiten (2015) then presented wild vervet monkeys with a two-action artificial fruit which could be opened by performing different actions (lift or slide) on the same door (thereby effectively ruling out local and stimulus enhancement as mechanisms). Depending on the group, models were trained to either slide the door (to the left or to the right) or to lift the door (Figure 2b). The results showed a strong positive correlation between techniques witnessed by each individual (i.e. the technique used by their model) and the technique they adopted, with monkeys showing preferences for the technique modeled in their group. These findings showed that wild primates are capable of transmitting behaviors through imitation and/or emulation, going beyond the simpler forms of stimulus and local enhancement. However, another field experiment which used a two-step task found that wild vervet monkeys failed to copy a sequence of actions (van de Waal & Bshary, 2011), thereby displaying some limitations of their social learning compared with humans (McGuigan, Whiten, Flynn, & Horner, 2007). This likely has important implications for the differences in our observed cultures and reinforces the importance of investigation with wild primates.

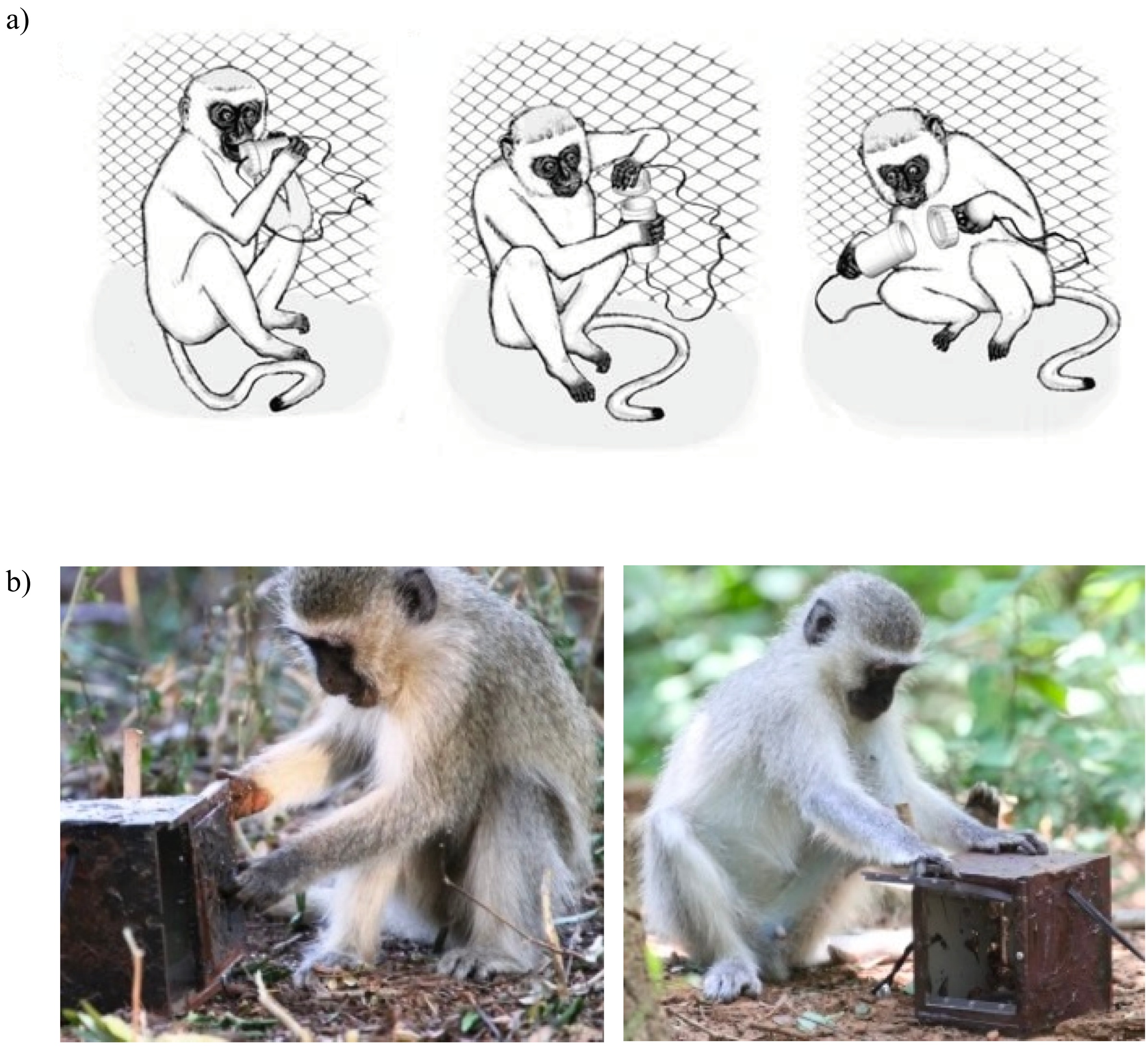

Figure 2: a) the three different techniques to open the canister used in van de Waal & Whiten, 2012; b) the artificial fruit used in van de Waal et al., 2015: door being slid to right, door being lifted.

5.2 Social learning rules: sex, kinship and majority bias

In addition to the learning mechanisms involved in social information transfer, researchers are also interested in the biases that may govern when and between whom this information is transferred. One main question to answer is whether the identity of the model (i.e. sex, age, kinship, group affiliation) affects the occurrence of social transmission. The 'social model' and 'directed social learning' hypotheses suggest that, for primates with structured social groups, some individuals are more likely to be copied than others, such as kin, or knowledgeable, older, perhaps high ranking members of the same group and species (de Waal, 2001; Coussi-Korbel & Fragaszy, 1995). To provide a better understanding of the various rules driving social learning, several experiments have been performed in foraging contexts. Some early studies have suggested sex, kinship and dominance biases in hens and birds (Nicol & Pope, 1999; Schwab, Bugnyar, Schloegl, & Kotrschal, 2008; Katz & Lachlan, 2003; Benskin, Mann, Lachlan, & Slater, 2002), and two experiments with captive chimpanzees have revealed apparent dominance and prestige biases (Horner, Proctor, Bonnie, Whiten, & de Waal*,* 2010; Kendal *et al.*, 2015; although see Watson *et al.*, 2017). An observational study highlighted a sex-based attention bias in wild vervet monkeys; under natural conditions (foraging or grooming contexts), group members paid significantly more attention to adult females rather than adult males (Renevey, Bshary, & van de Waal, 2013). A sex-based copying bias towards females was revealed using a two-action experiment; monkeys opened a box using the method demonstrated to them when it was demonstrated by a dominant female, but not by a dominant male (van de Waal, Renevey, Favre, & Bshary, 2010). Analyses showed that this was due to selective attention toward the female demonstrators, as opposed to other potential factors. This selective attention to females may be because females are philopatric in this species (remaining their whole lives in their natal group) and thus have a better knowledge about local resources and food than males who disperse when they reach sexual maturity. In addition, in a recent study, Bono and collaborators (2018), showed a payoff-bias in male, but not in female vervet monkeys. When the payoff received by male and female models was equal, participants preferentially copied the foraging method of the females. However, in conditions where male models gained a higher payoff than female models, males significantly copied male models while females continued to copy the female models. These results highlight the flexibility of male preferences toward the 'most efficient' choice while females maintained their attention to female models in both conditions These differences may be explained by the necessity of being adaptive in new groups for males as the dispersing sex, and being conservative for females as the philopatric sex.

In the latter studies, as in many studies of primate social learning, all models were dominant individuals (both females and males), thus showing that vervet monkeys are capable of learning from dominant individuals. However, in a recent experimental study, researchers trained both high- and low-ranked female models and did not find any group-level bias towards learning from dominant individuals over lower-ranking models in this species (Botting, Whiten, Grampp, & van de Waal, 2018).

A kinship-based bias has also been observed in wild vervet monkeys. Vertical transmission (from the mother to her infant offspring) was apparent when the vervet monkeys cleaned food presented by researchers which was covered in sand; while several cleaning methods emerged within the groups, infants used the same cleaning method as their mother (van de Waal, Krützen, Hula, Goudet, & Bshary, 2012; van de Waal, Bshary, & Whiten, 2014), as opposed to other females. The importance of shared foraging time in the daily time-budget could affect this social transmission by increasing the observation time of the matriline members (van de Waal *et al.*, 2012), and is consistent with observations from other primate species which has highlighted the role of the mother as primary model in a primate's early life (Biro *et al.*, 2003; Schuppli *et al.*, 2016).

Research with wild vervet groups has also indicated majority-biased transmission in social learning. In a further experiment (van de Waal, Borgeaud, & Whiten, 2013b), two boxes of corn, dyed different colors, were presented to the whole group. In the initial training phase, the monkeys learned that one color of corn was palatable, whilst a bitter taste was added to the other color (red vs blue color; Figure 3), making it unpalatable. Five months after these first presentations, and following the birth of several infants, the two colors were presented without any bitter taste. The monkeys continued to ignore the previously bitter color of corn and just ate the color they had learned was palatable. The naive infants went directly to the group's corn of choice, ignoring the other color and thereby showing that from an early age, these infants' food choices are being guided through social learning.

Figure 3: Groups trained to prefer different colors of dyed corn (palatable food in red on the left and in blue on the right).

However, this experiment also provided insight into social learning at a different life stage. During the five months gap between the training and test presentations, a number of males migrated between the neighboring groups, serendipitously coming from groups trained with one palatable color and entering groups with the opposite trained preference. When tested in their new groups, these males chose the color preferred by their new group even though it was the color they had previously learned, through direct experience, was unpalatable (van de Waal *et al.*, 2013b). This abandonment of their previous preferences in favor of their new group's preference, known as conformity (Whiten & van de Waal, 2016) is striking and draws obvious parallels to the seminal experiments on human conformity by Asch (1951). Asch's experiments showed important fluctuations in human conformity; participants did or did not conform depending on several external factors (e.g., whether it was an unanimous majority, whether the answer was public or private, sex of the participant). In addition, humans conformed to majority even though they knew that their statement was wrong (Asch, 1951). In the vervet studies, the males had prior personally-acquired information that their new group's favored color was distasteful; however they had also moved to a new territory upon immigration to their new group. It remains to be seen whether their conformity was socially-motivated (normative) or by the need to acquire new, territory specific information about food quality (informative, see Claidière & Whiten, 2012 and van Leeuwen, Acerbi, Kendal, Tennie, & Haun*,* 2016; for a debate on the evidence for conformity). Nevertheless, these experiments highlight a potentially important link between the social learning processes of humans and primates. In a follow-up of this experiment, females showed social conformity after group fission (van de Waal, van Schaik, & Whiten, 2017). As high-ranked females often monopolized the preferred color, low-ranked females ate a lot of the previously unpalatable color and thus learned that it was now equally palatable. Nevertheless, after a group fission, low-ranked females who formed a new splinter group demonstrated a 100% preference for the same food color as their initial group, despite their individual knowledge that both colors were equally palatable (van de Waal *et al.*, 2017). Similar findings of conformity have also been seen in birds (Aplin *et al.*, 2015), suggesting that it may be an adaptable, widespread, and thus convergent, phenomenon throughout the animal kingdom.

These findings, such as the differing biases exhibited by the philopatric and dispersing sex, highlight the powerful effect of environmental pressures upon the development of social learning rules in vervet monkeys. By understanding how specific pressures may lead to the emergence of certain biases in primates, we can further our knowledge of how specific social learning biases arose in human evolution. Indeed, experimental studies have already found evidence of many of these biases in humans both in terms of model identity and context (Wood *et al.*, 2013; Rendell *et al.*, 2011; Cross *et al.*, 2017). Human children exhibit several biases in whom they learn from (Wood, Kendal, & Flynn, 2013; Lucas *et al.*, 2017; Frick, Clément, &

Gruber, 2017); they are more likely to learn from familiar than from unfamiliar individuals (Corriveau & Harris, 2009), and are also sensitive to majority bias (Haun & Tomasello, 2011; Haun, Rekers, & Tomasello, 2012). Indeed, food preferences and eating habits in human children are shown to be influenced by familial and social factors (Patrick & Nicklas, 2005), potentially comparable to the behavior of vervet infants within matrilines previously described.

Looking beyond the primates at our more distant relatives, social learning and cultural transmission have been observed in many different species including insects (Leadbeater and Chittka, 2007), birds (Slagsvold and Wiebe, 2011) and fish (Laland, Atton, & Webster, 2011). In particular, the cetaceans show some of the most impressive evidence for cultural transmission in nonhumans [e.g., transmission of humpback whales' song (Garland *et al.*, 2011) and lobtail feeding (Allen, Weinrich, Hoppitt, & Rendell, 2013)]. This therefore indicates that culture is highly adaptable and an example of convergent evolution. Nonetheless, the phylogenetic closeness of primates suggests that our own sophisticated culture likely has its evolutionary roots in the culture and social learning abilities displayed by our nearest relatives.

Thus, social learning experiments on wild primates represent a valuable resource for our understanding of how social learning in humans may compare to that in other animals, why certain strategies may have evolved and more broadly, the effect these may have had on the ontogeny of culture in humans. There are of course still many questions remaining, particularly how multiple biases may interact in the same individual (Kendal *et al.*, 2018) and why social learning abilities apparently do not necessarily result in the emergence of cultural behaviors. Further research with humans, primates and more distantly related taxa will undoubtedly help answer these questions.

6 Conclusion

By comparing the cognitive capabilities of humans and primates, we can gain valuable insight into the evolution of these capabilities. Whilst a large number of comparative studies with captive chimpanzees have provided us with important results, particularly in the areas of social learning and cooperation, observations and particularly field experiments with wild groups of primates have allowed us to assess many social cognitive skills in their natural setting. Here we have focused specifically on the contribution of studies with vervet monkeys to the field of social cognition. The widespread and semi-terrestrial nature of this species has allowed for relatively easy habituation and observation by researchers, providing many insights into the behaviors of these monkeys in the wild. Additionally, their social organisation with multi-male, multi-female groups and linear hierarchies has allowed researchers to explore a wide range of topics within the field of social cognition.

As we have discussed in this review, a number of social cognitive behaviors in humans and vervet monkeys share similar properties. Although human language is unique to our own species, by investigating primate communication systems, we have been able to understand more about the evolution of this ability. Despite the current debates regarding these findings, studies into vervet monkey vocalizations have provided valuable evidence of referentiality and semanticity (Seyfarth *et al.*, 1980; Cheney & Seyfarth, 1982b), properties shared with human language. Human language also encompasses a number of other features, such as intentionality (Tomasello, 2008), and syntax (Lemasson & Barbu, 2011) and more broadly pragmatics (Price *et al.*, 2015), all representing useful avenues to explore in vervet monkeys. On the other hand, further research on gestural communication in this species could provide a more complete picture, and allow other proto-linguistic properties to be investigated.

Similarly, studies with vervet monkeys helped to develop early models of monkey cooperation and commodity exchange (Seyfarth, 1977). Whilst not reaching the high level of human trade and cooperation, reciprocity and trading systems have been shown in vervet monkeys, who use grooming as a valuable currency to exchange for reciprocal grooming (Fruteau *et al.*, 2011a), tolerance (Borgeaud & Bshary, 2015) and support in conflicts (Arseneau-Robar *et al.*, 2016a), as well as in food access and infant handling (respectively, Fruteau *et al.*, 2009 and Fruteau *et al.*, 2011b). Further investigation of other forms of reciprocity and exchange of commodities other than grooming, would be an interesting avenue for future research with vervet monkeys, particularly with regard to delayed reciprocity (e.g., delayed reciprocity for help during agonistic encounters observed in chimpanzees, de Waal & Luttrell, 1988) to further understand the extent and limitations of their cooperative behaviors and how these compare to human cooperation.

Finally, we have discussed the contribution that vervet monkey studies have made to the growing field of cultural evolution and social learning processes (Richerson & Boyd, 2005). Field experiments have provided evidence for not only local enhancement, but also emulation and/or imitation in this species (van de Waal & Bshary, 2011; van de Waal *et al.*, 2015). Infants have been shown to selectively copy their mothers (van de Waal *et al.*, 2014) and migrating males appear to forgo their individually learned information for the preferences of their new group (van de Waal *et al.*, 2013b). These findings highlight both the similarities and differences between human and nonhuman social learning and add to our understanding of how our uniquely human culture has evolved. However, whilst cultural behaviors have already been observed at the group level in a handful of primate species (e.g., Whiten & van Schaik, 2007; van Schaik *et al.*, 2003; Perry *et al.*, 2003; Santorelli *et al.*, 2011), we do not yet have clear evidence for culture, or the lack thereof in vervet monkeys (although there is tentative evidence of foraging related group differences, Tournier *et al.*, 2014). Further research with this species could focus on exploration of other domains, such as communication and social behaviors, in search of potential cultural behaviors, as well as continuing to examine how multiple social learning biases operate in a variety of contexts. By following these multiple avenues of investigation across these many areas of cognition, we can continue to add to the already significant contribution that studies of primates in the wild have made to our understanding of the evolution of our own minds and continue to discover which capacities are, and are not, unique to humans.

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Captions for supplementary material

S1. Sound track of vervet monkey alarm call for raptor (copyright Stéphanie Mercier).

S2. Sound track of vervet monkey alarm call for ground predator (copyright Stéphanie Mercier).

S3. Sound track of vervet monkey alarm call for snakes (copyright Stéphanie Mercier).