Construction grammar for monkeys?

Animal communication and its implications for language evolution in the light of usage-based linguistic theory

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Abstract

In recent years, multiple researchers working on the evolution of language have put forward the idea that the theoretical framework of usage-based approaches and Construction Grammar is highly suitable for modelling the emergence of human language from pre-linguistic or proto-linguistic communication systems. This also raises the question of whether usage-based and constructionist approaches can be integrated with the analysis of animal communication systems. In this paper, we review possible avenues where usage-based, constructionist approaches can make contact with animal communication research, which in turn also has implications for theories of language evolution. To this end, we first give an overview of key assumptions of usage-based and constructionist approaches before reviewing some key issues in animal communication research through the lens of usage-based, constructionist approaches. Specifically, we will discuss how research on alarm calls, gestural communication and symbol-trained animals can be brought into contact with usage-based, constructionist theorizing. We argue that a constructionist view of animal communication can yield new perspectives on its relation to human language, which in turn has important implications regarding the evolution of language. Importantly, this theoretical approach also generates hypotheses that have the

potential of complementing and extending results from the more formalist approaches that often underlie current animal communication research.

1. Introduction

Research that compares human language with animal communication systems is a key source of evidence for any account of the evolution of language (see e.g. Fitch, 2017). As Tallerman & Gibson (2012, p. 2) point out, “[i]n every meaningful sense, language is an autapomorphy, i.e. a derived trait found only in our lineage, and not shared with other branches of our monophyletic group”. However, much of current research on language evolution has suggested that most, if not all, differences between human language and animal communication systems are gradual rather than qualitative, which opens up new ways of comparing them. Also, both the field of linguistics and biological approaches to communication systems have seen interesting paradigm shifts in recent years and decades. This is pointed out, for example, by Hakansson & Westander (2013, p. 1), who emphasise “the shift of paradigm from the signaller-message-receiver perspective to a dynamic and interactive view of communication.” In linguistics, one group of approaches taking such a view are usage-based linguistic theory and constructionist approaches. These approaches stress the importance not only of the dynamic and interactive nature of communication, but also of general cognitive factors, learning, and usage in shaping communication systems. They have also started to take a more “holistic”, multimodal perspective on language, thus broadening the scope of the discipline, e.g. by recognizing gestures as an integral part of linguistic communication (see e.g. Müller, 2013).

These and other developments have led to new perspectives on human language and its relation to animal communication systems. Interestingly, a number of scholars have suggested that a Construction Grammar approach might prove helpful in accounting for the evolution of

language out of non-linguistic or pre-linguistic communication systems (e.g. Steels, 2004; Arbib, 2012, Hurford, 2012, Johansson, 2016). Hurford (2012, p. 81) first mentions Construction Grammar in his discussion of complex hierarchical structure in birdsong. This raises the question of whether reconsidering comparative evidence in the light of Construction Grammar could shed new light on animal communication systems and help understand their commonalities with and differences to human language. In this paper we explore this question in more detail. By reviewing the relevant current literature, we argue that a reconsideration of existing evidence from a usage-based and constructionist point of view can yield interesting new insights into the phenomena at stake. This is especially the case as much of the previous comparative research from a linguistic perspective has been conducted in a more formal-semantic framework and usage-based, constructionist can complement these approaches. In addition, such theoretical comparisons can feed into theorizing and research on language evolution. However, we also want to hint at another possibility, which so far has been underexplored, namely the question whether concepts and research from usage-based, constructionist approaches could be a helpful tool in analysing animal communication. Tomasello (2006), for example, argues that the goal of theories of language acquisition should be to specify a “construction grammar for kids” that explains children’s language processing in terms of psychologically real categories based on the cognitive and social skills children are known to possess. When it comes to research on non-human communication systems, is it also possible, then, to create, for example, a ‘construction grammar for monkeys?’ We will present first steps towards answering this question.

The paper is structured as follows: We first give an overview of constructionist approaches in the context of usage-based linguistic theory. Then we turn to the question of how constructionist approaches have been applied in research on the evolution of language, before we discuss major approaches to the study non-human animal (animal hereafter) communication systems

and their possible relation to usage-based linguistic theory. Specifically, we will discuss research on alarm calls, gestural communication, and attempts at teaching artificial and language-like communication systems to animals. Finally, we discuss how these strands of research could be combined by outlining first steps towards a usage-based, constructionist approach to animal communication systems. We also outline some specific testable hypotheses that follow from a constructionist approach to animal communication systems. These proposals are as follows: Firstly, if human constructions exhibit different types of combinatoriality, we should be able to find at least some correspondences between different types of combinatoriality found in animal communication and those found in linguistic constructions, such as probabilistic combinatoriality and componentiality. One further such feature, which is also hypothesised to have characterised early protolanguage, is a high degree of semantic polysemy, which leads to our second proposal that polysemy should also be found in some animal communication systems, and should in principle also be learnable by at least some animals in artificial language learning paradigms. Lastly, three-slot constructional patterns, which can be found in human linguistic constructions, should be present in at least some animal communication systems and should in principle be learnable in artificial grammar learning paradigms by at least some animals, as opposed to merge-based hypotheses that restrict animal communication to only exhibit dual-compartment frames.

Our main goal, however, is to present a comprehensive overview of current research on animal communication and language evolution through a usage-based, constructionist lens. As we argue a large proportion of this research indeed converges on a usage-based perspective and is highly compatible with constructionist accounts.

2. Usage-based linguistic theory and constructionist approaches

In this section, we give a brief overview of usage-based linguistic theory and constructionist approaches. Both are fairly broad cover terms for a variety of paradigms, and both intersect to a considerable degree: While there are “flavours” of Construction Grammar that emphasise formalisation and are less interested in usage (see e.g. Goldberg, 2013, p. 16), most constructionist approaches actually commit to the key role of usage. The term “usage-based” was coined by Langacker (1987, 1988), although the basic tenets of usage-based theories are of course shared by multiple approaches that precede the label (see Kemmer & Barlow, 2000). As the name suggests, usage-based theory assumes that linguistic knowledge is acquired and continually shaped by language use. As Tomasello (2009, p. 69) puts it, “meaning is use – structure emerges from use.” Consequently, usage-based approaches reject the assumption of an innate language faculty or Universal Grammar (see Pleyer & Hartmann, 2019). Kemmer and Barlow (2000) summarise the key properties of usage-based models of language as follows: Most importantly, they posit an intimate relation between linguistic structure and instances of use. This means that a language is learnt by abstracting away schemas from actual usage events. This leads to the emergence of a network of linguistic units (usually conceived of as form-meaning pairs, labeled “symbolic units” in Langacker’s Cognitive Grammar and “constructions” in Construction Grammar). In principle, each and every usage event can lead to a reconfiguration of this network, not only in first language acquisition, but throughout the entire lifespan (cf. Langacker, 1987, p. 376). A number of other central properties of usage-based approaches follow from this overarching assumption: They see comprehension and production as integral, rather than peripheral, to the linguistic system; they focus on learning and experience in language acquisition; they see linguistic representations as emergent, rather than stored as fixed entities; and they assign a key role to frequency (Kemmer & Barlow, 2000, p. viii–xii). Two further aspects mentioned by Kemmer and Barlow (2000) are of central

importance: Firstly, usage-based models posit an “intimate relation between usage, synchronic variation, and diachronic change” (Kemmer and Barlow, 2000, p. xviii). Secondly, they emphasise “[t]he interconnectedness of the linguistic system with non-linguistic cognitive systems” (Kemmer & Barlow, 2000, p. xx). In this regard, usage-based approaches strongly overlap with emergentist ones (see e.g. MacWhinney, 2015) as well as with the broader framework of Cognitive Linguistics (e.g. Evans, 2019), which “explicitly rejects the idea that the systems and processes that support language are unique to language, which is instead seen as reliant on the same systems and processes that are involved in non-linguistic domains of cognition” (Hart 2016, p. 337). Also, both aspects are strongly connected to grammaticalisation, i.e. the emergence of (more) grammatical forms from (more) lexical ones (see e.g. Hopper & Traugott, 2003). It is usually assumed that in the various heterogeneous processes that constitute grammaticalisation, different cognitive mechanisms such as abstraction and generalisation as well as metaphor and metonymy interact to give rise to increased grammatical complexity.

Importantly, it has been suggested that grammaticalisation is not only a key process in the traceable history of human languages but also gave rise to the very first grammatical constructions, i.e. units that go beyond one-word utterances or simple mono-clausal propositions at most (Heine & Kuteva 2007, 2012). This is where usage-based theory and grammaticalisation theory not only intersect with each other but also with other frameworks. Note, for example, that Progovac (2015) offers an account very similar to the one proposed by Heine & Kuteva (2007). Heine & Kuteva (2007) assume different “layers” of grammatical development, starting with a purely lexical protolanguage gradually giving rise to grammatical constructions. Progovac (2015) also assumes that there are “linguistic fossils” in modern languages that represent different protolinguistic stages of development. For example, she argues that “small clauses” such as *Problem solved*, in which two elements are paratactically

combined, can be seen as the predecessors of more complex syntactic constructions.

According to this proposal, Tense Phrases (TPs) are “built upon the foundation of the small clause” (Progovac, 2015: 10), as are more complex transitive structures. We will take a closer look at these proposals in Section 3 below.

Another framework with which both usage-based approaches and grammaticalisation theory intersect is complex systems theory (Beckner et al., 2009, Massip-Bonet & Bastardas-Boada [eds.], 2013, among others). On this view, language is seen as a complex adaptive system, i.e. a system whose global properties emerge from independent actions of multiple agents at a local level (see e.g. Frank & Gontier 2010) – a view partly prefigured in Keller’s (1994) invisible-hand theory of language change. Finally, it has been suggested that the shared intentionality framework proposed by Tomasello and colleagues (Tomasello et al., 2005, Tomasello, 2008) can bridge the gap between non-human communication and the basic protolanguage presupposed in a grammaticalisation framework along the lines of Heine & Kuteva (see e.g. Hurford, 2007, 2012; Pleyer & Winters, 2014; Pleyer, 2017, among others).

From a usage-based perspective, then, the challenge in accounting for the evolution of language is explaining the emergence of the relationship between linguistic forms and the meanings they encode. This is where another framework fits in naturally that shows a considerable amount of overlap with the usage-based approaches mentioned so far, namely Construction Grammar (CxG). As already hinted at above, CxG is not a unified framework but has rather evolved into a diverse set of approaches that show considerable differences with regard to their scope, their foundational assumptions, and their methodologies (see Goldberg, 2013, for an overview). What these approaches share, however, is that they make constructions, i.e. form-meaning pairs at various levels of abstraction, the main unit of linguistic analysis. Constructions can be lexically specific patterns, e.g. idioms like *kick the bucket*, partially lexically specific patterns like *The X-er the Y-er*, or highly abstract schemas such as

syntactic patterns. In addition, individual words are sometimes also seen as constructions (see e.g. Dąbrowska, 2009, for discussion; also see Diessel, 2019, p. 11).

This concept of a continuum from (more) fixed to (more) schematic constructions, sometimes termed the lexicon-grammar continuum, is also one of the aspects that makes Construction Grammar an interesting framework from an evolutionary point of view, which is the topic that we are going to turn to next.

3. Constructionist approaches to language evolution

Johansson (2016) argues that the different types of constructions – e.g. morphological constructions, syntactic constructions, constructional idioms, etc. – form “a hierarchy of increasingly demanding types”, which opens up the possibility that they evolved successively. This would also be in line with the layering model proposed by Heine & Kuteva (2007), which hypothesises that grammatical evolution proceeds from a one-word stage with nouns and verbs to increasingly complex grammatical patterns. Their argument is based on findings from grammaticalisation studies, which have given rise to “grammaticalisation theory” (but see Börjars et al. 2015 for a criticism of this term). According to Heine & Kuteva (2012: 518), “[g]rammaticalization theory offers a tool for reconstructing the rise and development of grammatical forms and constructions.” This approach is of course based on a uniformitarian preassumption: “There is no intrinsic reason to doubt that language change and the functional motivations underlying it were of the same kind in early language as observed in modern languages” (*ibid.*). As pointed out in Section 2, Progovac (e.g. 2015) takes a similar stance in arguing that there are “living fossils” of early grammar in the grammars of today’s languages, e.g. unaccusative small clauses ([*the milk [will [spill ~~the milk~~]]*]) or exocentric compounds (*cry-baby*). According to Progovac (2015: 75), the commonalities between these structures – and

others like e.g. absolutes – make sense if they are seen “as survivors from a two-word proto-syntax stage, which could only accommodate one argument per verb, and which did not have the means to distinguish between subjects and objects.”

Johansson (2016) sees the emergence of constructions with gaps as a key evolutionary step. It is preceded by a stage in which words are simply juxtaposed. This is in line with the concept of a lexical protolanguage, which “consists of single proto-words, initially uttered separately and slowly, and subsequently joined in short, fairly random sequences” (Tallerman, 2012, p. 480). Note that these ideas share many similarities with the usage-based approach to first language acquisition, which assumes that children first acquire “holophrases” before starting to use language productively with the help of frame-and-slot patterns, i.e. constructions with a lexically fixed part and an open slot such as *What’s X?* or *More X* (see e.g. Tomasello 2003). These parallels to child language acquisition can also be found in other accounts that offer concrete hypotheses about how fully-fledged language might have developed out of a more rudimentary protolanguage – for instance, Heine & Kuteva’s (2007) model shows certain parallels to ontogenetic development. In addition, both Jackendoff (2002) and Progovac (2015) also adduce evidence from language acquisition in their models of hypothesised protolinguistic stages. In particular, Progovac (2015, p. 49-52) presents evidence that development from small clauses to Tensed Phrases (TPs) argued for in her model of language evolution can also be found in children’s developing language, who start out with untensed small clauses such as *Eve gone* and *Kitty hiding* and then go on to construct more complex tensed clauses building on this small clause layer. On the one hand, this could be seen as a reason to treat such models with caution as they might seem like naive transfers from language acquisition to language evolution. On the other hand, there are good reasons to expect such parallels. As e.g. Studdert-Kennedy (1990: 759) points out, despite the fact that the idea that ontogeny recapitulates phylogeny has been refuted, “in an adaptively complex system, such as language, where the function of any one part

may depend crucially on another, at least the broad lines of development are likely to be parallel, phyletically and ontogenetically". Moreover, as Progovac (2015, p. 50) makes clear, the key argument here is not that we should expect ontogeny literally recapitulating phylogeny, but that data from ontogenetic development can be used as corroborating evidence for evolutionary proposals.

Johansson (2016) further argues for the key relevance of pragmatics in the earliest stages of (proto-)language: At first, words are pragmatically juxtaposed, and only gradually does grammar partially replace pragmatics. The key relevance of pragmatics in early language(s) has been spelled out in more detail in a variety of other approaches. For instance, Smith (2008) and Scott-Phillips (2015) emphasise that focusing on Gricean cooperative communication can bridge the gap between the conflicting accounts of "analytic" and "holistic" protolanguage: Depending on the context, the meaning of a proto-utterance could have been simpler or more complex (Smith 2008: 110). Pleyer (2017: 87) argues that non-human communicative units are even more context-dependent and pragmatic in nature than words and constructions in human languages. Many of these ideas are highly compatible with accounts of the emergence of linguistic constructions as proposed by, among others, Traugott & Trousdale (2013). To quote Scott-Phillips' (2015: 119) example, *man bites dog* and *dog bites man* would be indistinguishable in a hypothetical protolanguage as the mere juxtaposition of words does not carry any meaning yet that goes beyond the individual units that are combined. But as soon as the ordering of words is taken to imply a subject-predicate-object interpretation, it has developed into a construction in its own right. Importantly, the ostensive-inferential nature of communication highlighted by Scott-Phillips (2015) plays a crucial role in the process of constructionalization as the construction is, ultimately, a fossilised inferential deduction that has become sufficiently conventionalised to be seen as part of the "grammar" of a language. To a

certain extent, then, it could be argued that the emergence of grammatical constructions entails “depragmaticalization”, as conventions are established that apply across different contexts.

The view that Construction Grammar may provide a suitable framework for the evolution of language has been expressed explicitly by Steels (2004), Arbib (2012, p. x), and Hurford (2012, p. 177). Arbib (2012, p. 252) sees one major advantage of Construction Grammar in its unified approach, “abandoning segregated rule systems for syntax, semantics, and phonology.”

The basic idea of constructions as form-meaning pairs is formalised and computationally implemented in the framework of Fluid Construction Grammar (FCG), which has been used to model the emergence and diachronic development of language using computer simulations, some of them using robotic agents (see e.g. Spranger, 2016, Steels, 2017). FCG incorporates the idea that linguistic constructions are inherently dynamic by modelling linguistic units as transient structures and constructions as feature structures that operate on those transient structures and define a bi-directional pairing between aspects of meaning and aspects of form (Steels, 2011, pp. 17–19). FCG has been used to investigate how populations of speakers converge on a shared inventory of symbols. Specifically, it has been used in so-called Naming Games, in which an agent draws the attention of another agent to an object in their shared context by naming a particular salient feature. Using this method, it has been shown that autonomous agents could self-organise an inventory of proper names to refer to objects in their environment (Steels & Loetzsch, 2011).

From a more theoretical perspective, Pleyer (2017) proposes ad-hoc constructionalisation as a foundational mechanism in the evolution of language. The term “constructionalisation” refers to the emergence of a new construction – more specifically, Traugott & Trousdale (2013, p. 22) define constructionalisation as “the creation of form_{new}-meaning_{new} (combinations of) signs.” For example, the emergence of the English *going to* future construction from a fully compositional

pattern qualifies as an instance of (grammatical) constructionalisation. The term ad-hoc constructionalisation refers to the spontaneous emergence of linguistic conventions in online discourse. According to Brône & Zima (2014), interlocutors regularly establish local routines in dialogue, which gives rise to ad hoc constructions. An ad hoc construction is defined as “a grammatical pattern that emerges in the course of an ongoing interaction through the known processes of schematization, instantiation and extension.” (Brône & Zima, 2014, p. 467).

According to this scenario, then, the way to the first proto-constructions would have started with semantically promiscuous communicative units that are locally “micro-entrenched” in interaction, which gradually gave rise to full-fledged constructions which become increasingly conventionalised. This is very much in line with the account proposed by Arbib (2012), who suggests a development “from holistic protolanguages to Construction Grammar” (Arbib, 2012, p. 252). He hypothesises that a holistic protolanguage may have consisted of holophrases, which encoded concepts for frequently occurring and highly significant situations like “The alpha male has killed a meat animal and now the tribe has a chance to feast together. Yum, yum!” (Arbib, 2012, p. 258) Tallerman (2012), however, raises a number of objections against the idea of a holistic protolanguage, especially against the idea that the holophrases were subsequently fractionated into shorter utterances. She refers to overwhelming evidence from research on grammaticalisation, according to which “grammatical constructions are overwhelmingly formed by composition when adjacent elements fuse, not by breaking complex elements apart” (Tallerman, 2012, p. 488). However, assuming a holistic protolanguage does not necessarily entail the assumption that the original holophrases were broken down into smaller parts: Instead, more complex scenarios of reanalysis and semantic change can be conceived, which would also be compatible with what can be observed in grammaticalisation and in instances of historical language change.

In sum, then, we can state that Construction Grammar has repeatedly been suggested as a helpful framework for language evolution research because it offers an inherently dynamic model of linguistic knowledge and language use. As such, it allows for modelling the gradual evolution of a “constructicon”, i.e. a network of form-meaning pairs, starting with the use of ad-hoc constructions that emerge in context and the emergence of a semantically polysemous protolanguage which becomes increasingly conventionalised and diversified. This leaves us with the question of the relationship between human language and animal communication systems. In the next section, we will briefly review current research on the latter.

4. Approaches to animal communication

In this section, we outline some of the key topics in animal communication research. This discussion can then serve as a stepping stone for addressing the question what contribution a usage-based, constructionist perspective can make to research on animal communication. In addition, animal communication research also has potential to feed back into usage-based and constructionist theorising. Again, however, the purpose of this section is not to propose entirely new ideas but instead to review which aspects of animal-communication are potentially relevant for a usage-based, constructionist account of language evolution.

Animal communication research is a complex field of research which draws on a multitude of research and results from different disciplines and animal species (e.g. Hauser, 1996; Hakansson & Westander, 2013; Stegmann, 2013). Three areas of animal communication research have been seen as especially important for questions surrounding the evolution of language: The structure and meaning of alarm calls, the meaning and use of gestural communication, and the capacities of symbol- or language-trained animals. We will briefly discuss each of them and their relation to language evolution research.

Alarm calls

A number of mammal (Townsend & Manser, 2013) and bird (Gill & Bierema, 2013) species emit alarm calls in response to specific predators. Among mammals, these species include different monkey species, e.g., vervet monkeys (Seyfarth et al., 1980), Campbell's monkeys, (Outtara et al., 2009), putty-nosed monkeys (Arnold & Zuberbühler, 2006) and titi monkeys (Berthet et al., 2019) as well as prairie dogs (Kirazis & Slobodchikoff, 2006) and meerkats (Manser, 2001). Among birds, they include the American Robin (Eason & Vanderhoff, 2009), great tits (Suzuki, 2012) and a small number of others (Gill & Bierema, 2013). Vervet monkeys, for example, emit different alarm calls for eagles, leopards, and snakes, which are all linked to differential responsive behaviours in receivers (however, see Price et al., 2015 for a recent re-analysis showing that the picture seems to be more complicated). In language evolution research, it has often been asked to what extent alarm calls like these can be seen as evolutionary precursors, either homologous or analogous, to human words (e.g. Bickerton, 2009).

However, the question of what these alarm calls mean and to what extent they are employed intentionally to refer to something and communicate information has been hotly debated (cf. Vonk 2020). In a seminal paper, Macedonia & Evans (1993) argued that calls of these types could be seen as “functionally referential signals.” It should be noted here that alarm calls are not the only type of potentially functionally referential signal used by animals, as a number of species, such as chimpanzees (Schel et al., 2013) and marmosets (Kitzmann & Caine, 2009) also produce functionally referential food calls, and other species, such as rhesus macaques, produce calls with social meaning (Townsend & Manser, 2012). However, we will focus on alarm calls here, with the note that similar considerations apply to these types of calls.

As alarm calls are reliably produced in specific contexts and in response to a specific stimulus, such as an aerial predator, and because animals who hear the call react as if they had observed

the predator themselves, an alarm call can be said to functionally refer to a specific predator or predation event. In this way, it could be seen as similar to a form-meaning pair – a construction – in human language. However, there are several open and widely-discussed questions: Do animals producing alarm calls intentionally communicate concepts such as EAGLE, or do they simply express a motivational state such as “I am very scared (of something above us)” that is interpreted by receivers in certain ways under specific contextual conditions? In addition, do alarm calls simply evoke specific behavioural responses in receivers or do other animals form actual concepts upon hearing a conspecific utter an alarm call? Note that this question also applies to infants’ very early understanding of language. As Tincoff and Jusczyk (1999) have shown, six-month-old human infants look longer at a picture of their father when they hear the word ‘daddy’ and longer at a picture of their mother when they hear the word ‘mommy’. But at this age, does this indicate an understanding of referential meaning, “[o]r do they instead simply associate labels and objects or events, in the way we might associate the bell of an ice cream truck with a delicious treat?” (Johnson & White, 2019).

This question of course does not only relate to alarm calls (and linguistic units in child language and child-directed speech), but to communicative signals more generally. There is evidence that Diana monkeys retain information about predators after hearing alarm calls (Zuberbühler et al., 1999; cf. Hurford, 2007). Moreover, in Japanese tits, hearing a snake-specific alarm call evokes a visual search image for snake-like objects in receivers (Suzuki, 2018). In addition, on the production side, orangutans avoid gestures that previously failed to achieve their goals, whereas they retain successful gestures and redeploy them. This indicates that they are able to learn and store gestures in memory that are associated with more or less communicative success (Cartmill & Maestriperi, 2012; cf. Bar-On, 2018). So there is evidence across domains and different species that at least some animals associate some kind of stored “meaning” with communicative signals. Studies of the acquisition of referential meaning in humans and of the

meaning of animal communicative signals are therefore faced with similar difficulties. However, it is currently not clear if progress in one of these fields can be translated into progress and new ideas for the other one. Kershenbaum et al. (2016), for example, decry the “lack of connection between theories of human semantics, and theories of animal communication”, although this situation might slowly be beginning to change (e.g. Schlenker et al., 2016; Bar-On & Moore, 2018; Bar-On, 2018). However, this overall situation has led many researchers to investigate two key components that underlie interpretations of the meaning of animal signals independent of theories of human semantics. On the one hand, interpretations of the ‘meaning’ of alarm calls have been related to questions of how animals categorise and conceptualise entities and events (see e.g. Hurford, 2007, Andrews, 2016, Smith et al., 2016 for discussion). On the other hand, interpretations are related to our understanding of the sociocognitive and intentional processes involved in animal communication and interaction. Faced with such difficulties, Wheeler & Fischer (2012) suggest that the concept of “functional reference” should be abandoned, as it proves not to be of any use as a guide to the evolution of referential semantics in human language, whereas others keep defending its utility (e.g. Scarantino & Clay, 2015). One important difference between linguistic constructions and alarm calls is that calls seem to be largely innate, with animals having little control over the structure of these calls (e.g. Hammerschmidt & Fischer, 2008; Janik & Slater, 2000). Overall, non-human primates have very limited capacities of vocal production learning (Fischer 2017). Unlike human words, then, they cannot be said to be learned form-meaning mappings. They do, however, have some control over when to use these innate calls (Fischer et al., 2015, Watson et al., 2015; cf. Fischer, 2017). In addition, there is good evidence for usage learning in monkey species, meaning that they need to learn what a particular call stands for even though the call itself is innate (Fischer, 2002). This and other evidence point towards the importance of pragmatic factors in animal alarm calls, albeit to a much stronger degree on the receiver’s side (Wheeler & Fischer, 2012; Fischer, 2017). Indeed, alarm call interpretation seems to be strongly context-dependent

(Scarantino & Clay, 2015, p. e1). This indicates that “signals can functionally refer by virtue of contextual cues and in the absence of a strong correlation with their referents” (Scarantino & Clay, 2015, p. e1). Therefore, although untangling the meaning of alarm calls is beset with difficulties, it seems clear that for alarm calls and other communicative signals in monkeys and apes meaning emerges from an integration of signal and social context (Seyfarth & Cheney, 2017). With regard to the evolution of language, then, the pragmatic dimension of the production, usage, learning, and reception of alarm calls is therefore of the greatest interest when investigating possible continuities between animal communication and human language.

Gestural communication

Given the limited productive control, as well as the small number of signals in animal vocal communication, a number of researchers have proposed that the flexible and intentional gestural communication of primates holds much greater interest when looking for evolutionary continuity between animal and human communication (e.g. Pollick & De Waal, 2007; Tomasello, 2008).

What makes great ape gestures especially interesting from an evolutionary perspective is that they differ from alarm calls in two important aspects. On the one hand, the gesture repertoires of primates seem to be much larger than call repertoires found in other animals. For different great apes, the repertoires that have been documented range from 66 (in chimpanzees, Hobaiter & Byrne, 2014) to 102 (in gorillas, Genty et al., 2009; cf. Byrne et al., 2017). In addition, recent evidence suggests it is not only great apes who possess a complex repertoire of gestures that they use flexibly and intentionally. Molesti et al. (2019), for instance, found that olive baboons use a repertoire of 67 gestures in the visual, tactile and audible modality across different contexts. On the other hand, the second distinguishing feature of gestures is that they seem to

be used in a more flexible and intentional manner than alarm calls. That is, the context-dependence established for alarm calls seems to be even more pronounced in gestural communication. Indeed, great ape gestures “are all characterized by the use of several different gestures in a single context and the use of a single gesture in multiple contexts” (Liebal et al., 2014, p. 155). In a sense then, great ape gestures can be said to be polysemous (Moore 2014, cf. Pleyer 2017). As Genty & Zuberbühler (2015) point out, this places a strong emphasis on the pragmatic dimension of gestural communication. Different gestures can have different meanings according to context, so that just like alarm calls, they can be said to be contextually modulated. However, as pointed out by Liebal and Oña (2018), currently ‘meaning’ is operationalised quite differently in research on vocal vs. gestural communication. In addition, the methodologies in these two areas of research also are quite different. This leads Liebal and Oña (2018) to the conclusion that “it is currently not possible to generalize findings across these modalities” and we should keep this caveat in mind. Just as with alarm calls, it is a crucial question to which degree the ontogenetic development of these repertoires can be said to be genetically channeled or whether and to what extent it is learned and socioculturally acquired (cf. Cartmill & Hobaiter, 2019). One position is that these gestures are to a significant degree acquired by a process of ‘ontogenetic ritualization’, “in which individuals learn their gestures in the context of regularly occurring dyadic interactions such that parts of fully functional social behaviors become ritualized” (Halina et al., 2013, p. 654). For example, the ‘arm raise’ gesture of young chimpanzees used to initiate play can be analysed to have developed out of an actual preparation to play-hit another youngster. Through processes of ritualization and anticipation the first step of this sequence then turns into a gesture initiating play behaviour (Halina et al., 2013, p. 654; Tomasello, 2008, p. 23). From this view, the flexible usage of ape gestures marks them as learned behavioural strategies (Halina et al., 2013, p. 653). Hobaiter & Byrne (2011), however, found no support for the hypothesis that gestures are acquired by ontogenetic ritualization. Instead, the distribution of gestures has been found to indicate a universal

repertoire that is species-typical. However, not only are most gestures species-typical, but the majority of gestures seems to be ‘family-typical’ (Genty et al., 2009; Liebal et al., 2014, Byrne et al., 2017), that is, the same gestures can be found in different great apes. Based on current estimates, the great ape family (chimpanzees, bonobos, gorillas, and orangutans) shares around 36 gestures, whereas the subfamily of African apes (chimpanzees, bonobos, and gorillas) share an additional 30 gestures, with the genus pan (chimpanzees, bonobos) sharing an additional three (Byrne et al., 2017). Overall then, the number of species-specific gestures seems to be quite small, ranging from two (chimpanzees) to eight (gorillas) (Byrne et al., 2017). In addition, there are gestures that are present both in human infants and the chimpanzee gesture repertoire (Kersken et al., 2019). This lends further support to the genetic channeling account, with interesting implications for human evolution. More specifically, the data are consistent with the assumption “that the cognitive skills underlying usage of manual gestures may have been present in our last common ancestor and are shared within Hominoidea” (Roberts et al., 2012).

Overall, one of the most important findings from the perspective of language evolution research seems to be the pragmatic dimension of meaning construal in ape gestures. This suggests that the evolutionary platform on which human language is built is characterised by the ability to communicate intentionally, is flexible, and rests on a sophisticated sociocognitive basis.

Artificial Communication Systems

The previous discussion of research on animal communication has dealt with the ‘natural’ communicative systems of animals. However, much research has also concentrated on

teaching animals 'human language' or artificial symbolic systems. Andrews (2016) lists 18 completed or ongoing long-term projects, ranging from 1933 to 2011, involving chimpanzees, but also bonobos, a gorilla, orangutans, a sea lion, four bottlenose dolphins, an African Grey Parrot, and a border collie. However, most of these studies have focussed on great apes, especially chimpanzees. These programmes have come to be known as "ape language research" (Lyn, 2012). According to Lyn (2012), in the last 40 years of research there have been peer-reviewed data for 16 chimpanzees, 3 bonobos, and 2 gorillas. While the popularity of "ape language" research programmes has declined significantly, they are still of great interest when discussing language evolution for contrasting the symbolic and syntactic capacities of humans with that of animals. In linguistics, this popularity is evidenced, for example, by the fact that many introductions to linguistics (e.g. Akmajian et al., 2017; Yule, 2016; Fasold & Connor-Linton, 2014), as well as those to language acquisition (e.g. Rowland, 2014; Saxton, 2017; Hoff, 2013) feature sections on these research programmes. The key interest behind many of these studies investigating whether animals could be trained to use complex linguistics or language-like systems was to probe deeper into animals' cognitive and communicative capacities beyond what they exhibited in the wild. Here, research focussed mostly on two issues: (1) The question whether animals exhibited syntactic competence not found in their natural communication systems, (2) the question whether animals could acquire semantics, that is if they could acquire arbitrary symbols with referential, stand-for meanings. For ape language studies, the general consensus seems to be that language-trained apes do not exhibit complex hierarchical structure or grammatical structuring neither in production or comprehension (e.g. Gibson, 2012; Lyn, 2012; Hurford, 2012; Truswell, 2017). However, the degree to which apes have something akin to proto-syntactic capacities is still being debated. Whereas some researchers insist that symbol-trained apes have basically no understanding of ordering principles in communicative utterances at all (e.g. Terrace et al., 1979; Anderson, 2006), other researchers have presented evidence that apes such as Kanzi at least possess some kind of ordering structure in

comprehension and production and at least minimal grammatical competence, possibly even some kind of semantic ordering principles (Rumbaugh et al., 1993; Hurford, 2012; Hurford, 2012; Lyn, 2012). There also has been keen interest in studying artificial grammar learning in a wide range of animals, especially birds and primates (see, e.g., ten Cate, 2017; ten Cate & Petkov, 2019 for reviews). But as with ape language research, current evidence on artificial grammar learning is “insufficient to arrive at firm conclusions concerning the limitations of animal grammatical abilities.” (ten Cate 2017). However, there is accumulating evidence that at least some of the core combinatorial processes used by children in their very early language acquisition are evolutionary shared across a range of species. This includes, for example, neural processes adapting to the repetition of stimuli, and the ability to detect at least some limited dependencies and regularities in structured sequences (Petkov & ten Cate, 2020). Such results indicating at least very basic continuity between animal learning and human language learning are consistent both with the usage-based, constructionist perspective adopted here as well as more generally with approaches whose goal it is to decompose syntax to its simplest combinatorial strategies, such as that of Progovac (2015, p. 84).

The second area of research, whether animals are able to acquire symbols, is characterised by more agreement. Here research has shown evidence that animals are able to acquire object-symbol pairings, and in some animals there is even evidence for the acquisition of more abstract concepts such as ‘same’ and ‘different’ (e.g. Hurford, 2007). What is more, some symbol-trained animals seem to not only be able to learn the referents of individual symbols, but also to understand relations between symbols, which in Deacon’s (1997) analysis is the true hallmark of symbolic cognition (cf. Gibson, 2012). According to Hurford (2012: 494), therefore, the capacity to acquire a “network of inferential relations between object-symbol pairings” is present in both chimpanzees and humans, with the difference being a matter of degree and not a qualitative difference. This assessment is of course of great interest for usage-based and

constructionist approaches to language evolution, as on this perspective, the assumption that language is a structured network of related constructions is of central importance. However, it has to be noted that the human capacity for “massive storage” (Hurford, 2012) of constructions in the form of a structured network seems to go well beyond the repertoires reported for language-trained animals, which in themselves are already many times larger than communicative repertoires found in the wild. For language-trained apes, the productive vocabularies range from 68 to, 256+ signs in peer-reviewed publications to over 1000 in other types of publications (Lyn, 2012). For other species, the grey parrot Alex has been shown to label “>50 objects, seven colors, five shapes, quantities to eight, three categories (color, shape, material) and used “no,” “come here,” “wanna go X,” and “want Y” (X,Y being appropriate location or item labels). He combined labels to identify, request, comment on, or refuse > 150 items and to alter his environment. (Pepperberg, 2012, p. 297). Dogs also have been shown to be able to acquire a large number of sound-item mappings, with border collie Rico having an inventory of about 200 of such mappings (Kaminski et al., 2004) and border collie Chaser being able to retrieve 1,022 toys by name (Pilley & Reed, 2011).

The human network of constructions is several orders of magnitudes bigger than that of language-trained animals. At 25 months of age children’s vocabulary range lies between 100 and 600 words (Fenson et al., 1994) and therefore already well above the repertoire of language-trained animals. By 6 years of age, with about 14,000 words (Templin, 1957), children lie well above even generous estimates in non-peer-reviewed studies on language-trained animals, and adults are estimated to know between 40,000 to 150,000 unique items. From a constructionist perspective, this number increases exponentially if we add knowledge of relations between these items and the ways in which they can be combined (cf. Pleyer, 2017). Mollica & Piantadosi (2019) estimate that during language acquisition, adults have stored about

12.5 million bits of information about syntax, word frequency, lexical semantics, word forms, and phonemes.

There are a number of important factors influencing the evolution of our capacity for massive storage of constructions. One contributing factor certainly was the evolution of an increasing capacity for storing and managing social information that comes with bigger group sizes as well as more complex social interaction and forms of cooperation. In addition, human evolution is characterised by ecological challenges which required an increasing ability to learn complex behaviours such as tool use as well as increased planning abilities. All these factors certainly led to increasing memory demands in the course of human brain evolution (e.g. Dunbar & Shultz 2007, Schoenemann 2009; 2017; Manrique & Walker 2017; González-Forero & Gardner 2018). However, beyond these factors, there likely was a co-evolutionary relationship between the memory demands of learning, an increasing number of form-function pairings, and the evolution of the storage capacity of human memory. The view that brain evolution was in part influenced by the demands of (proto)language goes as far back as Darwin (1874, cf. Progovac 2019a). It is also expressed by Hurford (2012: 581): “The symbolic niche gradually created by humans contained increasing numbers of constructions. Humans adapted by a gradual growth in the natural limits of their storage space for learned meaning–form pairings.” That is, selection pressure for learning a vast amount of constructions itself likely was a key driving factor for the evolution our capacity for massive storage, leading to a coevolution of (proto)language and the brain (cf. Deacon 1997; Schoenemann 2009)

The human network of constructions therefore clearly looks very different from both natural animal communication systems and from the repertoires acquired by language-trained animals. This assessment holds for conceptual content, repertoire size, as well as combinatorial and compositional properties. However, for investigations of the evolution of language, it is important not only to spell out how these systems differ in general, but to specify the precise ways in

which human and animal communication is similar, and in which ways it is different. In this review, we argue that usage-based and constructionist approaches can offer an interesting framework to investigate some of these similarities and differences. This topic is what we are going to turn to next.

5. A usage-based, constructionist approach to animal communication

What can a usage-based, constructionist perspective bring to the study of animal communication? And conversely, from an evolutionary point of view, what can usage-based and constructionist approaches contribute to questions regarding the relationship of animal communication systems and human language? Answering these questions requires an extended dialogue between usage-based and constructionist researchers and animal communication researchers. This review is meant as a stepping stone towards such a dialogue. In the following, we will outline possible points of contact. Specifically, we will outline possible contributions of a usage-based, constructionist perspective to a number of key topics in research on human and animal communication. Of course, it is clear that actual progress will only be made by deriving specific, testable proposals from the usage-based, constructionist approaches to language evolution outlined in this review. For this reason, in this section we also mention a number of specific hypotheses that emerge from this perspective.

“Design features” of language and the architecture of the construction

There have been many proposals regarding the aspects that make language unique compared to animal communication systems. Perhaps most famously, Hockett (1960) has suggested thirteen “design features” of language, including e.g. displacement – the ability to talk about things that are remote in space and time – or duality of patterning, i.e. the combination of a relatively small inventory of meaningless sounds to meaningful elements (see e.g. de Boer et al., 2012). He argued that most, if not all, of those features can also be found in animal communication systems but argued that the specific configuration of features is specific to human language. In the decades since Hockett’s seminal paper, research on animal communication has made enormous strides in amassing data relevant for Hockett’s design features.

If we ask to what extent concepts from usage-based Construction Grammar can be used to describe non-human communication systems, a crucial question is which features distinguish the human construction, or structured network of constructions, from the inventories of calls and other signals that e.g. monkeys possess. One major open question, as already discussed in the previous section, is whether we can legitimately say that signals in non-human communication systems exhibit anything that approaches semantics (cf. Hurford, 2007; Schlenker et al., 2016).

This in turn begs the question of what exactly we mean when we speak of the “meaning” of words and constructions. While a long-standing tradition in linguistic semantics has upheld a fairly strict division between semantics and pragmatics, usage-based and constructionist approaches tend to emphasise the interactional, context-dependent and emergent nature of meaning. Arguably, this also has implications for non-human communication systems. For example, Schlenker et al. (2016) analyse monkey alarm calls using formal semantics, hoping to gain insight into precursors of human language. However, usage-based approaches argue that

what humans do when they communicate is not adequately captured by formal logic (see e.g. Ariel, 2015, p. 605 and *passim*).

Constructionist approaches usually subscribe to a broad conceptualisation of semantics which explicitly includes sociopragmatic aspects that cannot be modelled in truth-conditional terms.

For example, the much-discussed *What's X doing Y?* construction (*What are you doing with the knife?!?*, see e.g. Kay & Fillmore, 1999) is argued to convey a strong, conventionalised implication of disapproval that has emerged through frequent usage in contexts in which the speaker expresses a negative stance towards the interlocutor's action (Bybee, 2010, p. 29).

Here we can draw parallels to the work on animal communication reviewed above, according to which the meaning of communicative signals in monkeys and apes emerges from the integration of the signal and the social context (cf. Seyfarth & Cheney, 2017). However, a further important aspect regarding meaning is that human language features strong degrees of conventionalisation, and that it is culturally transmitted. As e.g. Smith (2004, p. 128) points out, it has been argued that true, cumulative cultural transmission does not exist in non-human species (see e.g. Tomasello et al., 1997, Tomasello, 1999). For human language, on the other hand, as e.g. Imo & Ziegler (2019, p. 79) point out, language always oscillates between the poles of "emergence" on the one hand and routinisation or "sedimentation" on the other. On this view, constructions are routinised and conventionalised interactional cues. For Tomasello (2019, p. 112f.), the aspect of conventionalisation is what sets apart human language from other communication systems:

Linguistic communication is an extension of natural gestures. Both are invitations to jointly attend to an external situation for one of several cooperative motives. The difference is that linguistic communication achieves these functions via social conventions. This means that achieving joint attention and expressing emotions and attitudes within a linguistic act are achieved through means that reside in, and only in, the cultural common ground of our, and only our, linguistic community.

Whereas other communication systems, such as great ape gestures, feature degrees of ritualisation and routinization, the concept of conventionalisation goes beyond this. The crucial difference is that conventionalization also relates to a metacognitive understanding that social conventions such as language are normative and are shared by members of a community (i.e. “this is the way we do things”). In Tomasello’s (2019) view, conventionalization so defined, as being dependent on shared social agreements, group-mindedness and capacities for collective intentionality, is absent in other communication systems and emerges in children around three to four years of age.

Note, however, that the view of constructions as conventionalised cues is neither tied to a specific modality nor to the kinds of communicative behaviour that are traditionally regarded as “language” proper. In addition, it is important to note that whereas cumulative cultural transmission seems to be absent in animals, there is a wealth of evidence for processes of transmission in animals (see e.g. Whiten, 2017, p. 2019 for a review), indicating that this distinction might again not be captured in absolute all-or-nothing terms. For monkey alarm calls, it has also been shown that features of the environment, such as the presence or absence of particular predators, can lead to ‘dialectal variation’ in the meaning of alarm calls (Schlenker et al., 2014).

Regarding semantics, another key distinction is the open-endedness and productivity of human language. As outlined in the previous section, on the one hand, this relates to the sheer number of form-function associations stored in human memory. On the other hand, it also relates to the types of concepts and meanings that can be expressed. As Fitch (2019) points out, “animal communication systems appear to be intrinsically limited to a smallish set of fitness-relevant messages that relate to such factors as food, danger, aggression, appeasement or personal prowess”, while humans can express virtually all concepts they possess (see also Schlenker et al., 2017).

The capacity for “massive storage” (Hurford, 2012) of constructions therefore seems to be a clear distinguishing factor between humans and animals (cf. Pleyer & Lindner 2014; Pleyer & Winters 2014). However, from a usage-based, constructionist point of view it is crucial that humans do not simply have “more storage space” for form-function pairings. Importantly, the human construction is characterised by its network structure, in which constructions of differing degrees of specificity and abstractness are related via analogical links and relations, contextual factors as well as frequency measures (e.g. Diessel, 2019). This would mean that the key explanandum in the evolution of language is the emergence of a large number of constructions, as well as the human ability to integrate these constructions into a structured, inter-related network. This view of the cognitive architecture of human language also opens up new avenues for comparisons of human language and animal communication. For instance, from a usage-based perspective, “human cognition, including language cognition, would be captured better in probabilistic terms than by means of all-or-nothing rules” (Divjak, 2019, p. 10). If language and animal communication systems make use of many of the same basic, evolutionarily conserved mechanisms, this leads to the testable prediction that probabilistic systems should also be found in animal communication. Interestingly, probabilistic communication systems are indeed not only found in human language. For example, Berthet et al. (2019) present evidence that some primate communication systems, such as Titi monkey call sequences, are systems that generate probabilistic meaning.

The constructionist view has the added benefit that it can integrate different types of form-function pairings into a unified framework. There is not one type of rule system at work in human language, but a complex network of different types of constructions. This means that according to this view, there is just not one path by which language evolved (e.g. through the evolution of a Merge-like operation), but that different aspects of the construction might have different, interactive and interrelated evolutionary trajectories. This is in line with recent proposals by

Engesser & Townsend (2019), who argue that combinatorial systems should “be decomposed into finer, transitional forms (e.g., affixation).” They hold that different types of combinatoriality are present in different animal communication systems. Overall, this opens up the possibility of investigating similarities and differences between specific types of constructions and specific animal communication systems, as different constructional types also exhibit different types of combinatoriality.. Some construction types might therefore have homologous or analogous processes in different species and we might find particular types of constructional patterns in different species.

For example, as outlined above, research in construction grammar has shown that much more linguistic units than previously assumed are in fact non-compositional in nature (and therefore qualify as constructions in the classic definition by Goldberg, 1995). Such constructions can then be fruitfully compared to animal communication systems with idiomatic, non-compositional sequences, as the systems of putty-nosed monkeys, for example (Arnold & Zuberbühler, 2012).

A constructionist, usage-based approach therefore leads to different hypotheses and different research programmes. This is also expressed by Zuberbühler (2018):

An alternative hypothesis suggests that everyday language use is not very generative at all, but based on accessing pre-fabricated phrases from a vast stock. Although such utterances may be described in terms of their syntactic structure, language users do not normally generate any of them, but deploy them ‘wholesale’ in adequate situations. If this view is correct, then evolutionary investigations of syntax should primarily focus on non-generative, combinatorial systems, as frequently seen in animal communication.

Zuberbühler (2018) also notes that a usage-based view entails different evolutionary scenarios for language evolution research. On this view, the key factor yielding human combinatoriality might be the significant “brain expansion that took place from *Homo habilis* to early *Homo*

sapiens over little more than 1 million years, which have led to massively powerful acoustic storage and pattern searching devices.” This perspective squares well with models that propose that communicative pressure for increasing the number of signals in a language can lead to the emergence of productivity (Piantadosi & Fedorenko, 2017). One proposal for a pathway towards such productivity and the emergence of structured networks of constructions is to see them as following from the dynamic and shifting balancing of pressures for learnability and expressivity (Smith et al., 2013; Pleyer & Winters, 2014). On this view, linguistic structure emerges through pressures for simplicity (or “compressibility”) on the one hand and expressivity on the other (see e.g. Smith et al. 2013). While the idea of these competing pressures can be traced back at least to the 19th century (see Hartmann 2020), it has gained much traction in recent language evolution research (see e.g. Winters et al. 2018, Nölle et al. 2018). A semantically promiscuous protolanguage would be highly compressible, i.e. contain fewer forms, but it would be limited in its expressivity in that the forms would be highly ambiguous. The emergence of constructions leads to conventionalised form-function mappings and can thus be seen as an important stepping stone towards more expressive (and hence also more learnable, see Kirby et al. 2015) grammars. However, there is an additional solution to balancing the competing pressures of expressivity and compressive and that is building polysemous networks of constructions. If protolanguage was indeed highly polysemous, this offers a way out of having to memorise a vast array of unrelated items, as items are easier to learn and to represent in memory if they are connected in a network (Karuza et al 2016).

One specific, testable proposal that emerges from positing a semantically promiscuous protolanguage is that polysemous constructions should be cognitively basic, e.g. that they should easily be acquired by children, and potentially be also found in animal communication. As discussed in Section 4 for great ape gestures, there are indeed animal communication systems that exhibit polysemy. In addition, research in language acquisition demonstrates that

polysemous words with multiple related meanings are indeed easy for children to acquire, and are in fact easier to acquire than homonyms with unrelated meanings (Floyd & Goldberg 2020). Moreover, we would expect polysemy to still play a major part in modern languages as a “linguistic fossil” that could also be found in protolanguage. Indeed, polysemy is ubiquitous in human languages and it can also be observed to be an important mechanism in language change (Vicente & Falkum 2017). For English, for example, there are estimates that up to 84% of English words exhibit degrees of polysemy (cf. Floyd & Goldberg 2020). One further specific proposal that emerges from this with regard to animal communication and cognition is that polysemy should also be learnable by at least some animals. If, for example, great apes, really do exhibit polysemy where the same element can have different ‘meanings’ one prediction we can make based on this observation is that they should also be able to learn polysemous elements, in symbol-training and artificial grammar learning paradigms (AGL) (Petkov & ten Cate 2020).

In the light of usage-based, constructionist approaches, particular communicative structures might appear to be of much higher relevance to investigations of the evolution of language than previously assumed. For example, Schlenker et al. (2017) stress that the similarities between monkey languages and human language are very limited. While we absolutely agree with these authors that there are many “important dissimilarities” between these two systems, we still argue that constructionist, usage-based approaches have the potential of shedding new light on the nature of these similarities and differences. Take, for example, the process of repetition in call sequences. Schlenker et al. (2017), for example, state that “monkey languages display numerous cases of call repetition, which have no equivalent in human language”. However, evidence from a wide variety of – especially non-European – languages shows that “[r]eduplication is a very widespread construction in the world’s languages.” (Inkelas, 2014). As such it has an important role in derivational morphology and word-formation in many languages

and can be seen as a “productive and lexical means of word-formation” (Schwaiger, 2015). It also figures quite prominently in the structure of ideophones (Dingemanse, 2018). Reduplication can therefore be seen as a general strategy to extend communicative systems, which is employed in animal communication, as well as in human language. Of course, it is important to note that reduplication can have multiple different functions in different systems. In human languages, reduplication often takes on specific grammatical functions such as plurality and collectivity, intensification, expressing aspectual categories such as frequency, repetition, continuation and progression, and a wide range of other functions (Inkelas 2014). In animal communication, no such clear semantic functions are apparent in reduplication. However, the argument is that reduplication is available as a resource for the extension of communication systems in both human languages and animal communication systems, with each system making different use of this potential. This is in line with a systems approach to human language and animal communication, which considers the structural and functional relationships of different components of a signalling system to each other, and how their interactions change over time (Hebets et al, 2016).. In the case of many animal signalling systems that exhibit repetition, this redundancy increases the robustness of the system, enabling the system to maintain function, for example under conditions of noise and lossy transmission, as in the display call of the king penguin (Aubin & Jouventin, 2002). However, such redundant elements can then be evolutionarily exapted to become pluripotent. This means that a structure can take on new functions, thereby increasing the functional diversity of the system (Hebets et al., 2016), with reduplication in human languages being a case in point.

It is important to note that this multicomponent view of language is not only adopted by usage-based, constructionist approaches and research paradigms in animal communication such as that espoused by Engesser & Townsend (2019). It is also consistent with the emerging trend in language evolution towards multicomponent (Fitch, 2017; Balari & Lorenzo, 2016), “mosaic”

(Benítez-Burraco & Boeckx, 2014; Gong et al., 2018) conceptions of the language-ready brain (cf. Pleyer & Hartmann, 2019). Of course, it is also highly compatible with approaches that try to decompose language into its more primitive component parts to yield possible protolinguistic stages (e.g. Progovac, 2015; Jackendoff & Witek, 2017).

In the remainder of this section, we want to outline possible areas of investigation where usage-based, constructionist approaches might help inform animal communication research. Currently, we see the most potential for convergence in investigations of the structure and storage of animal communication systems, and in the question of animals learn and represent to usage communicative utterances.

Animal Vocalisations and Gestures as Constructions

As outlined in Section 2, usage-based, constructionist approaches describe language in terms of a network of constructions, that is, as form-function pairings or as pairings of a form and a meaning potential with differing degrees of schematicity and abstraction. Does describing animal signals as constructions (or proto-constructions) yield any potential for further additional insights? We think this is a question in need of thorough exploration without a definitive answer at the moment. However, what we want to argue for here is that describing animal communication in terms of constructions is able to at least capture many of the important properties of animal communication. In addition, it provides a new, different perspective regarding the combination of items in animal communication. Specifically, this perspective has the potential to highlight similarities and differences between human language and animal communication that are not captured in a rule-based, merge-based, generative computational view and so can add to insights gained from research in other frameworks.

As an example of such a different perspective, consider Miyagawa & Clarke's (2019) analysis of the system underlying old world monkey communication, such as putty-nosed monkeys and Campbell's monkeys. As Miyagawa & Clark (2019) argue, "the system used by these monkeys contains a dual-compartment frame that allows them to acquire a two-part call. The two-part call is not the result of some combinatorial operation such as Merge, but rather, the nonhuman primate possesses this dual-compartment frame for creating utterances." From a constructionist perspective, such dual-compartment frames can be seen as a constructional frame-and-slot pattern, and as a first step towards more abstract constructions "with gaps" (Tomasello, 2003). Usage-based, constructionist research on language acquisition has shown that the emergence of such frame-and-slot patterns is a crucial step in children's development of more complex constructions. Miyagawa & Clarke (2019) as well as others argue that humans have evolved an additional computational operation, merge that allows for infinite combinations of units.

A usage-based perspective, on the other hand, would argue for the evolution of additional complex frame-slot patterns through processes of usage, analogy, abstraction and schematisation. From a usage-based, constructionist point of view, it would therefore be of interest to compare dual compartment constructions found in old world monkey communication systems with the change from holophrastic utterances to pivot schemas and first word combinations found in children between approximately 14 to approximately 18 months of age (Tomasello, 2003). These types of utterances do not yet involve any syntactic marking, but already have empty slots, a system that becomes more abstract as children grow older. This model also makes different predictions for what we can find in nature.

Whereas Miyagawa & Clarke (2019) argue that there should be no animal communication systems combining three elements, this finding would be consistent with a constructionist view of animal communication. In theory, this presents a specific, testable proposal of the usage-based, constructionist approach. Presently, however, it is still true that "[a]ll reported known

cases for meaningful call combinations in animals involve only two meaningful units.” (Suzuki et al., 2020). However, this proposal could be tested in the future using Artificial Grammar Learning (AGL) paradigms. One advantage of AGL is that these studies can tap into cognitive abilities and learning mechanisms that animals generally exhibit, but do not display in their vocalizations (Petkov & ten Cate 2020), and it is such general cognitive abilities and mechanisms that usage-based, constructionist approaches are interested in.

However, it is of course indeed possible that animals do not exhibit systems combining more than two elements due to them possessing only limited merge capacities (Rizzi, 2016, Miyagawa & Clarke, 2019). The existence of a merge-like process is consistent with usage-based, constructionist theory (MacWhinney 2015; Pleyer & Hartmann 2019). However, such a process would not operate on syntactic operations, as in a generative model. Instead, merge-like processes would operate on constructions and their network connections via processes such as abstraction. In addition, again the limitation of merge-like processes might be explained not in all-or-nothing terms but be captured by working memory constraints and increasing capacities for pattern finding and abstraction (cf. Hurford, 2012; Zuberbühler, 2019). Such a position is also in line with criticism from within biolinguistic approaches that explanation of language evolution often demonstrate an over-reliance on merge to the detriment of other important processes (Progovac, 2019b; cf. Martin & Boeckx, 2019). This of course also means that there is potential for convergence with such approaches.

Animal Communication, Constructions and Multimodality

In addition, constructionist approaches have the added benefit that they have increasingly integrated multimodality into their models. As research on multimodal construction grammar has shown, many constructions integrate not only vocal-auditory, but also gestural and other

modalities, calling for an integrated system of speech, gesture, and other modalities (e.g. Steen & Turner, 2013; Ziem, 2017; Hall et al., 2019). Given that primate communication is also fundamentally multimodal in nature to a large degree (e.g. Liebal et al., 2014; Wilke et al., 2017), both fields have much to offer each other in this regard. Usage-based, constructionist approaches to both sign languages (e.g. Lepic, 2019) and co-speech gesture (e.g. Zima & Bergs, 2017) represent a burgeoning field with a wealth of theoretical and empirical developments that promise to be highly relevant for studies of ape gestures. This is especially so given that many models both in animal communication and linguistics treat vocal and gestural signals very differently (Liebal & Oña, 2018), a problem that might be overcome with the help of multimodal construction grammar.

Multimodal communication is also highly relevant to evolving theories of combinatoriality and compositionality both in human and animal communication as multimodality does not fall neatly into existing categories of syntactic combination that do not take a multimodal view (cf. Authors et al., in preparation). Oña et al. (2019), for example, suggest that multimodal gestural-facial communication in chimpanzees exhibit “componentiality” in that different combinations of gestures and facial expressions yield different communicative effects. As they argue, such componentiality is a crucial stepping stone towards compositionality. From a usage-based, constructionist perspective this leads to the prediction that human language also exhibits componential parts, along with compositionality.

Animal Communication, Constructions and Learning Mechanisms

A final contribution by usage-based, constructionist approaches we briefly want to outline is the possible relevance of research on learning and storage of items. Traditionally, generative and biolinguistic approaches have, following Chomsky (1959), eschewed learning theory and

research on associative learning in animals when investigating questions of language learning and evolution. However, usage-based approaches see general processes of learning, association, and abstraction as crucial to explaining language. On this view, many of the general principles of learning found in animals can also be found in humans when they use and learn language. Indeed, learning theory has shown that in many regards learning in both animals and humans is supported by similar cognitive processes. This suggests that many of the processes uncovered by learning theory are relevant for both the question of how animals acquire communication systems, and how humans learn language (cf. Divjak, 2019). Usage-based approaches therefore promise to be much more compatible with research on animal learning than traditional generative approaches, for example. A continuing dialogue would therefore be highly fruitful between researchers who investigate how animals learn their communication systems, and between researchers who investigate language learning from a usage-based perspective. This perspective could help in establishing the ways in which, e.g., the learning of alarm calls is similar or dissimilar to human language learning, without making all-or-nothing pronouncements. This approach of course is also in line with more ‘progressive’ applications of generative frameworks to language evolution that decompose linguistic operations into simpler constructs and cognitive operations, such as those of Progovac (2015, 2019b), Jackendoff and Wittenberg (2017) and Rizzi (2016). These approaches can therefore work together in uncovering foundational cognitive mechanisms of both protolanguage and language, and relate them to research on cognitive and learning mechanisms in cognitive science and animal communication research.

Of course, there are some important distinguishing features between animal communication and human language. Both animal calls and gestures seem to be genetically channelled to an important degree, whereas the linguistic structures of individual languages are learned. Note of course that just because linguistic structures are learned, this does not preclude the possibility

of innate constraint of various types, such as architectural constraints, to influence human language acquisition and the learning mechanisms themselves being innately constrained (cf. Pleyer & Hartmann 2019; Dehaene 2020). Regardless of the stronger inherent genetic channeling of animal communication, three of the defining dimensions of how animal calls and gestures come to be acquired relate to explicit learning processes: comprehension learning, usage learning, and production learning (Janik & Slater, 2000; ten Cate & Scharff, 2019). In addition, these dimensions are also highly relevant for the emergence of call and gesture combinations. Research on animal communication and usage-based approaches both investigate cognitive and other processes involved in how signallers learn to produce, comprehend and use signals. A dialogue between these areas of research therefore is a highly promising endeavour when investigating the emergence of language. One particular concept that can be fruitfully adapted to issues of call and gesture learning in animals as well as sequence learning is that of entrenchment. Entrenchment is a foundational concept in usage-based approaches and refers to the way that processes of association, routinisation, as well as schematisation and automation affect the storage and representation of frequently occurring structures in memory (cf. Blumenthal-Dramé, 2012; Schmid, 2018; Divjak, 2019). In outlining how structures become entrenched through language use, usage-based approaches integrate existing models on learning, frequency effects, salience, attention, and memory consolidation from other disciplines in cognitive science. Many of these effects are seen to be domain-general, and in fact, many, if not most, of the cognitive processes usage-based approaches see as critical in explaining the emergence and use of language are also present in animals. It is therefore worthwhile to investigate whether usage-based models of cognitive processes involved in the emergence of language can also be applied to animal communication systems. For instance, Divjak (2019) discusses three types of entrenchment which, we argue, are also highly relevant when investigating the emergence of meaningful calls and gestures, as well as sequences of these. First of all, the more frequently a particular unit is activated, e.g. the more

frequently a call is being emitted in response to a predator, the higher the reduction in cognitive effort and increase in automatization. Secondly, as Divjak (2019) puts it, “Units that occur together, refer together.” The frequent co-occurrence of structures leads to unit formation facilitating access and retrieval. Clearly, the cognitive and neurological processes underlying this kind of entrenchment are highly relevant for possible models of the emergence of call and gesture sequences. Lastly, in Divjak’s (2019) words, “Units that occur together, blur together.” Frequently co-occurring structures are subject to processes of ‘chunking’ and ‘fusion.’ This entrenchment process could be instrumental in investigating the way that call combinations such as “pyow-hack” in putty-nosed monkeys or “krak-oo” in Campbell’s monkeys are stored and represented as units with a ‘blurred’, blended meaning, due to processes of memory formation. Applying these processes both to human language and animal communication would lead both of them to appear in quite a different light. In the light of usage-based approaches, both animal communication and human language might be based on many of the same general cognitive and neurological processes. These include, for instance, the types of entrenchment and memory formation discussed by Divjak (2019), and the neural processes underlying the ability to detect regularities in structured sequences evident in artificial grammar learning paradigms (cf. Petkov & ten Cate, 2020).

6. Conclusion

Although there is virtually universal agreement that human language is fundamentally different from animal communication systems, findings from comparative research have increasingly led to the conclusion that the difference is a matter of degree. This is why various researchers have suggested that usage-based, constructionist approaches are well-suited for modelling the evolution of (proto-)language from non-linguistic/pre-linguistic communication systems. In this

review of animal communication through a usage-based, constructionist lens, we have followed this line of reasoning, arguing that a usage-based constructionist perspective offers new theoretical avenues for comparisons between human language and animal communication which are directly relevant for theories of language evolution. We have fleshed out this idea by discussing how concepts from Construction Grammar can potentially be applied to animal communication systems, especially to monkey alarm calls, which have been subject to considerable debate regarding the amount of combinatoriality and compositionality they exhibit, to the extent that their structure has been viewed as a precursor to linguistic morphology (Endress et al., 2009). We have argued that a constructionist approach can contribute to our understanding of commonalities and differences between different (linguistic and non-linguistic) communication systems. Construction Grammar is strongly semiotic in nature: The concept of a construction is basically an extension of the Saussurean sign, which has come to be applied to various non-linguistic sign systems as well (Larsen 1997: 2062). In recent years, construction grammarians have started to take phenomena into account that have previously been treated as epiphenomenal at best, e.g. multimodal constructions such as conventionalised co-speech gestures (Zima, 2014, Cienki, 2017) or memes (Dancygier & Vandelanotte, 2017). This also shows that language is not a nicely delineated, clear-cut entity, which fits in with the assumption of a continuum between non-linguistic and linguistic communication. In other words, gradualist approaches in comparative research share many foundational assumptions with usage-based approaches to language.

However, we do not want to claim that Construction Grammar is necessarily the best, let alone the only way of approaching animal communication systems from an evolutionary-linguistic point of view. In fact, recent years have seen increasing convergence between different approaches that were previously seen as irreconcilably different (see e.g. Pleyer & Hartmann 2019). This shows that today more than ever before, different theoretical approaches to the

same data can prove complementary in opening up different perspectives on the research questions and topics at hand. In fact, cross-fertilisation between usage-based, constructionist approaches to language evolution and explicit proposals of protolinguistic stages in other frameworks, such as that of Progovac (2015), those based in grammaticalisation research such as that of Heine and Kuteva (2007), or the linear grammar hypothesis of Jackendoff and Wittenberg (2017) present an important future step in fleshing out this approach. The perspective espoused here, then, is not meant to contradict existing proposals on protolinguistic stages, but to be complementary to such proposals by focussing on shared mechanisms in human languages and animal communication and by espousing a usage-based, constructionist perspective on these systems.

All in all, what is the added value, then, of analysing animal communication systems using the terminological and conceptual apparatus of Construction Grammar? In this paper, we have argued that constructionist approaches to animal communication offer new perspectives on various issues that are of key importance for understanding the evolution of language. First of all, a constructionist re-analysis of animal communication data can yield interesting implications regarding the question of what makes human language unique (see the discussion about the so-called design features of language). Secondly, we have argued that usage-based and constructionist approaches on the one hand and animal communication studies on the other can cross-fertilise each other by providing new perspectives on human and animal communication systems as well as the continuum between linguistic and non-linguistic communication. In our discussion, we highlighted three specific, testable proposals that emerge out of a usage-based, constructionist approach to language evolution and animal communication. Regarding the assumption of semantically polysemous protolanguage, we argued that semantic polysemy should be found in at least some animal communication systems. Indeed, great ape gestures represent one such polysemous system, and from a usage-based, constructionist perspective

we should take a closer look at possible instances of polysemy in animal communication systems. Moreover, we argued that if the ability to use and understand polysemous constructions is present in chimpanzees, and was likely present in our last common ancestor with other great apes, we would predict that great apes are able to learn polysemous constructions in artificial language learning experiments. Moreover, in accordance with Engesser & Townsend (2019), we argued that both language and animal communication make use of different types of combinatoriality. From this, we predicted that we should be able to find particular types of combinatoriality proposed by usage-based, constructionist approaches and animal communication research in both human language and animal communication, for example probabilistic combinatoriality and componentiality. Lastly, we predicted that given that there are no prohibiting constraints by working memory, in principle there could be animal communication systems making use of at least three distinct elements. Moreover, we predicted that animals should be able in principle to learn artificial grammars using three distinct elements in artificial grammar learning experiments. Importantly, as we stressed, these proposals should not be seen as alternative, contradictory proposals to existing models of protolinguistic elements in human language, such as that of Progovac (2015) and Jackendoff (2002; Jackendoff & Wittenberg 2017). Instead, these proposals serve as additional, complementary proposals to existing proposals on protolinguistic component parts that were integrated in the course of human evolution to yield human complex language. We hold that finding cross-relevance, and ways of cross-fertilization between these different frameworks will lead to progress in better understanding language evolution, and help open up the possibility to find additional testable proposals on protolinguistic features of human language that can also be found in animal communication.

Overall, aspects of construction grammar and usage-based linguistic theory show great potential to inform conceptualisations of animal communication. We believe that this endeavour

promises to be highly productive and profitable, but that it requires concerted interdisciplinary efforts from and dialogue between usage-based, constructionist theorists and evolutionary linguists on the one hand, and animal communication researchers on the other.

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