



Optionality in animal communication: a novel framework for examining the evolution of arbitrariness

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ABSTRACT

A critical feature of language is that the form of words need not bear any perceptual similarity to their function – these relationships can be ‘arbitrary’. The capacity to process these arbitrary form–function associations facilitates the enormous expressive power of language. However, the evolutionary roots of our capacity for arbitrariness, i.e. the extent to which related abilities may be shared with animals, is largely unexamined. We argue this is due to the challenges of applying such an intrinsically linguistic concept to animal communication, and address this by proposing a novel conceptual framework highlighting a key underpinning of linguistic arbitrariness, which is nevertheless applicable to non-human species. Specifically, we focus on the capacity to associate alternative functions with a signal, or alternative signals with a function, a feature we refer to as *optionality*. We apply this framework to a broad survey of findings from animal communication studies and identify five key dimensions of communicative optionality: signal production, signal adjustment, signal usage, signal combinatoriality and signal perception. We find that optionality is widespread in non-human animals across each of these dimensions, although only humans demonstrate it in all five. Finally, we discuss the relevance of optionality to behavioural and cognitive domains outside of communication. This investigation provides a powerful new conceptual framework for the cross-species investigation of the origins of arbitrariness, and promises to generate original insights into animal communication and language evolution more generally.

Key words: arbitrariness, language evolution, animal communication, optionality, language origins.

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I. INTRODUCTION

A traditional view in linguistics is that the form and meaning of words are not connected by perceptual similarities, and that their relationship can therefore be described as ‘arbitrary’ (Hockett, 1958; Gasser, 2004; Monaghan *et al.*, 2014; Dingemanse *et al.*, 2015). For instance, the English word ‘jacket’ bears no resemblance to the category of objects being referred to – we could just as easily refer to them as ‘trousers’, ‘cats’ or ‘hoobles’. This arbitrariness is key to the expressive power of language. It allows for the invention and learning of new words (Gasser, 2004), and facilitates the emergence and evolution of terms for abstract concepts, which typically cannot tap into any perceptual similarity between words and their meanings (Clark, 1998; Dingemanse *et al.*, 2015). Recently, the position that language is entirely or even primarily arbitrary has given way to a new wave of research demonstrating that hitherto underestimated forms of non-arbitrariness (such as iconicity, where word forms resemble the properties of their referent, and systematicity, the existence of statistical patterns of similarity among word forms expressing similar meanings) permeate languages far more than traditionally assumed (Dingemanse *et al.*, 2015; Blasi *et al.*, 2016). Nevertheless, arbitrariness remains a crucial feature of language, and developing a comprehensive understanding of this capacity demands an in-depth analysis of its evolutionary history. At present, such an analysis is lacking.

While a linguistic comparative approach, contrasting languages both past and present, can be highly informative of the factors determining how languages change over time (Sicoli & Holton, 2014; Tamariz & Kirby, 2016; Greenhill *et al.*, 2017; Derungs *et al.*, 2018), its utility in answering evolutionary questions is limited by the relatively short period of recorded human history we have access to. Implementation of a cross-species, comparative framework is therefore necessary. Such an approach allows one to go beyond this narrow historical window and make powerful inferences about the evolutionary history of shared traits (Fitch, 2005, 2010). While this approach has been highly productive when applied to other features of language, such as semantics and syntax (Seyfarth & Cheney, 2017; Coye, Townsend & Lemasson, 2018; Suzuki, Wheatcroft & Griesser, 2020; Zuberbühler, 2020), it has yet to be applied to arbitrariness. An advance in this field is therefore necessary to decipher this critical missing piece in the puzzle of language evolution (Gasser, 2004).

Here we propose such an advance, by drawing together the rich literature on non-human animal communication within a novel conceptual framework and examining these data for shared features or antecedents of full-blown linguistic arbitrariness. Doing so is essential to shed light on the

evolutionary roots of linguistic arbitrariness and its underpinning cognitive abilities in the hominin lineage, as well as the selective pressures that may have acted upon them. One of the challenges when examining arbitrariness from an evolutionary perspective is that it is difficult to disentangle this notion from notions such as meaning or linguistic conventions (Glock, 2019; O’Connor, 2021), which makes direct comparisons with non-human (and therefore non-linguistic) animals problematic. For example, arbitrariness is traditionally tied to the concept of meaning (e.g. ‘a decoupling of the direct, one-to-one linkage between meaning and form’; Dingemanse *et al.*, 2015, p. 610). This is problematic in two respects. Firstly, the definition of meaning itself is a conceptual quagmire even within language (Lepore & Smith, 2008; Burgess & Sherman, 2014). Secondly, regardless of the definition adopted, whether animal signals can be said to have meaning at all is a highly contentious issue (Rendall, Owren & Ryan, 2009; Scott-Phillips, 2015). Focusing on meaning would therefore prevent a comparison with animal data *a priori*, and would make it impossible to detect any potential similarity between the processes underlying the association of form with meaning in language and those underlying the association of form with function in animals. We therefore rest our notion of optionality on the notion of a communicative function, a concept which remains open and inclusive of signals which may or may not carry semantic content. Of course, inferring the precise communicative function of animal signals is not straightforward. Nonetheless, animal signal functions can be determined through a variety of empirical methods, regardless of whether they carry semantic or lexical meaning (Rendall *et al.*, 2009; Schamberg, Wittig & Crockford, 2018). In this review, we propose a framework that allows for fruitful examination of the evolutionary origins of arbitrariness through a cross-species comparative approach, without necessarily invoking any other language-specific concepts.

Some of the animal behaviours we will discuss have previously been described under the broad conceptual heading of ‘communicative flexibility’. However, none of the specific notions found under this general heading appears suited to our purposes. Two specific forms of communicative flexibility have been identified as important to the evolution of human linguistic capacities and may at first seem relevant to the study of arbitrariness, but in fact concern quite different phenomena: ‘pragmatic flexibility’ and ‘functional flexibility’. Pragmatic flexibility can be broadly defined as the ability to decouple signals from specific contexts and to factor contextual information into the production or processing of signals (Seyfarth & Cheney, 2018). For example, the processing of primate vocalisations is known to be sensitive to contextual factors such as the presence and composition of the

audience, the signaller/listener's identity, the recent interactions between signaller and listener, or the signaller's expectations about the listener's response (Seyfarth & Cheney, 2018). Functional flexibility can be defined as the capacity to use signals to express different affective states in different situations (Clay, Archbold & Zuberbühler, 2015; Dezechache *et al.*, 2021; Taylor *et al.*, 2022). For example, it has been argued that human infants are capable of using individual protophones flexibly to express positive, negative, or neutral affect, in contrast with functionally fixed vocalisations such as crying and laughter, whose production is indicative of specific affective (Griebel & Oller, 2008; Oller *et al.*, 2013).

Crucially, neither pragmatic nor functional flexibility capture what we take to determine the arbitrariness of human words. Consider an arbitrary word like the English adjective 'tall'. 'Tall' is certainly contextually flexible: its production is not tied to specific contexts, and speakers and listeners take into account a variety of contextual cues in producing and interpreting the adjective. For example, we immediately understand that what counts as 'tall' is very different depending on whether we are having a conversation about pre-schoolers or basketball players. 'Tall' also qualifies as functionally flexible under the above definition of 'functional flexibility'. For example, though it may be regarded as fixed from a semantic standpoint (in the sense that it is semantically associated with designating the property of being tall), the adjective is not tied to any predetermined illocutionary function. English speakers can utter the sentence 'this mountain is tall' to express negative affect while facing an arduous climb, or to express positive affect in contemplating the majesty of natural scenery. However, the arbitrariness of 'tall' is conceptually distinct from its capacity to be used flexibly in different contexts, as well as from its ability to express a plurality of affective states. Paradigmatically, 'tall' is arbitrary because human speakers could, in principle, choose to change its semantic value, alter its form, or renegotiate both. We could easily decide that, from now on, 'tall' should be synonymous with 'blue', or alter the form of the adjective and spell it with an additional letter (say, 'twall'), or do both things at once: change the word-form 'tall' into 'twall' and use it to refer to the property of being blue (Lameira *et al.*, 2013; Monaghan *et al.*, 2014; Planer & Kalkman, 2019). While frameworks focussed on pragmatic and functional flexibility are of undoubted relevance for inquiring into the evolutionary origins of some capacities relevant to language, they were not designed to examine the specific set of capacities we associate with the arbitrariness of human words. We therefore need another framework: one capable of isolating with precision the specific dissociations between signal forms and functions (whether social, biological, or semantic) that fall within the purview of linguistic arbitrariness, while warranting application to linguistic and non-linguistic (e.g. non-human) systems alike. In this review, we propose the notion of 'optionality' to fulfil this goal.

We define optionality as the capacity to map alternative associations between signal forms and functions. Optionality

can be demonstrated in two basic ways. The first is the capacity to assign alternative functions to a signal-form. These alternative functions may be newly introduced, as in cases where existing words acquire functions that were not previously expressed anywhere else in the language (e.g. in recent decades 'application' has come to refer to computer software in addition to its previously existing meanings), or they may be extant, as in the case of homophones ('flour'/'flower') and polysemous words ('the water is cool' *versus* 'this song is cool'). Crucially in the former case, these alternative functions need not be simultaneously associated with the signal-form in question: signals may gain novel functions, lose them, or have their functions replaced with others, as in cases of lexical change where the extant meaning of a word is supplanted by another one (e.g. the adjective 'awful' once meant 'inspiring awe'; in contemporary English, it simply means 'bad'). Each of these scenarios would be demonstrative of optionality. The second way optionality can be demonstrated is through the capacity to associate a communicative function with alternative (novel or extant) signal forms. Examples from language would include synonyms, where multiple word-forms express the same meaning, or the systematic differences in pronunciation found in cases where a word is spoken in different dialects. Analogues from animal systems are readily drawn with these examples, such as chimpanzees using the same gesture to perform multiple communicative functions (Hobaiter & Byrne, 2011), or superb lyrebirds (*Menura novaehollandiae*) mapping the communicative function of a sexual display to the vast array of signal forms available to them through mimicry (Dalziell & Magrath, 2012). Naturally, a single species or individual can possess both the capacity to assign alternative functions to a single signal-form, and the capacity to associate the same communicative function with alternative signal forms.

Since the proposed characterisation of optionality appeals to functions, it bears emphasising that defining the 'function' of a signal is a complex enterprise, as this term is defined differently across disciplines, research foci and levels of analysis (Neander, 2009; Bateson & Laland, 2013; Schamberg *et al.*, 2018). Some researchers may, for example, lump all calls produced in social contexts under the broad functional class of 'social calls', whereas others may distinguish between them based on more specific social contexts (say, aggression or affiliation) depending on the relevant level of analysis for the research question. The notion of optionality is not bound to any single such definition, and can be applied across multiple ways of determining communicative functions. In this review, we therefore assume a rather general definition of a communicative function as being the biological or social activity, state or eliciting cause (e.g. feeding, aggression, predator sighting) determined by the current literature as being most closely associated with the signal. The degree of precision and confidence with which one can determine these functions for a particular species hinges on cutting-edge empirical work, and here we have done so to the best of our understanding of the existing literature.

Note also that while in ordinary parlance the concept of an 'option' is often associated with individual agency and

voluntary control, the question of intentionality is orthogonal to the technical sense in which we are appealing to the notion of optionality. By saying that a form–function mapping is ‘optional’ for an individual or a species, we simply mean to say that the mapping in question is a viable communicative possibility for them, irrespective of whether the transition between alternatives would occur as a result of voluntary decision-making, like choosing to make up a new word, or as a result of non-intentional processes. Naturally, none of this is meant to suggest that the relationship between optionality and intentionality is uninteresting, but rather that the latter is not a defining criterion of the former.

Finally, rather than focusing exclusively on a single area of communicative abilities (e.g. vocal learning), we view optionality as operating across multiple dimensions of signal production and comprehension. In particular, in the body of this text we identify and describe five key dimensions of optionality, and review the existing literature providing evidence for their presence in non-human animals (see Fig. 1 for examples). These five dimensions can be concisely introduced as follows: (1) signal production optionality: association of alternative signal forms with an extant or novel function; (2) signal adjustment optionality: association of alternative variants of an extant signal-form with an extant or novel function; (3) signal usage optionality: association of an extant signal-form with alternative functions; (4) combinatorial optionality: association

of alternative combinations of signal elements with extant or novel functions; and (5) signal perception optionality: receiver-based changes in signal–function associations.

Each of these dimensions of optionality is to be viewed as a continuous rather than binary trait, whose presence in a system is a matter of degree rather than an all-or-none phenomenon. For example, a system in which both the form and function of signals are tightly constrained, as well as the association between them such that one is 100% predictive of the other with no possibility of alteration, would have a minimal degree of signal production, adjustment and usage optionality. Conversely, a maximal degree of optionality is found in human languages, where associations between signals and functions are typically unbounded from such constraints (whether on the level of morphemes, words, or syntax). We may also quantify this capacity to some extent, in that a choice between 100 equally valid options demonstrates greater optionality than a choice of 10, or two, or one (Planer & Kalkman, 2019). In Fig. 2, we illustrate how such a framework might be conceptualised graphically. Importantly, each of the behaviours discussed below may fall into more than one of the five dimensions described, and their characterisation herein is partly our decision as to which dimension they are most illustrative of. In Table S1, we list a more extensive sample of the existing literature demonstrating candidate examples of optionality (including those

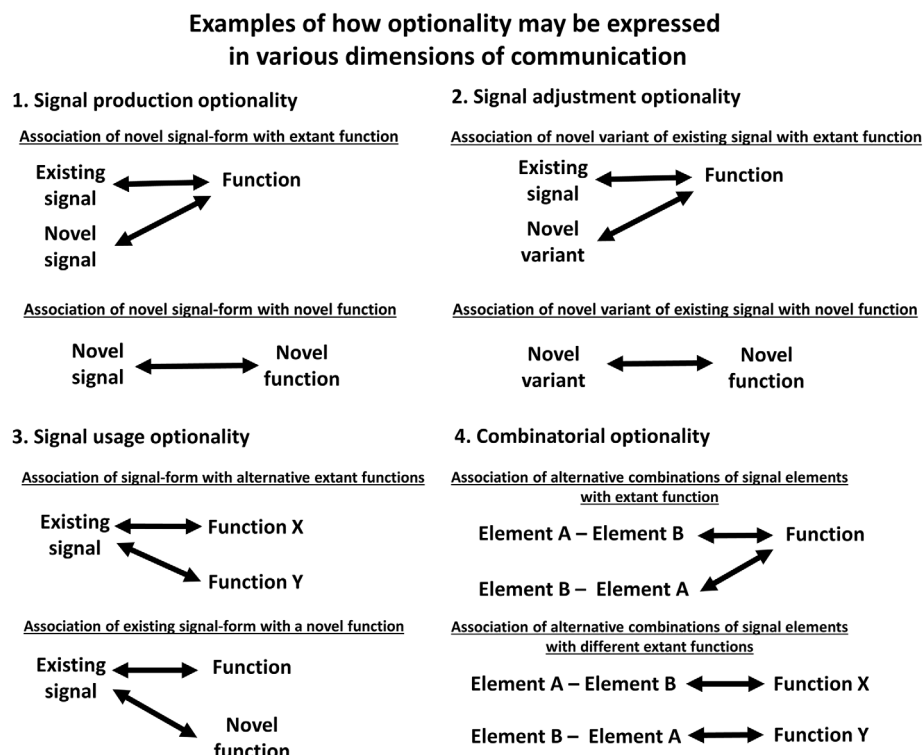


Fig. 1. Abstract examples of optionality corresponding to each dimension discussed in this review. These examples are not exhaustive, and other ways in which associations between form and function may exist, be created or be altered are discussed herein. Each of these may also be viewed from the perspective of receivers, representing our fifth aspect, ‘signal perception optionality’.

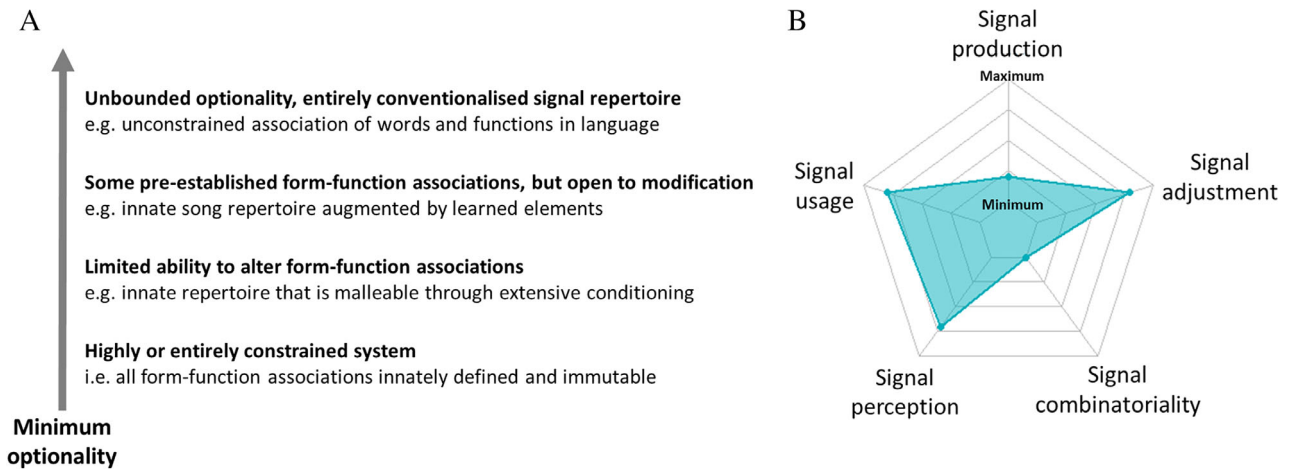


Fig. 2. (A) Spectrum of optionality with examples of each degree. The four degrees highlighted are not intended to be a prescriptive, quantitative evaluation of points on this spectrum but rather an aid for conceptualising our proposed framework. (B) Illustration of five dimensions of communicative optionality represented as separate axis on a radar plot. This plot represents a hypothetical species with a high degree of signal usage, perception and adjustment optionality but low degrees of signal production and combinatorial optionality.

not directly discussed here) and briefly describe their relevance to each dimension.

II. EVIDENCE OF OPTIONALITY IN ANIMAL COMMUNICATION

The communicative repertoires of our closest relatives, the primates, have been argued to be innate, with no opportunity for production learning of novel signal forms, and the structure and usage of existing signals largely governed by physiological and affective states rather than being under voluntary control (Wheeler & Fischer, 2012). It would follow, therefore, that these species are rather limited in the extent to which they can demonstrate optionality, and that the emergence of the unconstrained optionality found in language is likely to be a relatively recent evolutionary development in the hominin line. On the other hand, there is mounting evidence demonstrating significant control over the production, usage and comprehension of innate signals in our primate cousins, particularly the great apes (Townsend, Watson & Slocombe, 2020; Vernes *et al.*, 2021). Furthermore, sophisticated communicative behaviours have been observed outside of the primate order – with many of the most impressive examples coming from birds and marine mammals (Berwick *et al.*, 2013; Janik, 2014). To understand comprehensively the evolutionary trajectory of the cognition underpinning the enormous degree of optionality found in language, it is therefore necessary to compare the communicative abilities of humans with both our close phylogenetic relatives, and more distantly related species.

Below, we identify key examples of communicative behaviour which may be sufficient to demonstrate optionality in a

system. In each case, we begin with a brief justification of why the behaviour at stake is pertinent to optionality, followed by some of the most illustrative or intriguing examples, drawn from the existing literature, demonstrating their presence in animal systems. See also Table S1 for a summary of a larger array of empirical studies demonstrating candidate evidence for optionality in animals.

(1) Signal production optionality

The clearest way a species may demonstrate optionality is through the ability to produce novel signals and map them to new or existing functions, known as signal production learning (Pfenning *et al.*, 2014; Lattenkamp & Vernes, 2018; Martins & Boeckx, 2020). By doing so, they directly and unambiguously increase the number of signal forms mapped to a function. Humans demonstrate signal production learning throughout their lives. We can readily learn new word-forms (or signs) from others, or invent new ones ourselves, and map them to a function – thereby allowing for the enormous repertoires associated with contemporary languages. In animals, signal production learning has been primarily investigated in the domain of vocal behaviour (‘vocal production learning’; Tyack, 2020; Martins & Boeckx, 2020; Vernes *et al.*, 2021) due to the perceived relevance of this modality to the riddle of language evolution (Christiansen & Kirby, 2003; Oller, Griebel & Warlaumont, 2016). Such examples are therefore predominant, but our interest is not limited to any single domain of behaviour, and when referring to signal production learning we mean the production of any novel signal, irrespective of modality. In another respect, our use of signal production learning is restrictive, in that we exclude instances of learning that only modify or recombine pre-existing signals (behaviours that we discuss instead in Sections II.2 and II.4).

Many classic examples of signal production learning are found in avian species, such as parrots imitating human speech (Montes-Medina, Salinas-Melgoza & Renton, 2016; Wright & Dahlin, 2018), Lyrebirds imitating environmental sounds (Dalziell & Magrath, 2012), or passerines incorporating songs from neighbouring species into their own sexual and/or territorial displays (Boughey & Thompson, 1981; Derrickson, 1987). Because these species could, in principle, copy almost any sound in their environment, they demonstrate a remarkable degree of optionality in signal production. However, such learning is typically constrained to individual call types, rather than being a truly open-ended system where, for example, the signal forms of any and all call types within a repertoire could be supplemented by signal production learning. Indeed, it is conspicuous that most examples of signal production learning serve the function of sexual displays, supporting arguments that signal production learning may have originally evolved for a similar purpose in humans (Fitch, 2005). Nevertheless, counterexamples do exist: green-rumped parrotlets (*Forpus passerines*) develop idiosyncratic contact calls, which cross-fostering experiments have determined are partially modelled on those produced by their primary caregiver, whether they are related individuals or not (Berg *et al.*, 2012). Similarly, bottlenose dolphins (*Tursiops truncatus*) use learned ‘signature whistles’, which appear to function as a way of identifying themselves to others. Furthermore, individuals learn to reproduce the whistles of their affiliates, thereby facilitating identification of close social partners and the maintenance of those relationships (Janik, 2014). These whistles were even found to be produced spontaneously to facilitate coordinated action in a cooperative button-pushing task (King *et al.*, 2021), suggesting that they either serve multiple functions naturally, or can be made to do so under certain conditions. Only a handful of other non-avian species have been found to spontaneously (i.e. without explicit training) demonstrate signal production learning. Specifically, elephants (Poole *et al.*, 2005; Stoeger *et al.*, 2012), pinnipeds (Ralls, Fiorelli & Gish, 1985; Sanvito, Galimberti & Miller, 2007; Reichmuth & Casey, 2014; Stansbury & Janik, 2019), bats (Esser, 1994; Knörnschild *et al.*, 2010; Knörnschild, 2014; Prat, Taub & Yovel, 2015) and various cetaceans (Janik, 2014) have demonstrated vocal production learning in both captivity and the wild. While such cases are rare, the taxonomic range of this list is striking, suggesting that while the interaction of necessary pre-existing traits (including those that allow for optionality) and selective pressures for signal production learning to evolve is relatively rare, it can arise under diverse circumstances.

Across species and taxa, almost all naturally observed cases of signal production learning pertain to social calls, as opposed to stimulus-specific and ‘functionally referential’ signals, e.g. alarm calls (Seyfarth & Cheney, 1980) and food calls (Slocombe & Zuberbühler, 2005*b*), which are often argued to be an evolutionary precursor to linguistic reference (Zuberbühler, 2000; Manser, 2013; Schlenker *et al.*, 2014). This contrast is notable as it suggests that form–function

associations are generally more tightly constrained in some signal types relative to others, a feature which may be useful in guiding future explorations of optionality. A rare counterexample to this is the kleptoparasitic fork-tailed drongo (*Dicurus adsimilis*), which produce their own predator alarm calls but also mimic those of sympatric living species such as meerkats (*Suricata suricatta*) and southern pied babbler (*Turdoides bicolor*). These calls are not produced in a social context, but rather in response to both genuine predator sightings and as a means of scaring away the mimicked species to steal their food (Flower, 2011). However, even in this example, while the repertoire of novel *signals* being associated with functions has expanded, the corresponding repertoire of *functions* to which they could be assigned has not. Naturally occurring examples of optionality in animal signal production learning therefore seem to possess a key discontinuity with human linguistic learning, which can increase not only the number of signals but also the functions to which they may be associated. As we will discuss in the next section, this observation is also reflected in the literature on signal adjustment learning.

Conspicuously absent in the list of vocal production learners above, given their close evolutionary relationship to humans, are primates (Martins & Boeckx, 2020). In contrast to the many songbird species who readily integrate novel sounds into their vocal repertoires (Willbrecht & Nottebohm, 2003), there is no evidence that the signal forms of primate repertoires are learned (although some aspects of their functional associations might be, see Section II.3). As a particularly illustrative example, squirrel monkeys (*Saimiri sciureus*) develop a full and acoustically typical adult vocal repertoire even when deaf or socially isolated from birth (Winter *et al.*, 1973; Hammerschmidt, Jürgens & Freudenstein, 2001), although it has not been determined whether these calls in fact elicit species-typical responses in receivers. Similarly, cross-fostered rhesus (*Macaca mulatta*) and Japanese macaque (*M. fuscata*) infants developed largely species-typical vocal repertoires (Cheney *et al.*, 1992), indicating that they were unable to learn entirely novel vocalisations even from closely related species whom they perceived as conspecifics. It seems that this lack of learning is not due to anatomical constraints on the vocal apparatus, as it has been found that the vocal tracts of rhesus macaques (and so presumably other primates too) are ‘speech ready’ in terms of the sounds they are physically capable of producing (Fitch *et al.*, 2016). Yet, despite these anatomical possibilities, these species seem unable to add novel vocalisations to their repertoire (Egnor & Hauser, 2004), suggesting rigid neurological constraints (Wheeler & Fischer, 2012; Fitch *et al.*, 2016).

With that said, there are a handful of examples of signal production learning in great apes. Captive chimpanzees (*Pan troglodytes*), for example, have been found to produce acoustically novel ‘extended grunt’ and ‘raspberry’ sounds, which are not found in wild populations and function as an attention-getter directed towards their human caretakers (Hopkins, Tagliatela & Leavens, 2007). These sounds, and their function, can be socially learned by offspring from

their mothers (Tagliapietra *et al.*, 2012) as well as instilled through operant conditioning (Russell *et al.*, 2013). Orangutans (*Pongo pygmaeus*) also demonstrate a high degree of control over their vocal system, with captive individuals having been found to produce several different novel vocal behaviours including whistling (Wich *et al.*, 2009) and novel ‘wookie’ calls (Lameira *et al.*, 2016). Orangutans may even engage in signal production learning in wild conditions, with certain call types apparently existing in one population but not another, which appears difficult to explain *via* genetic or environmental differences, and is therefore likely the result of some form of learning (Wich *et al.*, 2012). However, it is not yet settled whether the different groups actually possess different repertoires of signal forms, or rather exhibit learned differences with respect to how fully these repertoires are deployed – perhaps due to a different suite of communicative needs characteristic to their social or physical environment (but see Lameira *et al.*, 2022). The first explanation would support the presence of genuine signal production learning, whereas the latter may demonstrate learned differences in how signals are used (see Section II.3).

Quite remarkable data also exist for so-called ‘enculturated’ apes (Call & Tomasello, 1996), individuals who, having been raised in human environments and given extensive exposure or even training with language, provide intriguing insights into the extent to which apes are capable of optionality. For instance, several chimpanzee, orangutan, gorilla (*Gorilla gorilla*) and bonobo (*Pan paniscus*) subjects successfully learned to produce a large number of American Sign Language signs and correctly associate them with their function (Hixson, 1998). An enculturated bonobo named Kanzi also successfully learned to use a ‘lexigram’ – a keyboard-like object where each of over 200 symbols was associated with a referent (for example, food, places or people familiar to Kanzi) – to communicate with humans (Savage-Rumbaugh *et al.*, 1993; Brakke & Savage-Rumbaugh, 1995, 1996). These subjects demonstrate optionality in their ability both to (i) learn how to produce novel signals and (ii) map them to functions that do not exist in their respective species-typical signal repertoires. It is striking that these ‘success stories’ occur in domains of behaviour more closely aligned with gestural than vocal communication, suggesting that the gestural repertoires of great apes may be less constrained with regards to demonstrating optionality in comparison to their vocal repertoires. However, while natural gestural communication of primates is still somewhat under-examined, and many species of primate remain entirely unstudied, the evidence so far suggests that the gestural repertoires of wild primates are as rigid as vocal ones. The associations between signal forms and functions found in the gestural repertoires of wild apes do not vary much between populations (Byrne & Cochet, 2017) and are even shared between species (Genty *et al.*, 2009; Hobaiter & Byrne, 2011; Graham *et al.*, 2018; Fröhlich *et al.*, 2019), suggesting an ancestrally shared, innate repertoire. While the enculturated individuals described above are highly unusual in terms of their upbringing and training received, they nevertheless demonstrate that the

learning of novel signals and mapping them to functions (both in and outside of the species’ typical communicative range) is within the absolute limits of cognition for all great ape species. From this we can infer that such feats may also have been possible for our common ancestors, if given the same opportunities.

(2) Signal adjustment optionality

As opposed to adding new signals to one’s repertoire and assigning them a novel or existing function (as with signal production learning), another dimension in which optionality may be expressed involves altering the form of *existing* signals and assigning them a novel or existing function, i.e. ‘signal adjustment optionality’. An example of signal adjustment optionality would be an English speaker’s ability to modify the form of the adjective ‘big’ to ‘biiig’ to intensify the meaning of the adjective and convey that something is very big (Schlenker, 2018). In everyday communication, it is also common for conversation partners to converge on the prosodic and/or structural features of one another’s language use to facilitate social bonding, or to signal group identity in a process known as ‘accommodation’ (Bernhold & Giles, 2020). Each of these cases involves an ability to alter the form of existing signals (whether with or without an associated change in function) and is therefore demonstrative of signal adjustment optionality.

In animals, the ability to adjust existing signals appears to be relatively widespread compared to signal production learning (Martins & Boeckx, 2020). In these species, the repertoire of call types may be entirely fixed, but the acoustic structures of these calls may nevertheless be modified for a range of purposes. Analogous to accommodation in language use, some species modify existing signals to become more similar to those produced by social partners, resulting in short-term or persistent acoustic convergence between two or more individuals. For example, yellow-naped Amazon parrots (*Amazona auropalliata*) develop regional ‘dialects’ which are thought to be used for identification, social cohesion and attracting affiliated social partners to their foraging party (Wright, 1996), with individuals who live between regions even using both dialects interchangeably. These birds are therefore capable of associating multiple learned signal variants with an existing function. In primates, male chimpanzees produce an individually identifiable social contact call known as a ‘pant-hoot’ which may serve a range of possible functions including territorial and sexual displays, group coordination and more (Notman & Rendall, 2005; Fedurek, Donnellan & Slocombe, 2014). When this call-type is produced in chorus, a behaviour that reflects an affiliative bond between two individuals, males dynamically adjust the acoustic and temporal features of their calls to make them more similar to one another (Mitani & Gros-Louis, 1998). Furthermore, chimpanzees are able to alter the acoustic structure of their pant-hoots on a long-term basis by converging on stable, group-wide pant-hoot profiles that differentiate them from neighbouring communities (Marshall, Wrangham &

Arcadi, 1999; Crockford *et al.*, 2004; Desai *et al.*, 2021). Chimpanzees can, therefore, both dynamically modify the structure of their pant-hoots (dyadic convergence), as well as ‘save’ modifications on a more long-term basis to form a new template for this call-type (group signatures). While any changes to the function of these calls corresponding with such acoustic modifications are unexplored, these data minimally demonstrate that although the acquisition of pant-hoots is innately rooted, there is nevertheless a degree of optionality in how they can be produced.

Unfortunately, due to the difficulty of obtaining detailed, long-term acoustic data on the same individuals in the wild, we can often only observe the endpoint of such long-term acoustic changes and have little insight into the exact processes underlying them. Observing this process in action would allow us to understand better the cognitive biases and other factors influencing which acoustic modifications take place, and how neighbouring groups avoid making the same modifications. Indeed, research in other, captive primates has succeeded in examining this process under experimental conditions. For example, a series of translocation experiments (Zürcher, Willems & Burkart, 2019) found that common marmosets (*Callithrix jacchus*) who are moved to live with a new population, and who previously demonstrated an acoustically different dialect (Zürcher & Burkart, 2017), converge on the acoustic structure of the new population in multiple call types. Crucially, the authors first moved the individuals to the novel environment, but prevented social and acoustic contact with the new population, and did not observe any persistent changes to call structure, thus ruling out environmental effects as an explanation for the changes observed after social contact was made (Fischer, Wheeler & Higham, 2015; Watson *et al.*, 2015a). Relatedly, pygmy marmosets (*Cebuella pygmaea*) converge on the acoustic structure of their partners’ ‘trill’ contact calls when paired with a new mate (Snowdon & Elowson, 1999). Similar findings also exist for other non-primate species, including avians (Henry *et al.*, 2015), pinnipeds (Ravignani *et al.*, 2016; Stansbury & Janik, 2019), cetaceans (Janik, 2014) and naked mole rats (*Heterocephalus glaber*) (Barker *et al.*, 2021). Taken together, these data suggest an evolutionarily ancient capacity to alter the acoustic structure of signals within pre-existing form–function associations.

Interestingly, much like the examples of signal production optionality described above, signal adjustment has also been identified almost exclusively within the functional category of social contact calls. However, one counterexample has been identified in chimpanzees. Chimpanzees produce ‘rough grunts’ in response to finding food. These grunts differ acoustically relative to the caller’s preference for that food type (higher frequency grunts being associated with higher value food items), and listeners can use them to guide their own search for food (Slocombe & Zuberbühler, 2005b). When a group of chimpanzees were brought to Edinburgh Zoo to be integrated with an existing community, Watson *et al.* (2015b) found that each sub-group possessed different group-level preference values for apples (high value for the

‘local’ sub-group, and low value for the newcomer sub-group) and produced acoustically different grunts in response to finding this food. However, after 3 years, once the groups had fully socially integrated, the authors found that the ‘immigrant’ sub-group had converged on the acoustic structure of the grunts produced by their hosts, despite *not* changing their preference for apples (Watson *et al.*, 2015a,b). This not only demonstrates learned adjustment of a signal-form, but an ability to decouple certain features of signal forms from their innately corresponding function. Whether chimpanzees are capable of going further and fully dissociating a call from its function, such as producing a rough grunt to function as a contact call, is unclear. However, there is evidence that optional associations between existing signals and novel functions is within the capabilities of other primate species (see Section II.3).

Beyond identifying more examples of signal adjustment optionality, an important next step would be examining what, if any, are the actual adaptive benefits of this behaviour. For instance, despite the apparently strong motivation individuals from many species have to share similar signal forms with their close social partners (Henry *et al.*, 2015), it is currently unclear whether individuals who do not converge on group-specific variations of signals face any costs. If one does not converge on the signal forms of groupmates, is it more challenging to coordinate and/or understand the function of their signals? Or do individuals who fail to converge on such norms suffer some form of social consequences, much as humans often demonstrate negative bias towards out-group speakers (Iacozza, Meyer & Lev-Ari, 2020)? Conformity towards group-wide behavioural ‘norms’ seems to be present in the foraging behaviour of several animal species (van de Waal, Borgeaud & Whiten, 2013; Aplin *et al.*, 2015), but the proximate causes of behavioural convergence and consequences for non-conformists are as unclear as with vocal accommodation. Finally, it is not currently known whether individuals who converge on a new long-term call structure still have ready access to the previously used form. In other words, are individuals capable of simultaneously producing both old and new variants, or does the latter ‘overwrite’ the former? This would have important implications for whether we understand examples of signal adjustment learning as cumulative, long-term increases in optionality of signal forms associated with a function, or rather a temporary widening (during the adjustment process) and subsequent winnowing (once the process is complete) of signalling options. Another possibility is that even if the novel variant ‘overwrites’ the previous form, it may subsequently be easier to ‘relearn’ it than other novel forms, analogous to an individual ‘losing’ their original accent after moving to a new region, but quickly regaining it if they return.

(3) Signal usage optionality

In the previous section, we focused on the particular dimension of optionality found in the adjustment of the form of existing signals (i.e. optionality in how a signal is *produced*).

We now turn to another dimension of optionality: the association of existing signal forms to different functions (i.e. optionality in how a signal is *used*). For instance, consider a human infant visiting the park who points and utters ‘Ducky!’ at waterbirds as diverse as ducks, swans, geese and moorhens, before gradually refining their usage of the word. Here, a stable signal-form (the word ‘Ducky’) is associated with a change in function. Even species with largely fixed signal repertoires may undergo changes in the usage of existing vocalisations that reflect optionality, whether this occurs by way of an ontogenetic process in the development of an adult repertoire, or by way of learning to use existing calls for novel functions. A classic example of the former case, analogous to the ‘Ducky’ example, has been identified in vervet monkey (*Chlorocebus pygerythrus*) infants. Initially, these monkeys produce alarm calls in response to any aerial disturbance, but eventually refine their usage so that the calls are only produced in response to the ‘correct’ stimuli of aerial predators (Seyfarth & Cheney, 1980, 1986). Exactly what causes this process is currently unclear: it may be developmentally fixed, a result of feedback from conspecifics, or simply a result of differences in what causes a state of alarm in an infant compared to an adult. Further study of this behaviour may determine whether these findings reflect a change in the number of functions assigned to the signal, a replacement of a ‘generalised’ alert signal with a more precise one, or more simply an increase in the precision with which the original function is applied by signalers. What we do know is that surrounding adults are likely to ignore the calls of these infants until they reach maturity, indicating that receivers are capable of understanding that others may use signals for ‘incorrect’ functions (Seyfarth & Cheney, 1980, 1986). This example therefore demonstrates some level of optionality on the part of both producers (refining the function of a signal over time) and receiver (understanding that the same signal can refer to both ‘predator’ and ‘disturbance’ – we consider this further in Section II.5).

Individuals can also demonstrate signal usage optionality by mapping existing signals to previously unassociated functions (as opposed to the previous example, where functions were winnowed). In English, for example, words with originally negative connotations such as ‘bad’, ‘wicked’ and ‘sick’ have gained positive ones in slang dialects over time. This ability to map additional, even diametrically opposed functions to an existing signal is difficult to examine in animals under wild conditions. The types of environments encountered by a species are typically static, at least within observable timescales, and they are therefore unlikely to encounter novel contexts at a frequency that would warrant such changes, even if they were capable of them. However, under captive conditions, signal usage optionality can be elicited or developed through training. Pig-tailed macaques (*Macaca nemestrina*) naturally produce a ‘coo’ call in social contexts, which researchers have trained them to produce under experimental conditions, functioning as a human-directed request for food (Coudé *et al.*, 2011). Interestingly, in contrast to ‘spontaneous’ calls, where motor regions of the brain activate during call production, these trained calls elicited brain

activity before the onset of the call, indicating pre-planning or voluntary control over the production. In a similar study, one Japanese macaque was trained to produce coo calls to ‘request’ a stick-tool for a food-raking task (Hihara *et al.*, 2003b), thereby demonstrating signal usage optionality. Once this behaviour had been instilled, the monkey spontaneously demonstrated signal adjustment optionality by altering the acoustic structure of the ‘coo’ calls produced in this function so that they were acoustically distinct from the original call-type. This potentially demonstrates a motivation to differentiate signal forms in response to differentiations in signal functions where possible. Similar evidence exists for several other species, including spear-nosed bats (*Phyllostomus discolor*) (Lattenkamp, Vernes & Wiegrecbe, 2020), white-handed gibbons (*Hylobates lar*) (Kato *et al.*, 2007) and budgerigars (*Melopsittacus undulatus*) (Manabe & Dooling, 1997). While these studies typically have small sample sizes of individuals living under extremely unusual conditions, they do at least demonstrate that these species (a) possess the ability to associate innate calls with novel functions under specific circumstances (signal usage optionality) and (b) are spontaneously motivated to differentiate the functions of calls through modification of their form (signal adjustment optionality).

While these studies demonstrate signal usage optionality is within the absolute limits of cognition of their target species, this raises the question of why this is not demonstrated more readily under natural conditions. One likely explanation is that the relative stability of natural environments provides insufficient motivation to change the innate set of form–function associations in their repertoire, which already meets the demands of their social and ecological environment. Another tantalising possibility is that such instances have simply gone unrecorded in many species. Due to the difficulty of collecting sufficiently extensive, comparable data on multiple populations of the same species, explicit cross-population comparisons of signal usage are rare. However, where such data do exist, there are hints that optional signal usage may indeed occur under natural conditions. For instance, while the vast majority of chimpanzee gesture forms and functions appear to be innately tied in their association (Byrne & Cochet, 2017; Motes-Rodrigo & Tennie, 2021), a handful of gestures (most notably ‘leaf clipping’) are used for particular functions by some communities but not others (Whiten *et al.*, 1999; Kalan & Boesch, 2018). Assuming that there is no genetic explanation for this variation, we can infer that chimpanzees possess some degree of optionality in the functional associations of their gestural repertoire. It is therefore possible that for some species, we are observing the ‘end-state’ of processes that have shaped their use of signals over many years. Recent work also shows that applying experimental methods to wild populations can indeed illuminate optionality in signal usage: Wegdell, Hammerschmidt & Fischer (2019) report that, in response to the introduction of a novel flying drone, western green monkeys (*Chlorocebus sabaues*) produced an ancestral call-type, which was not previously used under normal circumstances for aerial predators or disturbances, but was similar to the eagle-specific predator

alarm calls produced by closely related species, thus demonstrating the ability to associate pre-existing calls with novel stimuli. Approaches such as this could prove highly fruitful in exploring how wild animals communicate about novel stimuli in their environment.

(4) Combinatorial optionality

It is well understood that speakers of a natural language can express the same propositions by different choices of words (e.g. ‘Fatima gives a book to the boy’ *versus* ‘Fatima gives the boy a book’ – combination of different forms to achieve the same function). This case involves alternative combinations of the constituents of a sentence with the same communicative function. However, different combinations of an identical set of words can also drastically alter their meaning (e.g. ‘a man bites a dog’ *versus* ‘a dog bites a man’ – recombination of the same forms to achieve different functions). This case involves recombining the constituents of a sentence to achieve a different communicative function. This seems to point to an additional dimension of optionality, distinct from signal production, signal adjustment, and signal usage: the altering of the function of a signal based on the combinatorial context in which it is placed. This combinatorial optionality of signals is key to the full expressive power of language, as it allows us to combine a finite number of elements (i.e. words) into a theoretically unlimited number of larger, meaningful structures (i.e. sentences). A pertinent avenue of research is, therefore, the extent to which animals also demonstrate combinatorial optionality in signal structures.

Song is by far the primary domain of animal communication exhibiting significant levels of combinatorial optionality, found in species as diverse as birds (Slabbekoorn & Smith, 2002), marine mammals (McDonald, Mesnick & Hildebrand, 2006; Cholewiak, Sousa-Lima & Cerchio, 2013; Oleson *et al.*, 2014), bats (Davidson & Wilkinson, 2004; Bohn, Smarsh & Smotherman, 2013), rock hyrax (*Procapra capensis*) (Koren & Geffen, 2009) and even mice (Banerjee, Phelps & Long, 2019). Hundreds of different variations on a song may exist within a species, or even a single individual. For instance, in song sparrows (*Melospiza melodia*), ~1100 different songs were recorded from just 12 individuals living in New York (Podos *et al.*, 1992). Such examples indicate both producers and receivers can associate a diverse range of signal combination structures, including novel ones, to the same function (typically a territorial or sexual display). Interestingly, virtually all known examples of song in non-human animals are limited to territorial and mating displays. While different combinations of elements may express information about the caller, such as mate quality or group identity (Hardy & Parker, 1997; Davidson & Wilkinson, 2004), restructuring these songs does not alter their general function. This represents a key discontinuity with language, where changing the composition of a sentence can drastically alter its meaning. One exception to this is the white-handed gibbon (Geissmann, 2002), who, in addition to duet songs in which pair-bonded individuals converge on a song structure over a

number of years, also produce alarm songs produced in response to threats such as leopards and eagles (Clarke, Reichard & Zuberbühler, 2006; Andrieu *et al.*, 2020). Both duet songs and alarm songs are composed of an identical repertoire of notes, but contain differences in the prevalence of certain notes and how they are combined (Clarke *et al.*, 2006). This presents a so-far unique example where the rearrangement of song elements drastically alters the function of the song (from contact call to alarm call). The structure of these songs is subject to learning, with evidence suggesting a role of maternal feedback in the development of these songs in female offspring (Koda *et al.*, 2013) and pair-bonded individuals converging on dyad-specific duets (Geissmann, 2002).

Outside of song, relevant examples of signal combinations are rarer, but do exist (Engesser & Townsend, 2019). A stand-out example which may reflect multiple dimensions of optionality comes from chestnut-crowned babblers (*Pomatostomus ruficeps*) (but see also Suzuki, Wheatcroft & Griesser, 2016), a species of cooperatively breeding songbird. These birds produce two structurally similar, but functionally distinct, combinations of the same two acoustic elements: ‘B-A-B’ and ‘A-B’, where A and B are acoustically distinct sounds which are never produced alone or in other combinations. These calls have very different functions, with ‘A-B’ sequences being produced during flight and ‘B-A-B’ sequences produced while provisioning nestlings (Engesser *et al.*, 2015, 2019). The addition of the ‘B’ element is therefore not an additive change to the function of the call, as one would expect from the repetition of a note indicating heightened arousal (for example due to probable predator threat), such as the number of additional ‘D’ notes in the alarm calls of black-capped chickadees (*Parus atricapillus*) (Templeton, Greene & Davis, 2005). Chestnut-crowned babblers may therefore demonstrate optionality in terms of both (i) the function of individual elements produced in combinations (As and Bs are individually not tied to any individual function) and (ii) the relationships between them (different combination of the *same* elements results in a different function). Various examples of combinatorial optionality also appear to be present in non-bird species such as dwarf mongooses (*Helogale parvula*) (Collier *et al.*, 2020), dingoes (*Canis lupus dingo*) (Déaux *et al.*, 2016), bonobos (Clay & Zuberbühler, 2009), gorillas (Hedwig *et al.*, 2014; Watson *et al.*, 2020b), chimpanzees (Leroux *et al.*, 2021) and Campbell’s monkeys (*Cercopithecus campbelli*) (Schlenker *et al.*, 2014).

(5) Signal perception optionality

Until this point, we have largely focussed on optionality on the part of signallers, rather than receivers. However, for each of the dimensions of optionality described above, its counterpart in signal perception is also crucial for effective communication. As a case in point, for linguistic communication to be effective, receivers must be able to decode the intended function of a producer’s utterance even if they use a novel word (signal production optionality), unfamiliar pronunciation of a sentence (signal adjustment optionality), or an

unconventional composition (combinatorial optionality). While we have occasionally touched on the receiver side of the five dimensions of optionality in each of the sections above, we believe the subject warrants separate consideration. In the remainder of this section, we discuss it under the general heading of ‘signal perception optionality’.

Just as there would be no point for humans in inventing a new word if no one could interpret it correctly, the costly neurological and vocal apparatus necessary for vocal learning would be unlikely to evolve if such modifications could not be effectively processed by receivers (Fischer & Hammerschmidt, 2020). To illustrate, male humpback whales (*Megaptera novaeangliae*) have been found to alter their songs (thought to function as sexual displays; Tyack, 1981) gradually over time to increase complexity, leading to occasional ‘cultural revolutions’ where a highly complex song is disposed of and a simplified version of a neighbouring community’s song is adopted instead (Noad *et al.*, 2000; Allen *et al.*, 2018). This demonstration of optionality in signal production and adjustment must be met with an equivalent degree of optionality in signal perception. For instance, it is of critical importance that receivers are able quickly to associate both more complex and simple variants of songs, as well as entirely novel ones, with an extant communicative function, rather than infer that a brand-new call-type has been invented.

Signal perception optionality is also necessary for receivers who need to process examples of signal usage optionality effectively. For example, chimpanzees, bonobos and gorillas appear to use identical gestural forms to serve a variety of communicative functions (Genty *et al.*, 2009; Hobaiter & Byrne, 2011; Graham, Furuichi & Byrne, 2017). Receivers in these species seem, therefore, to be capable of mapping multiple functions to the same gesture and disambiguating between them based on, for example, social and contextual information (Roberts, Vick & Buchanan-Smith, 2012). However, it is currently unclear whether these examples are truly demonstrative of a capacity to associate a single signal with multiple alternative functions, or rather are indicative of pragmatic flexibility, i.e. of the ability to use information from context to disambiguate call meanings (Seyfarth & Cheney, 2018). It is worth noting that if receivers are overly inclusive in the signals they lump together under a single function, they risk overlooking nuanced differences that may cue them into valuable additional information. One prediction would therefore be that optionality is likely to be less readily expressed in both the production and processing of urgent signals, such as alarm calls (Green, Brandley & Nowicki, 2020). On the other hand, some degree of optionality in the perception of such call types is likely to be beneficial in the face of rapid environmental change or the introduction of a novel predator. One avenue for experimentally probing receiver-side optionality in signal usage could be akin to classic associative learning experiments involving forming a novel association between two stimuli in a learner. For example, a common paradigm involves subjects learning to associate the pulling of one lever with receiving food and another with no reward or an aversive stimulus, before the association

is subsequently reversed by experimenters to examine the factors influencing how quickly subjects can remap these predictive cues (Izquierdo *et al.*, 2017). A similar approach, but using recordings of a species’ own signals as stimuli, might be one means of examining this process in the communicative domain, i.e. the ease with which individuals can associate additional ‘functions’ (in this case, a simple predictive relationship to food) to existing signals in their repertoires, or from those of other species.

In many cases, single call types are acoustically ‘graded’ according to their urgency, resulting in a system where important information may be carried by subtle perceptual differences between signals. For example, chimpanzee screams vary substantially in their acoustic structure according to the signaller’s role in an agonistic encounter (aggressor or victim), and according to the severity of the event (Slocombe & Zuberbühler, 2005a). Being able to process these fine-grained acoustic cues and extract the encoded information (i.e. determine whether it has been emitted by a victim or by an aggressor) may be very useful to receivers in deciding whether to engage with the conflict, or in keeping track of important third-party alliances (Gilby *et al.*, 2013). Of course, caution must be taken regarding whether the statistical differences researchers detect between signal variants are perceptible to conspecific receivers. Instead of revealing genuine signal perception optionality, the phenomenon might simply be due to the fact that the perceptual system of the subjects tested is not sensitive enough to register the differences between the variants. Researchers examined this by playing back recordings of the screams of groupmates to wild chimpanzees and found that they were able to differentiate between aggressor and victim screams produced by the same individual, demonstrating a capacity in receivers to discriminate between perceptually similar signal forms and assign them separate functions (Slocombe, Townsend & Zuberbühler, 2009; Slocombe *et al.*, 2010).

It is worth noting that signal perception optionality need not be limited to the processing of signals produced by conspecifics. The ability to ‘eavesdrop’ on heterospecific alarm calls and correctly associate them with their corresponding functions is crucial to avoiding predation for a wide range of species, such as birds, mongooses, primates and reptiles (Magrath *et al.*, 2015a). Although it may be that some species have evolved an innate understanding of the alarm calls of certain heterospecifics, in others there is perhaps evidence of a genuine component of perception optionality. For instance, Magrath *et al.* (2015b) found that fairy-wrens (*Malurus cyaneus*) quickly learned to associate playbacks of an unfamiliar species’ alarm calls (chestnut-rumped thornbills, *Acanthiza uropygialis*) with the presence of a model predator. The learning process involved was demonstrated to be independent of sound structure: the birds learned to associate synthetic computer sounds with the predator just as rapidly as real calls, suggesting that they were not simply reacting to fixed, biologically widespread acoustic cues in calls elicited by predation contexts. However, it could be argued that examples of interspecific eavesdropping are not an example

of ‘signal’ processing at all, but rather that these stimuli are processed more as environmental cues (i.e. as smoke is a cue towards fire, or thunder a cue towards lightning).

The ability to eavesdrop on the alarm systems of other species may therefore demonstrate one way in which a high degree of signal perception optionality can bestow significant fitness benefits. Yet, we should bear in mind that high degrees of signal perception optionality may also bear potential negative repercussions. For example, let us imagine a socially living individual who is highly predisposed to associate novel functions to the signals they receive. A conspecific signaller produces an aerial alarm call towards an aerial predator at the same moment that a car is passing by. However, our receiver only observes the car and is ignorant of the predator. If our receiver is too quick to form lasting associations between signals and their apparent functions, they may misunderstand future aerial alarm calls as referring to the presence of a car and behave suboptimally as a result, with potentially deadly consequences. Receivers must therefore find a balance between flexibility and conservatism, and, in order to prevent such ‘runaway optionality’, may stand to benefit from allowing for a low degree of signal perception optionality for contextually urgent signal types, such as alarm calls. The dilemma of ‘splitting *versus* lumping’ of perceptually similar signals will be familiar to scientists studying animal communication, who must themselves often decide how best to categorise groups of signals. It may be some small comfort that this is also likely to be an important issue for their subjects.

Finally, although many species do not produce combinatorial calls/signals (Engesser & Townsend, 2019) and hence appear incapable of combinatorial optionality, this may be due to limitations of the production system rather than constraints on processing such sequences. Artificial grammar studies, in which researchers probe the ability of individuals to process relationships between strings of artificial sounds, may help us shed light on this question. Primates (Fitch & Hauser, 2004; Ravignani *et al.*, 2013; Watson *et al.*, 2020a), birds (Abe & Watanabe, 2011) and rats (de la Mora & Toro, 2013), have all shown impressive capabilities for learning complex ‘artificial grammars’ that far exceed the degree of combinatorial complexity found in their natural production systems. While most of these experiments were passive designs, which did not instil any functional associations with the sequences (therefore not meeting our criteria for optionality), some species have been found able to make such associations. For example, zebra finches (*Taeniopygia castanotis*) were trained on a ‘Go/No-Go’ paradigm in which they would peck a sensor, or not, depending on the composition of sequences (constructed from their own song elements) played back to them (van Heijningen *et al.*, 2013). All subjects were able to discriminate between training sequences, and some were even able to generalise spontaneously (i.e. without reward) the underlying compositional patterns to novel structures. These data may suggest that even species which do not produce complex combinatorial structures may nevertheless be able to demonstrate optionality in their perception (Beckers *et al.*, 2017).

III. CONTEXTUALISING OPTIONALITY AND FUTURE DIRECTIONS

In the preceding sections we evaluated the animal communication literature for evidence of optionality, the capacity to establish alternative mappings between signal forms and functions, which we argue to be one fundamental feature underlying linguistic arbitrariness. We searched for optionality across five key dimensions of communicative behaviour in animals, ultimately finding evidence to be taxonomically widespread, but varying greatly across species (see Table S1 for a more exhaustive list of candidate evidence). Furthermore, we found that individual species may possess variable degrees of each of the dimensions of optionality we have surveyed. For instance, amphibians alter call structure to optimise transmission in different environments (Ziegler, Arim & Narins, 2011) or to combat background noise (Brumm & Zollinger, 2011), demonstrating a degree of signal adjustment optionality. However, they do not appear to demonstrate any other dimensions of optionality. This contrasts with birds and primates, certain species of which exhibit evidence in many of the dimensions of optionality we have described above (although research bias towards such species may explain some taxonomic skew of evidence). To our knowledge, only humans unambiguously express optionality in every one of the aspects described.

An important next step for the framework we have introduced would be to determine which cognitive and neural features underpin the expression of optionality in each of the dimensions discussed here, and whether these factors are in fact similar across species. This could be complemented with ongoing research into the social [e.g. social complexity (Knörnschild, Fernandez & Nagy, 2020); dominance styles (Kavanagh *et al.*, 2021)] and physical factors (e.g. environmental change; McMullen, Schmidt & Kunc, 2014) that may select for the abilities underpinning optionality. It would also be important to establish whether the five dimensions of optionality described in this review typically correlate within species. If so, this would indicate a fundamental capacity for optionality that can be differentially expressed in the domains of signal production, signal adjustment, signal usage, signal combination, and signal perception.

Although we have examined optionality as a feature of communicative behaviour, it is also possible that the examples discussed may be demonstrative of a more domain-general capacity for associative mapping which scaffolds, but is not exclusive to, communication and language. One hypothesis worth exploring is that optionality in the communicative domain may be related to cognitive processes underlying individuals’ ability to modify behaviour patterns or associations in non-communicative domains. For example, the phenomenon of ‘functional fixedness’ in object use or problem solving refers to an individual being unwilling or unable to go beyond the first-learned function for a particular tool or apparatus (German & Defeyter, 2000). A high degree of functional fixedness has, for instance, been identified in

chimpanzees (Davis *et al.*, 2016), who were unwilling to switch from their first-learned method of retrieving food from a tube apparatus even when the alternative demonstrated was considerably more efficient (Davis *et al.*, 2016; but see Watson *et al.*, 2017). It is straightforward to draw a conceptual parallel between (a) a proclivity (or lack thereof) to associate a single tool with multiple functions, or to perform the same function with a variety of tools, and (b) optionality in the communicative domain. One way to explore this issue would be to examine whether optionality in the communicative domain correlates with, for example the ease with which a species associates tools with multiple functions.

An additional possibility is that optionality may be constrained by a more domain-general ability to process ‘opaque’ relationships between causes and effects (and by extension, forms and functions). For signals whose form is strongly shaped by underlying body anatomy (e.g. body size; Reby & McComb, 2003) or emotional states (i.e. signals on the lower end of the spectrum illustrated in Fig. 2) there is, in a sense, a causal and perceptible relationship between form and function. For example, emotionally urgent contexts such as predator sightings increase tension in the body of the signaller, including their vocal folds, resulting in higher pitched vocalisations. These vocalisations can be readily decoded by receivers as being produced with high emotional arousal, even across species (Bryant & Barrett, 2008; Filippi *et al.*, 2017), suggesting that form–function associations between signals and clear causal factors are relatively easy to form. An analogue can be drawn here with language, where vocabulary learned by infants is often rich in iconicity (a perceptual similarity between word and meaning), which is thought to aid acquisition (Monaghan, Mattock & Walker, 2012). Other signals, on the other hand, are ‘causally opaque’ in that there is no apparent causal or correlational relationship between the form of a signal and its function – with most examples of arbitrary language (and many examples of signal production learning) falling into this category. The ability to process opaque causal relationships in the physical domain, i.e. direct causal connections between stimuli (such as two objects, or an acoustic cue and a reward) which are not clearly perceivable, has been examined in human and non-human apes. This research indicates that apes are constrained in this ability, as are children up to the age of 4 years old, after which such associations are readily formed (Civelek, Call & Seed, 2020). Strikingly, language acquisition studies find that arbitrary sound–meaning mappings in the vocabulary typically acquired by children also arise sharply at the age of 4 years (Monaghan *et al.*, 2014).

Humans also have a pervasive tendency to copy causally opaque actions demonstrated by others, even when they have no apparent causal relationship with the actor’s goal (known as ‘overimitation’), with this proclivity also appearing from around 4–5 years of age (Hoehl *et al.*, 2019). Cognitive adaptation for processing these seemingly causally disconnected behaviours as being effective is critical for the highly conventionalised and technologically complex nature of human culture. For instance, if fully understanding the causal chain

between pushing a button and activating any of the myriad technologies in our home were to be a necessary condition for learning how to use them, they would be rendered wildly impractical. Great apes, on the other hand, are less inclined to make such dissociated connections between behaviour and function (McGuigan *et al.*, 2007; Nielsen & Susianto, 2010; Clay & Tennie, 2018). Taken together, these correlations between the ability of humans to process abstract (i.e. not perceptually apparent) relationships between causes and effects in the physical domain, as well as forms and meanings in the context of language, potentially supports a domain-general process underlying optionality across domains.

While currently speculative, these potentially related areas of research may be fruitful avenues for exploring relevant cognitive processes that may be acting across domains. Specifically, if communicative optionality represents a domain-specific manifestation of a domain-general capacity, we should find within-species correlations in evidence across these other domains of behaviour. Such an effect could be examined either directly, through the application of a battery of tests probing different potentially related behaviours in one (e.g. Watson *et al.*, 2018) or many (e.g. ManyPrimates *et al.*, 2019) species, or even *via* meta-analyses once a sufficient number of individual studies has accumulated. If such a correlation between domains were to be identified, this may lend support to arguments that the unique cognitive achievements of humans do not depend on excellence in any one particular domain of cognition, but rather on a feedback loop of interactions and reinforcement between domains (Laland & Seed, 2021). Along these lines, it may be that an interaction of optionality, not qualitatively different to that found in animals, with other language-relevant abilities allows for the full-blown arbitrariness found in human language. Through further examination of optionality and its limitations, we may be able to identify more acutely the processes involved in the evolution of linguistic arbitrariness.

Finally, a natural complement to the current review would be to apply the optionality framework to human language in order to identify more precisely parallels between examples of optionality in animals and linguistic arbitrariness. For example, while optionality is probably a crucial underpinning of linguistic arbitrariness, the former does not exhaust the latter. We could therefore task further conceptual research with identifying what additional features, if any, must accompany optionality to warrant a diagnosis of full-blown arbitrariness. Another approach might be to examine the five dimensions of optionality described in this review in child language acquisition, to understand better their developmental trajectory in humans. We might investigate, for example, the relationship between some or all of these dimensions and the use of iconicity and systematicity (features of non-arbitrariness, see Section I), which are prevalent in early child language acquisition but eventually give way to more arbitrary language (Cassidy & Kelly, 1991; Fitneva, Christiansen & Monaghan, 2009; Monaghan *et al.*, 2012). Some populations and languages seem to make use of

non-arbitrary features more readily than others (Dingemanse & Akita, 2017), suggesting that linguistic phylogeny imposes constraints on how the expression of optionality evolves in language within and between speaker populations. Investigating this phenomenon could provide further insights into the role of optionality in terms of the cultural evolutionary forces acting upon languages themselves (Woodin *et al.*, 2020; Ćwiek *et al.*, 2021; O'Connor, 2021).

IV. CONCLUSIONS

(1) Our ability to associate the form of words arbitrarily with their meaning is often cited as a defining feature of language (Hockett, 1958; Gasser, 2004; Monaghan *et al.*, 2014; Dingemanse *et al.*, 2015). Despite this, examination of the evolutionary history of linguistic arbitrariness is largely absent, in large part due to the difficulty of drawing comparisons between arbitrary language and animal communication (Planer & Kalkman, 2019). A conceptual advance facilitating this comparative approach is therefore crucial in order to shed light on the evolutionary roots of this defining feature of language.

(2) In this review we present a novel framework for examining the cognitive foundations of linguistic arbitrariness. This framework is centred on the notion of optionality, i.e. the capacity to establish alternative mappings between signal forms and functions, which we argue is one key feature underlying linguistic arbitrariness. Because optionality is not inherently bound to language and can be applied to any communication system, this enables the cross-species, comparative approach necessary for shedding light on the evolutionary history of arbitrariness.

(3) Until now, many of the examples of optionality we have surveyed have been discussed under the generic umbrella term of ‘flexibility’ (e.g. Townsend *et al.*, 2020). However, the notion of ‘flexibility’ was not designed to characterise linguistic arbitrariness. By adopting the notion of optionality, we have provided a novel conceptual framework with which to examine animal communication literature for the characteristic features of arbitrariness.

(4) In accordance with this framework, we have reviewed some of the most pertinent existing evidence for optionality in animal communication across five key dimensions of animal communication: signal production, signal adjustment, signal usage, signal combinatoriality and signal perception. We also provide a more extensive sample of relevant literature in Table S1.

(5) There is considerable scope for expanding on this framework by examining the cognitive abilities likely to be underpinning the described examples of optionality, and whether these are demonstrative of a single, unitary (possibly domain-general) capacity or rather a diverse suite of processes.

(6) This preliminary foray into examining optionality has yielded novel insights into existing data, and identified

promising avenues for future research. We believe that further application of this framework will be a productive means of exploring the evolutionary roots of the cognitive abilities underlying both animal communication and human language.

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VI. REFERENCES

- References identified with an asterisk (*) are cited in the Supporting Information.
- *ABE, K. & WATANABE, D. (2011). Songbirds possess the spontaneous ability to discriminate syntactic rules. *Nature Neuroscience* **14**, 1067–1074.
- ALLEN, J. A., GARLAND, E. C., DUNLOP, R. A. & NOAD, M. J. (2018). Cultural revolutions reduce complexity in the songs of humpback whales. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20182088.
- *ANDRIEU, J., PENNY, S. G., BOUCHET, H., MALAIVIJITNOND, S., REICHARD, U. H. & ZUBERBÜHLER, K. (2020). White-handed gibbons discriminate context-specific song compositions. *PeerJ* **8**, e9477.
- APLIN, L. M., FARINE, D. R., MORAND-FERRON, J., COCKBURN, A., THORNTON, A. & SHELDON, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541.
- BANERJEE, A., PHELPS, S. M. & LONG, M. A. (2019). Singing mice. *Current Biology* **29**, 190–191.
- BARKER, A. J., VEVIURKO, G., BENNETT, N. C., HART, D. W., MOGRABY, L. & LEWIN, G. R. (2021). Cultural transmission of vocal dialect in the naked mole-rat. *Science* **371**, 503–507.
- BATESON, P. & LALAND, K. N. (2013). Tinbergen’s four questions: an appreciation and an update. *Trends in Ecology & Evolution* **28**, 712–718.
- BECKERS, G. J. L., BERWICK, R. C., OKANOYA, K. & BOLHUIS, J. J. (2017). What do animals learn in artificial grammar studies? *Neuroscience & Biobehavioral Reviews* **81**, 238–246.
- BERG, K. S., DELGADO, S., CORTOPASSI, K. A., BEISSINGER, S. R. & BRADBURY, J. W. (2012). Vertical transmission of learned signatures in a wild parrot. *Proceedings of the Royal Society B: Biological Sciences* **279**, 585–591.
- BERNHOLD, Q. S. & GILES, H. (2020). Vocal accommodation and mimicry. *Journal of Nonverbal Behavior* **44**, 41–62.
- *BERTHET, M., NEUMANN, C., MESBAHI, G., CĂSAR, C. & ZUBERBÜHLER, K. (2018). Contextual encoding in titi monkey alarm call sequences. *Behavioral Ecology and Sociobiology* **72**, 1–11.
- BERWICK, R. C., FRIEDERICI, A. D., CHOMSKY, N. & BOLHUIS, J. J. (2013). Evolution, brain, and the nature of language. *Trends in Cognitive Sciences* **17**, 89–98.
- BLASI, D. E., WICHMANN, S., HAMMARSTRÖM, H., STADLER, P. F. & CHRISTIANSEN, M. H. (2016). Sound–meaning association biases evidenced across thousands of languages. *Proceedings of the National Academy of Sciences* **113**, 10818–10823.
- *BOECKLE, M. & BUGNYAR, T. (2012). Long-term memory for affiliates in ravens. *Current Biology* **22**, 801–806.
- BOHN, K. M., SMARSH, G. C. & SMOTHERMAN, M. (2013). Social context evokes rapid changes in bat song syntax. *Animal Behaviour* **85**, 1485–1491.
- *BOUGHEY, M. J. & THOMPSON, N. S. (1981). Song variety in the brown thrasher (*Toxostoma rufum*). *Zeitschrift für Tierpsychologie* **56**, 47–58.

- BRASSE, K. E. & SAVAGE-RUMBAUGH, E. S. (1995). The development of language skills in bonobo and chimpanzee: I. Comprehension. *Language & Communication* **15**, 121–148.
- BRASSE, K. E. & SAVAGE-RUMBAUGH, E. S. (1996). The development of language skills in pan: II. Production. *Language & Communication* **16**, 361–380.
- *BRUCK, J. N. (2013). Decades-long social memory in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131726.
- BRUMM, H. & ZOLLINGER, S. A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* **148**, 1173–1198.
- BRYANT, G. & BARRETT, H. C. (2008). Vocal emotion recognition across disparate cultures. *Journal of Cognition and Culture* **8**, 135–148.
- BURGESS, A. & SHERMAN, B. (2014). *Metasemantics: New Essays on the Foundations of Meaning*. Oxford University Press, New York, NY.
- BYRNE, R. W. & COCHET, H. (2017). Where have all the (ape) gestures gone? *Psychonomic Bulletin & Review* **24**, 68–71.
- CALL, J. & TOMASELLO, M. (1996). The effect of humans on the cognitive development of apes. In *Reaching into Thought: The Minds of the Great Apes* (eds A. E. RUSSON, K. A. BARD and S. T. PARKER), pp. 371–403. Cambridge University Press, New York.
- *CÁSAK, C., ZUBERBÜHLER, K., YOUNG, R. J. & BYRNE, R. W. (2013). Titi monkey call sequences vary with predator location and type. *Biology Letters* **9**, 20130535.
- CASSIDY, K. W. & KELLY, M. H. (1991). Phonological information for grammatical category assignments. *Journal of Memory and Language* **30**, 348–369.
- CHENEY, D. L., OWREN, M. J., DIETER, J. A. & SEYFARTH, R. M. (1992). ‘Food’ calls produced by adult female rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques, their normally-raised offspring, and offspring cross-fostered between species. *Behaviour* **120**, 218–231.
- CHOLEWIAK, D. M., SOUSA-LIMA, R. S. & CERCHIO, S. (2013). Humpback whale song hierarchical structure: historical context and discussion of current classification issues. *Marine Mammal Science* **29**, E312–E332.
- CHRISTIANSEN, M. H. & KIRBY, S. (2003). Language evolution: consensus and controversies. *Trends in Cognitive Sciences* **7**, 300–307.
- CIVELEK, Z., CALL, J. & SEED, A. M. (2020). Inferring unseen causes: developmental and evolutionary origins. *Frontiers in Psychology* **11**, 1–17.
- CLARK, A. (1998). Magic words: how language augments human computation. In *Language and Meaning in Cognitive Science* (eds A. CLARK and J. TORIBIO), pp. 33–51. Routledge, New York, NY.
- *CLARKE, E., REICHARD, U. H. & ZUBERBÜHLER, K. (2006). The syntax and meaning of wild gibbon songs. *PLoS One* **1**, e73.
- *CLAY, Z., ARCHBOLD, J. & ZUBERBÜHLER, K. (2015). Functional flexibility in wild bonobo vocal behaviour. *PeerJ* **3**, e1124.
- CLAY, Z. & TENNIE, C. (2018). Is overimitation a uniquely human phenomenon? Insights from human children as compared to bonobos. *Child Development* **89**, 1535–1544.
- *CLAY, Z. & ZUBERBÜHLER, K. (2009). Food-associated calling sequences in bonobos. *Animal Behaviour* **77**, 1387–1396.
- *CLAY, Z. & ZUBERBÜHLER, K. (2011). Bonobos extract meaning from call sequences. *PLoS One* **6**, e18786.
- COLLIER, K., RADFORD, A. N., STOLL, S., WATSON, S. K., MANSER, M. B., BICKEL, B. & TOWNSEND, S. W. (2020). Dwarf mongoose alarm calls: investigating a complex non-human animal call. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20192514.
- *COUDÉ, G., FERRARI, P. F., RODÀ, F., MARANESI, M., BORELLI, E., VERONI, V., MONTI, F., ROZZI, S. & FOGASSI, L. (2011). Neurons controlling voluntary vocalization in the macaque ventral premotor cortex. *PLoS One* **6**, e26822.
- COYE, C., TOWNSEND, S. & LEMASSON, A. (2018). From animal communication to linguistics and back: insight from combinatorial abilities in monkeys and birds. In *Origins of Human Language: Continuities and Discontinuities with Nonhuman Primates* (eds L. BOÉ, J. FAGOT, P. PERRIER and J. L. SCHWARZ), pp. 187–232. Peter Lang, Bern.
- *CROCKFORD, C., HERBINGER, I., VIGILANT, L. & BOESCH, C. (2004). Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology* **110**, 221–243.
- ĆWIEK, A., FUCHS, S., DRAXLER, C., ASU, E. L., DEDIU, D., HIOVAIN, K., KAWAHARA, S., KOUTALIDIS, S., KRIFKA, M., LIPPUS, P., LUPYAN, G., OH, G. E., PAUL, J., PETRONE, C., RIDOUANE, R., ET AL. (2021). Novel vocalizations are understood across cultures. *Scientific Reports* **11**, 10108.
- *DALZIELL, A. H. & MAGRATH, R. D. (2012). Fooling the experts: accurate vocal mimicry in the song of the superb lyrebird, *Menura novaehollandiae*. *Animal Behaviour* **83**, 1401–1410.
- *DAVIDSON, S. M. & WILKINSON, G. S. (2004). Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Animal Behaviour* **67**, 883–891.
- DAVIS, S. J., VALE, G. L., SCHAPIRO, S. J., LAMBETH, S. P. & WHITEN, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*Pan troglodytes*). *Scientific Reports* **6**, 1–12.
- *DE LA MORA, D. M. & TORO, J. M. (2013). Rule learning over consonants and vowels in a non-human animal. *Cognition* **126**, 307–312.
- *DE WAAL, F. (1986). Deception in the natural communication of chimpanzees. In *Deception: Perspectives on Human and Nonhuman Deceit* (eds R. W. MITCHELL and N. S. THOMPSON), pp. 221–244. State University of New York Press.
- DÉAUX, E. C., ALLEN, A. P., CLARKE, J. A. & CHARRIER, I. (2016). Concatenation of ‘alert’ and ‘identity’ segments in dingoes’ alarm calls. *Scientific Reports* **6**, 30556.
- *DEECKE, V. B., FORD, J. K. & SPONG, P. (2000). Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour* **60**(5), 629–638.
- DERRICKSON, K. C. (1987). Yearly and situational changes in the estimate of repertoire size in northern mockingbirds (*Mimus polyglottos*). *The Auk* **104**, 198–207.
- *DERUITER, S. L., BOYD, I. L., CLARIDGE, D. E., CLARK, C. W., GAGNON, C., SOUTHALL, B. L. & TYACK, P. L. (2013). Delphinid whistle production and call matching during playback of simulated military sonar. *Marine Mammal Science* **29**, E46–E59.
- DERUNGS, C., KÖHL, M., WEIBEL, R. & BICKEL, B. (2018). Environmental factors drive language density more in food-producing than in hunter-gatherer populations. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20172851.
- DESAI, N. P., FEDUREK, P., SLOCOMBE, K. E. & WILSON, M. L. (2021). Chimpanzee pant-hoots encode information about individual but not group differences. *bioRxiv* doi:<https://doi.org/10.1101/2021.03.09.434515>
- DEZECACHE, G., ZUBERBÜHLER, K., DAVILA-ROSS, M. & DAHL, C. D. (2021). Flexibility in wild infant chimpanzee vocal behavior. *Journal of Language Evolution* **6**, 37–53.
- DINGEMANSE, M. & AKITA, K. (2017). An inverse relation between expressiveness and grammatical integration: on the morphosyntactic typology of ideophones, with special reference to Japanese 1. *Journal of Linguistics* **53**, 501–532.
- DINGEMANSE, M., BLASI, D. E., LUPYAN, G., CHRISTIANSEN, M. H. & MONAGHAN, P. (2015). Arbitrariness, iconicity, and systematicity in language. *Trends in Cognitive Sciences* **19**, 603–615.
- EGNOR, S. E. R. & HAUSER, M. D. (2004). A paradox in the evolution of primate vocal learning. *Trends in Neurosciences* **27**, 649–654.
- *ELOWSON, A. M. & SNOWDON, C. T. (1994). Pygmy marmosets, *Cebuella pygmaea*, modify vocal structure in response to changed social environment. *Animal Behaviour* **47**, 1267–1277.
- *ENGESSER, S., CRANE, J. M. S., SAVAGE, J. L., RUSSELL, A. F. & TOWNSEND, S. W. (2015). Experimental evidence for phonemic contrasts in a nonhuman vocal system. *PLoS Biology* **13**, e1002171.
- ENGESSER, S., HOLUB, J. L., O’NEILL, L. G., RUSSELL, A. F. & TOWNSEND, S. W. (2019). Chestnut-crowned babbler calls are composed of meaningless shared building blocks. *Proceedings of the National Academy of Sciences* **116**, 19579–19584.
- ENGESSER, S. & TOWNSEND, S. W. (2019). Combinatoricity in the vocal systems of nonhuman animals. *WIREs Cognitive Science* **10**, e1493.
- *ESSER, K.-H. (1994). Audio-vocal learning in a non-human mammal: the lesser spear-nosed bat *Phyllostomus discolor*. *NeuroReport* **5**, 1718–1720.
- *EY, E., RAHN, C., HAMMERSCHMIDT, K. & FISCHER, J. (2009). Wild female olive baboons adapt their grunt vocalizations to environmental conditions. *Ethology* **115**, 493–503.
- FEDUREK, P., DONNELLAN, E. & SLOCOMBE, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology* **68**, 1345–1355.
- FILIPPI, P., GONGDON, J. V., HOANG, J., BOWLING, D. L., REBER, S. A., PAŠUKONIS, A., HOESCHELE, M., OCKLENBURG, S., DE BOER, B., STURDY, C. B., NEWEN, A. & GÜNTÜRKÜN, O. (2017). Humans recognize emotional arousal in vocalizations across all classes of terrestrial vertebrates: evidence for acoustic universals. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20170990.
- FISCHER, J. & HAMMERSCHMIDT, K. (2020). Towards a new taxonomy of primate vocal production learning. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20190045.
- *FISCHER, J., HAMMERSCHMIDT, K. & TODT, D. (1998). Local variation in Barbary macaque shrill barks. *Animal Behaviour* **56**(3), 623–629.
- FISCHER, J., WHEELER, B. C. & HIGHAM, J. P. (2015). Is there any evidence for vocal learning in chimpanzee food calls? *Current Biology* **25**, R1028–R1029.
- FITCH, W. T. (2005). The evolution of language: a comparative review. *Biology and Philosophy* **20**, 193–203.
- FITCH, W. T. (2010). *The Evolution of Language*. Cambridge University Press, New York, NY.
- FITCH, W. T., DE BOER, B., MATHUR, N. & GHAZANFAR, A. A. (2016). Monkey vocal tracts are speech-ready. *Science Advances* **2**, 1–7.
- *FITCH, W. T. & HAUSER, M. D. (2004). Computational constraints on syntactic processing in a nonhuman primate. *Science* **303**, 377–380.
- FITNEVA, S. A., CHRISTIANSEN, M. H. & MONAGHAN, P. (2009). From sound to syntax: phonological constraints on children’s lexical categorization of new words. *Journal of Child Language* **36**, 967–997.
- *FLOWER, T. (2011). Fork-tailed drongos use deceptive mimicked alarm calls to steal food. *Proceedings of the Royal Society B: Biological Sciences* **278**, 1548–1555.
- *FOOTE, A. D., GRIFFIN, R. M., HOWITT, D., LARSSON, L., MILLER, P. J. & RUS HOELZEL, A. (2006). Killer whales are capable of vocal learning. *Biology Letters* **2**, 509–512.

- *FRIPP, D., OWEN, C., QUINTANA-RIZZO, E., SHAPIRO, A., BUCKSTAFF, K., JANKOWSKI, K., WELLS, R. & TYACK, P. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. *Animal Cognition* **8**, 17–26.
- FRÖHLICH, M., STEVERS, C., TOWNSEND, S. W., GRUBER, T. & VAN SCHAIK, C. P. (2019). Multimodal communication and language origins: integrating gestures and vocalizations. *Biological Reviews* **94**, 1809–1829.
- *GARLAND, E. C., GOLDIZEN, A. W., REKDAHL, M. L., CONSTANTINE, R., GARRIGUE, C., HAUSER, N. D., POOLE, M. M., ROBBINS, J. & NOAD, M. J. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology* **21**, 687–691.
- GASSER, M. (2004). The origins of arbitrariness in language. *Proceedings of the Annual Meeting of the Cognitive Science Society* **26**, 434–439.
- *GEISSMANN, T. (2002). Duet-splitting and the evolution of gibbon songs. *Biological Reviews* **77**, 57–76.
- GENTY, E., BREUER, T., HOBAITER, C. & BYRNE, R. W. (2009). Gestural communication of the gorilla (*Gorilla gorilla*): repertoire, intentionality and possible origins. *Animal Cognition* **12**, 527–546.
- GERMAN, T. P. & DEFNEYER, M. A. (2000). Immunity to functional fixedness in young children. *Psychonomic Bulletin & Review* **7**, 707–712.
- GILBY, I. C., BRENT, L. J. N., WROBLEWSKI, E. E., RUDICELL, R. S., HAHN, B. H., GOODALL, J. & PUSEY, A. E. (2013). Fitness benefits of coalitional aggression in male chimpanzees. *Behavioral Ecology and Sociobiology* **67**, 373–381.
- GLOCK, H.-J. (2019). The normativity of meaning. In *The Normative Animal?: On the Anthropological Significance of Social, Moral, and Linguistic Norms* (eds N. ROUGHLEY and K. BAYERZ), pp. 295–318. Oxford University Press, Oxford.
- *GOLDIN-MEADOW, S. (1996). Kanzi: the ape at the brink of the human mind. *International Journal of Primatology* **17**, 145–148.
- *GRAHAM, K. E., FURUICHI, T. & BYRNE, R. W. (2017). The gestural repertoire of the wild bonobo (*Pan paniscus*): a mutually understood communication system. *Animal Cognition* **20**, 171–177.
- GRAHAM, K. E., HOBAITER, C., OUNSLY, J., FURUICHI, T. & BYRNE, R. W. (2018). Bonobo and chimpanzee gestures overlap extensively in meaning. *PLoS Biology* **16**, e2004825.
- GREEN, P. A., BRANDLEY, N. C. & NOWICKI, S. (2020). Categorical perception in animal communication and decision-making. *Behavioral Ecology* **31**, 859–867.
- GREENHILL, S. J., WU, C.-H., HUA, X., DUNN, M., LEVINSON, S. C. & GRAY, R. D. (2017). Evolutionary dynamics of language systems. *Proceedings of the National Academy of Sciences* **114**, E8822–E8829.
- GRIEBEL, U. & OLLER, D. K. (2008). Evolutionary forces favoring contextual flexibility. In *Evolution of Communicative Flexibility: Complexity, Creativity and Adaptability in Human and Animal Communication* (eds D. K. OLLER and U. GRIEBEL), pp. 9–40. MIT Press, Cambridge, MA.
- *HAGE, S. R., GAVRILOV, N. & NIEDER, A. (2013). Cognitive control of distinct vocalizations in rhesus monkeys. *Journal of Cognitive Neuroscience* **25**, 1692–1701.
- HAMMERSCHMIDT, K., JÜRGENS, U. & FREUDENSTEIN, T. (2001). Vocal development in squirrel monkeys. *Behaviour* **138**, 1179–1204.
- *HARDY, J. W. & PARKER, T. A. (1997). The nature and probable function of vocal copying in Lawrence's thrush, *Turdus lawrencii*. *Ornithological Monographs* **48**, 307–320.
- *HARLEY, H. E. (2008). Whistle discrimination and categorization by the Atlantic bottlenose dolphin (*Tursiops truncatus*): a review of the signature whistle framework and a perceptual test. *Behavioural Processes* **77**, 243–268.
- *HAUSER, M. D. (1992). Articulatory and social factors influence the acoustic structure of rhesus monkey vocalizations: a learned mode of production? *The Journal of the Acoustical Society of America* **91**, 2175–2179.
- *HAYES, K. J. & HAYES, C. (1951). The intellectual development of a home-raised chimpanzee. *Proceedings of the American Philosophical Society* **95**, 105–109.
- *HEDWIG, D., HAMMERSCHMIDT, K., MUNDRY, R., ROBBINS, M. M. & BOESCH, C. (2014). Acoustic structure and variation in mountain and western gorilla close calls: a syntactic approach. *Behaviour* **151**, 1091–1120.
- HENRY, L., BARBU, S., LEMASSON, A. & HAUSBERGER, M. (2015). Dialects in animals: evidence, development and potential functions. *Animal Behavior and Cognition* **2**, 132–155.
- *HERMAN, L. M., ABICHANDANI, S. L., ELHAJJ, A. N., HERMAN, E. Y., SANCHEZ, J. L. & PACK, A. A. (1999). Dolphins (*Tursiops truncatus*) comprehend the referential character of the human pointing gesture. *Journal of Comparative Psychology* **113**, 347–364.
- *HIHARA, S., OBAYASHI, S., TANAKA, M. & IRIKI, A. (2003a). Rapid learning of sequential tool use by macaque monkeys. *Physiology & Behavior* **78**, 427–434.
- HIHARA, S., YAMADA, H., IRIKI, A. & OKANOYA, K. (2003b). Spontaneous vocal differentiation of coo-calls for tools and food in Japanese monkeys. *Neuroscience Research* **45**, 383–389.
- HIXSON, M. D. (1998). Ape language research: a review and behavioral perspective. *The Analysis of Verbal Behavior* **15**, 17–39.
- *HOBAITER, C. & BYRNE, R. W. (2011). The gestural repertoire of the wild chimpanzee. *Animal Cognition* **14**, 745–767.
- HOCKETT, C. F. (1958). *A Course in Modern Linguistics*. Macmillan, New York.
- HOEHL, S., KEUPP, S., SCHLEIHAUF, H., MCGUIGAN, N., BUTTELMANN, D. & WHITEN, A. (2019). 'Over-imitation': a review and appraisal of a decade of research. *Developmental Review* **51**, 90–108.
- *HOPKINS, W. D., TAGLIALATELA, J. P. & LEAVENS, D. A. (2007). Chimpanzees differentially produce novel vocalizations to capture the attention of a human. *Animal Behaviour* **73**, 281–286.
- IACOZZA, S., MEYER, A. S. & LEV-ARI, S. (2020). How in-group bias influences the level of detail of speaker-specific information encoded in novel lexical representations. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **46**, 894–906.
- IZQUIERDO, A., BRIGMAN, J. L., RADKE, A. K., RUDEBECK, P. H. & HOLMES, A. (2017). The neural basis of reversal learning: an updated perspective. *Neuroscience* **345**, 12–26.
- *JANIK, V. M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science* **289**, 1355–1357.
- JANIK, V. M. (2014). Cetacean vocal learning and communication. *Current Opinion in Neurobiology* **28**, 60–65.
- *JANIK, V. M. & SAYIGH, L. S. (2013). Communication in bottlenose dolphins: 50 years of signature whistle research. *Journal of Comparative Physiology A* **199**, 479–489.
- *JANIK, V. M. & SLATER, P. J. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour* **56**, 829–838.
- KALAN, A. K. & BOESCH, C. (2018). Re-emergence of the leaf clip gesture during an alpha takeover affects variation in male chimpanzee loud calls. *PeerJ* **6**, e5079.
- KATO, A., MASATAKA, N., KODA, H. & OYAKAWA, C. (2007). Experimental evidence for the voluntary control of vocal production in an immature gibbon. *Behaviour* **144**, 681–692.
- KAVANAGH, E., STREET, S. E., ANGWELA, F. O., BERGMAN, T. J., BLASZCZYK, M. B., BOLT, L. M., BRISEÑO-JARAMILLO, M., BROWN, M., CHEN-KRAUS, C., CLAY, Z., COYE, C., THOMPSON, M. E., ESTRADA, A., FICHTEL, C., FRUTH, B., ET AL. (2021). Dominance style is a key predictor of vocal use and evolution across nonhuman primates. *Royal Society Open Science* **8**, 210873.
- *KING, S. L., GUARINO, E., DONEGAN, K., McMULLEN, C. & JAAKKOLA, K. (2021). Evidence that bottlenose dolphins can communicate with vocal signals to solve a cooperative task. *Royal Society Open Science* **8**, 202073.
- KNÖRNSCHILD, M. (2014). Vocal production learning in bats. *Current Opinion in Neurobiology* **28**, 80–85.
- KNÖRNSCHILD, M., FERNANDEZ, A. A. & NAGY, M. (2020). Vocal information and the navigation of social decisions in bats: is social complexity linked to vocal complexity? *Functional Ecology* **34**, 322–331.
- KNÖRNSCHILD, M., NAGY, M., METZ, M., MAYER, F. & VON HELVERSEN, O. (2010). Complex vocal imitation during ontogeny in a bat. *Biology Letters* **6**, 156–159.
- *KODA, H., LEMASSON, A., OYAKAWA, C., RIZALDI, R., PAMUNGKAS, J. & MASATAKA, N. (2013). Possible role of mother-daughter vocal interactions on the development of species-specific song in gibbons. *PLoS One* **8**, e71432.
- KOREN, L. & GEFFEN, E. (2009). Complex call in male rock hyrax (*Procavia capensis*): a multi-information distributing channel. *Behavioral Ecology and Sociobiology* **63**, 581–590.
- *KREMERS, D., LEMASSON, A., ALMUNIA, J. & WANKER, R. (2012). Vocal sharing and individual acoustic distinctiveness within a group of captive orcas (*Orcinus orca*). *Journal of Comparative Psychology* **126**(4), 433–445.
- *LACHLAN, R. F. & NOWICKI, S. (2015). Context-dependent categorical perception in a songbird. *Proceedings of the National Academy of Sciences* **112**, 1892–1897.
- LALAND, K. & SEED, A. (2021). Understanding human cognitive uniqueness. *Annual Review of Psychology* **72**, 689–716.
- *LAMEIRA, A. R., HARDUS, M. E., KOWALSKY, B., DE VRIES, H., SPRUIJT, B. M., STERCK, E. H., SHUMAKER, R. W. & WICH, S. A. (2013). Orangutan (*Pongo* spp.) whistling and implications for the emergence of an open-ended call repertoire: a replication and extension. *The Journal of the Acoustical Society of America* **134**(3), 2326–2335.
- *LAMEIRA, A. R., HARDUS, M. E., MIELKE, A., WICH, S. A. & SHUMAKER, R. W. (2016). Vocal fold control beyond the species-specific repertoire in an orang-utan. *Scientific Reports* **6**, 30315.
- LAMEIRA, A. R., SANTAMARÍA-BONFIL, G., GALEONE, D., GAMBA, M., HARDUS, M. E., KNOTT, C. D., MORROGH-BERNARD, H., NOWAK, M. G., CAMPBELL-SMITH, G. & WICH, S. A. (2022). Sociality predicts orangutan vocal phenotype. *Nature Ecology & Evolution* **6**, 1–9.
- LATTENKAMP, E. Z. & VERNES, S. C. (2018). Vocal learning: a language-relevant trait in need of a broad cross-species approach. *Current Opinion in Behavioral Sciences* **21**, 209–215.
- *LATTENKAMP, E. Z., VERNES, S. C. & WIEGREBE, L. (2020). Vocal production learning in the pale spear-nosed bat, *Phyllostomus Discolor*. *Biology Letters* **16**, 20190928.
- LEPORE, E. & SMITH, B. C. (2008). *The Oxford Handbook of Philosophy of Language*. Oxford University Press, Oxford, UK.

- LEROUX, M., BOSSHARD, A. B., CHANDIA, B., MANSER, A., ZUBERBÜHLER, K. & TOWNSEND, S. W. (2021). Chimpanzees combine pant hoots with food calls into larger structures. *Animal Behaviour* **179**, 41–50.
- *LILLY, J. C. (1965). Vocal mimicry in *Tursiops*: ability to match numbers and durations of human vocal bursts. *Science* **147**, 300–301.
- MAGRATH, R. D., HAFF, T. M., FALLOW, P. M. & RADFORD, A. N. (2015a). Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biological Reviews* **90**, 560–586.
- MAGRATH, R. D., HAFF, T. M., MCLACHLAN, J. R. & IGIC, B. (2015b). Wild birds learn to eavesdrop on heterospecific alarm calls. *Current Biology* **25**, 2047–2050.
- *MANABE, K. & DOOLING, R. J. (1997). Control of vocal production in budgerigars (*Melopsittacus undulatus*): selective reinforcement, call differentiation, and stimulus control. *Behavioural Processes* **41**, 117–132.
- MANSER, M. B. (2013). Semantic communication in vervet monkeys and other animals. *Animal Behaviour* **86**, 491–496.
- MANYPRIMATES, ALTSCHUL, D. M., BERAN, M. J., BOHN, M., CALL, J., DETROY, S., DUGUID, S. J., EGELKAMP, C. L., FICHEL, C., FISCHER, J., FLESSERT, M., HANUS, D., HAUN, D. B. M., HAUX, L. M., HERNANDEZ-AGUILAR, R. A., ET AL. (2019). Establishing an infrastructure for collaboration in primate cognition research. *PLoS One* **14**, e0223675.
- *MARSHALL, A. J., WRANGHAM, R. W. & ARCADI, A. C. (1999). Does learning affect the structure of vocalizations in chimpanzees? *Animal Behaviour* **58**, 825–830.
- MARTINS, P. T. & BOECKX, C. (2020). Vocal learning: beyond the continuum. *PLoS Biology* **18**, e3000672.
- MCDONALD, M. A., MESNICK, S. L. & HILDEBRAND, J. A. (2006). Biogeographic characterization of blue whale song worldwide: using song to identify populations. *Journal of Cetacean Research and Management* **8**, 55–65.
- MCUGIGAN, N., WHITEN, A., FLYNN, E. & HORNER, V. (2007). Imitation of causally opaque versus causally transparent tool use by 3- and 5-year-old children. *Cognitive Development* **22**, 353–364.
- MC MULLEN, H., SCHMIDT, R. & KUNC, H. P. (2014). Anthropogenic noise affects vocal interactions. *Behavioural Processes* **103**, 125–128.
- *MIRSIS, J. L., TYACK, P. L. & BUCK, J. R. (2002). Captive dolphins, *Tursiops truncatus*, develop signature whistles that match acoustic features of human-made model sounds. *The Journal of the Acoustical Society of America* **112**, 728–739.
- *MITANI, J. & GROS-LOUIS, J. (1998). Chorusing and call convergence in chimpanzees: tests of three hypotheses. *Behaviour* **135**, 1041–1064.
- MONAGHAN, P., MATTOCK, K. & WALKER, P. (2012). The role of sound symbolism in language learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition* **38**, 1152–1164.
- MONAGHAN, P., SHILLCOCK, R. C., CHRISTIANSEN, M. H. & KIRBY, S. (2014). How arbitrary is language? *Philosophical Transactions of the Royal Society B: Biological Sciences* **369**, 20130299.
- MONTES-MEDINA, A. C., SALINAS-MELGOZA, A. & RENTON, K. (2016). Contextual flexibility in the vocal repertoire of an Amazon parrot. *Frontiers in Zoology* **13**, 40.
- MOTES-RODRIGO, A. & TENNIE, C. (2021). The method of local restriction: in search of potential great ape culture-dependent forms. *Biological Reviews* **96**, 1441–1461.
- NEANDER, K. (2009). Functional explanations. *Revue Philosophique de la France et de l'étranger* **134**, 5–34.
- NIELSEN, M. & SUSANTO, E. W. E. (2010). Failure to find over-imitation in captive orangutans (*Pongo pygmaeus*): implications for our understanding of cross-generation information transfer. In *Developmental Psychology*, pp. 153–167. Nova Science Publishers, New York.
- NOAD, M. J., CATO, D. H., BRYDEN, M. M., JENNER, M.-N. & JENNER, K. C. S. (2000). Cultural revolution in whale songs. *Nature* **408**, 537.
- NOTMAN, H. & RENDALL, D. (2005). Contextual variation in chimpanzee pant hoots and its implications for referential communication. *Animal Behaviour* **70**, 177–190.
- O'CONNOR, C. (2021). Measuring conventionality. *Australasian Journal of Philosophy* **99**, 579–596.
- OLESON, E. M., ŠIROVIĆ, A., BAYLESS, A. R. & HILDEBRAND, J. A. (2014). Synchronous seasonal change in fin whale song in the North Pacific. *PLoS One* **9**, e115678.
- OLLER, D. K., BUDER, E. H., RAMSDELL, H. L., WARLAUMONT, A. S., CHORNA, L. & BAKEMAN, R. (2013). Functional flexibility of infant vocalization and the emergence of language. *Proceedings of the National Academy of Sciences* **110**, 6318–6323.
- OLLER, D. K., GRIEBEL, U. & WARLAUMONT, A. S. (2016). Vocal development as a guide to modeling the evolution of language. *Topics in Cognitive Science* **8**, 382–392.
- *OWREN, M. J., DIETER, J. A., SEYFARTH, R. M. & CHENEY, D. L. (1993). Vocalizations of rhesus (*Macaca mulatta*) and Japanese (*M. fuscata*) macaques cross-fostered between species show evidence of only limited modification. *Developmental Psychobiology* **26**, 389–406.
- *PARKS, S. E., CLARK, C. W. & TYACK, P. L. (2007). Short- and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication. *The Journal of the Acoustical Society of America* **122**, 3725–3731.
- *PAYNE, K. (1983). Progressive changes in the songs of humpback whales *Megaptera novaeangliae*: a detailed analysis of two seasons in Hawaii. In *Communication and Behavior of Whales* (ed. R. PAYNE), pp. 9–57.
- PFFENING, A. R., HARA, E., WHITNEY, O., RIVAS, M. V., WANG, R., ROULHAC, P. L., HOWARD, J. T., WIRTHLIN, M., LOVELL, P. V., GANAPATHY, G., MOUNTCASTLE, J., MOSELEY, M. A., THOMPSON, J. W., SODERBLUM, E. J., IRIKI, A., ET AL. (2014). Convergent transcriptional specializations in the brains of humans and song-learning birds. *Science* **346**, 1256846.
- PLANER, R. J. & KALKMAN, D. (2019). Arbitrary signals and cognitive complexity. *The British Journal for the Philosophy of Science* **72**, axz018.
- *Podos, J., PETERS, S., RUDNICKY, T., MARLER, P. & NOWICKI, S. (1992). The organization of song repertoires in song sparrows: themes and variations. *Ethology* **90**, 89–106.
- *POOLE, J. H., TYACK, P. L., STOEGER-HORWATH, A. S. & WATWOOD, S. (2005). Elephants are capable of vocal learning. *Nature* **434**, 455–456.
- PRAT, Y., TAUB, M. & YOVEL, Y. (2015). Vocal learning in a social mammal: demonstrated by isolation and playback experiments in bats. *Science Advances* **1**, e1500019.
- RALLS, K., FIORELLI, P. & GISH, S. (1985). Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Canadian Journal of Zoology* **63**, 1050–1056.
- RAVIGNANI, A., FITCH, W. T., HANKE, F. D., HEINRICH, T., HURGITTSCH, B., KOTZ, S. A., SCHARFF, C., STOEGER, A. S. & DE BOER, B. (2016). What pinnipeds have to say about human speech, music, and the evolution of rhythm. *Frontiers in Neuroscience* **10**, 1–8.
- *RAVIGNANI, A., SONNWEBER, R.-S., STOBBE, N. & FITCH, W. T. (2013). Action at a distance: dependency sensitivity in a New World primate. *Biology Letters* **9**, 20130852.
- *REBER, S. A., ŠLIPOGOR, V., OH, J., RAVIGNANI, A., HOESCHELE, M., BUGNYAR, T. & FITCH, W. T. (2019). Common marmosets are sensitive to simple dependencies at variable distances in an artificial grammar. *Evolution and Human Behavior* **40**, 214–221.
- REBY, D. & MCCOMB, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* **65**, 519–530.
- REICHMUTH, C. & CASEY, C. (2014). Vocal learning in seals, sea lions, and walruses. *Current Opinion in Neurobiology* **28**, 66–71.
- RENDALL, D., OWREN, M. J. & RYAN, M. J. (2009). What do animal signals mean? *Animal Behaviour* **78**, 233–240.
- *RICHARDS, D. G., WOLZ, J. P. & HERMAN, L. M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. *Journal of Comparative Psychology* **98**, 10–28.
- *RIDGWAY, S., CARDER, D., JEFFRIES, M. & TODD, M. (2012). Spontaneous human speech mimicry by a cetacean. *Current Biology* **22**, R860–R861.
- *ROBERTS, A. I., VICK, S.-J. & BUCHANAN-SMITH, H. M. (2012). Usage and comprehension of manual gestures in wild chimpanzees. *Animal Behaviour* **84**, 459–470.
- *RUKSTALIS, M., FITE, J. E. & FRENCH, J. A. (2003). Social change affects vocal structure in a callitrichid primate (*Callithrix kuhlii*). *Ethology* **109**, 327–340.
- *RUSSELL, J. L., MCINTYRE, J. M., HOPKINS, W. D. & TAGLIALATELA, J. P. (2013). Vocal learning of a communicative signal in captive chimpanzees, *Pan troglodytes*. *Brain and Language* **127**, 520–525.
- SANVITO, S., GALIMBERTI, F. & MILLER, E. H. (2007). Observational evidences of vocal learning in southern elephant seals: a longitudinal study. *Ethology* **113**, 137–146.
- SAVAGE-RUMBAUGH, E. S., MURPHY, J., SEVCIK, R. A., BRAKKE, K. E., WILLIAMS, S. L., RUMBAUGH, D. M. & BATES, E. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development* **58**, i–252.
- SCHAMBERG, I., WITTIG, R. M. & CROCKFORD, C. (2018). Call type signals caller goal: a new take on ultimate and proximate influences in vocal production. *Biological Reviews* **93**, 2071–2082.
- SCHLENKER, P. (2018). Iconic pragmatics. *Natural Language & Linguistic Theory* **36**, 877–936.
- *SCHLENKER, P., CHEMLA, E., ARNOLD, K., LEMASSON, A., OUATTARA, K., KEENAN, S., STEPHAN, C., RYDER, R. & ZUBERBÜHLER, K. (2014). Monkey semantics: two 'dialects' of Campbell's monkey alarm calls. *Linguistics and Philosophy* **37**, 439–501.
- SCOTT-PHILLIPS, T. C. (2015). Meaning in animal and human communication. *Animal Cognition* **18**, 801–805.
- SEYFARTH, R. & CHENEY, D. (2018). Pragmatic flexibility in primate vocal production. *Current Opinion in Behavioral Sciences* **21**, 56–61.
- SEYFARTH, R. M. & CHENEY, D. L. (1980). The ontogeny of vervet monkey alarm calling behavior: a preliminary report. *Zeitschrift für Tierpsychologie* **54**, 37–56.
- *SEYFARTH, R. M. & CHENEY, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour* **34**, 1640–1658.
- SEYFARTH, R. M. & CHENEY, D. L. (2017). The origin of meaning in animal signals. *Animal Behaviour* **124**, 339–346.

- *SHAPIRO, A. D., SLATER, P. J. & JANIK, V. M. (2004). Call usage learning in gray seals (*Halichoerus grypus*). *Journal of Comparative Psychology* **118**, 447–454.
- SICOLI, M. A. & HOLTON, G. (2014). Linguistic phylogenies support back-migration from Beringia to Asia. *PLoS One* **9**, e91722.
- SLABBEKOORN, H. & SMITH, T. B. (2002). Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **357**, 493–503.
- *SLOCOMBE, K. E., KALLER, T., CALL, J. & ZUBERBÜHLER, K. (2010). Chimpanzees extract social information from agonistic screams. *PLoS One* **5**, e11473.
- *SLOCOMBE, K. E., TOWNSEND, S. W. & ZUBERBÜHLER, K. (2009). Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: evidence from a playback study. *Animal Cognition* **12**, 441–449.
- SLOCOMBE, K. E. & ZUBERBÜHLER, K. (2005a). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology* **119**, 67–77.
- SLOCOMBE, K. E. & ZUBERBÜHLER, K. (2005b). Functionally referential communication in a chimpanzee. *Current Biology* **15**, 1779–1784.
- *SLOCOMBE, K. E. & ZUBERBÜHLER, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Sciences* **104**, 17228–17233.
- *SNOWDON, C. T. & ELWSON, A. M. (1999). Pygmy marmosets modify call structure when paired. *Ethology* **105**, 893–908.
- STANSBURY, A. L. & JANIK, V. M. (2019). Formant modification through vocal production learning in gray seals. *Current Biology* **29**, 2244–2249.e4.
- *STOEGER, A. S., MIETCHEN, D., OH, S., DE SILVA, S., HERBST, C. T., KWON, S. & FITCH, W. T. (2012). An Asian elephant imitates human speech. *Current Biology* **22**, 2144–2148.
- SUZUKI, T. N., WHEATCROFT, D. & GRIESSER, M. (2016). Experimental evidence for compositional syntax in bird calls. *Nature Communications* **7**, 10986.
- SUZUKI, T. N., WHEATCROFT, D. & GRIESSER, M. (2020). The syntax–semantics interface in animal vocal communication. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20180405.
- *TAGLIALATELA, J. P., REAMER, L., SCHAPIRO, S. J. & HOPKINS, W. D. (2012). Social learning of a communicative signal in captive chimpanzees. *Biology Letters* **8**, 498–501.
- *TAKAHASHI, D. Y., FENLEY, A. R., TERAMOTO, Y., NARAYANAN, D. Z., BORJON, J. I., HOLMES, P. & GHAZANFAR, A. A. (2015). The developmental dynamics of marmoset monkey vocal production. *Science* **349**, 734–738.
- *TAKAHASHI, D. Y., LIAO, D. A. & GHAZANFAR, A. A. (2017). Vocal learning via social reinforcement by infant marmoset monkeys. *Current Biology* **27**, 1844–1852.
- TAMARIZ, M. & KIRBY, S. (2016). The cultural evolution of language. *Current Opinion in Psychology* **8**, 37–43.
- *TANAKA, T., SUGIURA, H. & MASATAKA, N. (2006). Cross-sectional and longitudinal studies of the development of group differences in acoustic features of coo calls in two groups of Japanese macaques. *Ethology* **112**, 7–21.
- TAYLOR, D., CLAY, Z., DAHL, C. D., ZUBERBÜHLER, K., DAVILA-ROSS, M. & DEZECACHE, G. (2022). Vocal functional flexibility: what it is and why it matters. *Animal Behaviour* **186**, 93–100.
- TEMPLETON, C. N., GREENE, E. & DAVIS, K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science* **308**, 1934–1937.
- *TEN CATE, C. & FULLAGER, P. J. (2021). Vocal imitations and production learning by Australian musk ducks (*Biziura lobata*). *Philosophical Transactions of the Royal Society B* **376**, 20200243.
- *TERVO, O. M., PARKS, S. E., CHRISTOFFERSEN, M. F., MILLER, L. A. & KRISTENSEN, R. M. (2011). Annual changes in the winter song of bowhead whales (*Balaena mysticetus*) in Disko Bay, Western Greenland. *Marine Mammal Science* **27**, E241–E252.
- TOWNSEND, S. W., WATSON, S. K. & SLOCOMBE, K. E. (2020). Flexibility in great ape vocal production. In *Chimpanzees in Context: A Comparative Perspective on Chimpanzee Behavior, Cognition, Conservation, and Welfare* (eds L. M. HOPPER and S. R. ROSS), pp. 260–280. University of Chicago Press, Chicago, IL.
- *TSUKASA, M., FUJII, Y., HASHIMOTO, T., SHIMODA, A., IJIMA, S., HAYASAKA, K., SHIROMA, N. & ARAI, K. (2012). Preliminary study of object labeling using sound production in a beluga. *International Journal of Comparative Psychology* **25**, 195–207.
- TYACK, P. L. (1981). Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behavioral Ecology and Sociobiology* **8**, 105–116.
- *TYACK, P. L. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? *Behavioral Ecology and Sociobiology* **18**, 251–257.
- TYACK, P. L. (2020). A taxonomy for vocal learning. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20180406.
- VAN DE WAAL, E., BORGEAUD, C. & WHITEN, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science* **340**, 483–485.
- *VAN HEIJNINGEN, C. A., CHEN, J., VAN LAATUM, I., VAN DER HULST, B. & TEN CATE, C. (2013). Rule learning by zebra finches in an artificial grammar learning task: which rule? *Animal Cognition* **16**, 165–175.
- *VERGARA, V. & BARRETT-LENNARD, L. G. (2008). Vocal development in a beluga calf (*Delphinapterus leucas*). *Aquatic Mammals* **34**, 123–143.
- VERNES, S. C., KRIENGWATANA, B. P., BEECK, V. C., FISCHER, J., TYACK, P. L., TEN CATE, C. & JANIK, V. M. (2021). The multi-dimensional nature of vocal learning. *Philosophical Transactions of the Royal Society B: Biological Sciences* **376**, 20200236.
- *WATSON, S. K., BURKART, J. M., SCHAPIRO, S. J., LAMBETH, S. P., MUELLER, J. L. & TOWNSEND, S. W. (2020a). Nonadjacent dependency processing in monkeys, apes, and humans. *Science Advances* **6**, eabb0725.
- WATSON, S. K., HEESSEN, R., HEDWIG, D., ROBBINS, M. M. & TOWNSEND, S. W. (2020b). An exploration of Menzerath's law in wild mountain gorilla vocal sequences. *Biology Letters* **16**, 20200380.
- WATSON, S. K., LAMBETH, S. P., SCHAPIRO, S. J. & WHITEN, A. (2018). Chimpanzees prioritise social information over pre-existing behaviours in a group context but not in dyads. *Animal Cognition* **21**, 407–418.
- WATSON, S. K., REAMER, L. A., MARENO, M. C., VALE, G., HARRISON, R. A., LAMBETH, S. P., SCHAPIRO, S. J. & WHITEN, A. (2017). Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. *American Journal of Primatology* **79**, e22642.
- WATSON, S. K., TOWNSEND, S. W., SCHEL, A. M., WILKE, C., WALLACE, E. K., CHENG, L., WEST, V. & SLOCOMBE, K. E. (2015a). Reply to Fischer ET AL. *Current Biology* **25**, R1030–R1031.
- *WATSON, S. K., TOWNSEND, S. W., SCHEL, A. M., WILKE, C., WALLACE, E. K., CHENG, L., WEST, V. & SLOCOMBE, K. E. (2015b). Vocal learning in the functionally referential food grunts of chimpanzees. *Current Biology* **25**, 495–499.
- *WEGDELL, F., HAMMERSCHMIDT, K. & FISCHER, J. (2019). Conserved alarm calls but rapid auditory learning in monkey responses to novel flying objects. *Nature Ecology & Evolution* **3**, 1039–1042.
- *WEISS, B. M., SYMONDS, H., SPONG, P. & LADICH, F. (2011). Call sharing across vocal clans of killer whales: evidence for vocal imitation? *Marine Mammal Science* **27**(2), E1–E13.
- WHEELER, B. C. & FISCHER, J. (2012). Functionally referential signals: a promising paradigm whose time has passed. *Evolutionary Anthropology: Issues, News, and Reviews* **21**, 195–205.
- WHITEN, A., GOODALL, J., MCGREW, W. C., NISHIDA, T., REYNOLDS, V., SUGIYAMA, Y., TUTIN, C. E., WRANGHAM, R. W. & BOESCH, C. (1999). Cultures in chimpanzees. *Nature* **399**, 682–685.
- *WICH, S. A., KRÜTZEN, M., LAMEIRA, A. R., NATER, A., ARORA, N., BASTIAN, M. L., MEULMAN, E., MORROGH-BERNARD, H. C., ATMOKO, S. S. U., PAMUNGKAS, J., PERWITASARI-FARAJALLAH, D., HARDUS, M. E., VAN NOORDWIJK, M. & VAN SCHAİK, C. P. (2012). Call cultures in orang-utans? *PLoS One* **7**, e36180.
- *WICH, S. A., SWARTZ, K. B., HARDUS, M. E., LAMEIRA, A. R., STROMBERG, E. & SHUMAKER, R. W. (2009). A case of spontaneous acquisition of a human sound by an orangutan. *Primates* **50**, 56–64.
- WILBRECHT, L. & NOTTEBOHM, F. (2003). Vocal learning in birds and humans. *Mental Retardation and Developmental Disabilities Research Reviews* **9**, 135–148.
- *WILSON, D. R. & MENNILL, D. J. (2010). Black-capped chickadees, *Parus atricapillus*, can use individually distinctive songs to discriminate among conspecifics. *Animal Behaviour* **79**, 1267–1275.
- WINTER, P., SCHOTT, D., PLOOG, D. & HANDLEY, P. (1973). Ontogeny of squirrel monkey calls under normal conditions and under acoustic isolation. *Behaviour* **47**, 230–239.
- WOODIN, G., WINTER, B., PERLMAN, M., LITTLEMORE, J. & MATLOCK, T. (2020). 'Tiny numbers' are actually tiny: evidence from gestures in the TV News Archive. *PLoS One* **15**, e0242142.
- *WRIGHT, T. F. (1996). Regional dialects in the contact call of a parrot. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **263**, 867–872.
- *WRIGHT, T. F. & DAHLIN, C. R. (2018). Vocal dialects in parrots: patterns and processes of cultural evolution. *The Emu* **118**, 50–66.
- ZIEGLER, L., ARIM, M. & NARINS, P. M. (2011). Linking amphibian call structure to the environment: the interplay between phenotypic flexibility and individual attributes. *Behavioral Ecology* **22**, 520–526.
- ZUBERBÜHLER, K. (2000). Interspecies semantic communication in two forest primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**, 713–718.
- ZUBERBÜHLER, K. (2020). Syntax and compositionality in animal communication. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20190062.
- *ZÜRCHER, Y. & BURKART, J. M. (2017). Evidence for dialects in three captive populations of common marmosets (*Callithrix jacchus*). *International Journal of Primatology* **38**, 780–793.
- *ZÜRCHER, Y., WILLEMS, E. P. & BURKART, J. M. (2019). Are dialects socially learned in marmoset monkeys? Evidence from translocation experiments. *PLoS One* **14**, e0222486.

VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Survey of candidate evidence for optionality in animal communication systems including studies not described in the main text.

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