Comparative perspectives on communication in human and nonhuman primates:

**Grounding meaning in broadly conserved processes of voice production,
perception, affect and cognition**

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This is a draft of a chapter/article that has been accepted for publication by Oxford University Press in the forthcoming book [The Oxford Handbook of Voice Perception] edited by Pascal Belin and Sascha Fruholz, due for publication in December 2019. More information and pre-order can be found here:

<https://global.oup.com/academic/product/the-oxford-handbook-of-voice-perception-9780198743187?cc=us&lang=en&#>

Introduction

Comparative perspectives on primate and human communication have varied historically and been marked by two equally untenable extremes, one being that language is special, the other that it is not. The former, conventional stance, assumes language is special, unique, and without significant evolutionary precedent. It has struggled, therefore, to explain the origins and evolution of a complex faculty from scratch (Chomsky 1968; Pinker 1994). The latter stance reflects more recent comparative research on systems of communication in nonhuman primates which, in general, has been extremely productive (Fitch 2010). At times, however, research on systems of primate communication has been focused quite narrowly on high-level linguistic constructs, like *meaning*, *information* and *syntax*, and in an effort to demonstrate continuity to language has often appropriated and applied these constructs to primates in relatively loose and metaphorical ways that can distort their linguistic significance (Rendall, Owren & Ryan 2009; Rendall & Owren 2010; Owren, Rendall & Ryan 2010). In the process, such approaches risk trivializing the distinctive properties of language and overstating continuity with primate communication, thereby leaving little to explain about the *evolution* of language.

Here we try to strike a balance and identify fertile common ground between human and primate communication by focusing on what is indisputably shared, namely the basic units of sound that are the building blocks of vocal communication in each. We then consider how these basic building blocks combine with additional commonalities in fundamental processes of voice perception, affect and cognition to yield functional outcomes for communication in each group. Critically, this approach points to some novel possibilities

for how some of the more complex semantic dimensions of language, not shared with primates, might nevertheless be grounded in and bootstrapped from basic dimensions of voice production and perception that *are* shared. The hope is that this approach will also promote further productive integration in research on both groups and develop some common terms and modes of analysis to facilitate that.

We begin by focusing on language and with a discussion of the pressures for human languages to be both learnable and expressible (Kirby, Cornish, Smith, 2006). We outline the outcomes of those pressures in producing languages that take advantage of perceptuo-cognitive processes of human language learners operating on fundamental elements of voice production and perception.

To forecast the arguments in brief, we suggest that humans have a suite of perceptual biases that make certain associations between words and meanings more salient than they would be otherwise. For example, ‘moo’ is a good word for the sound that a cow makes because it is imitative of the sound of that event [onomatopoeia], and thus potentially more memorable for a naïve language learner. Beyond these simple types of imitative word-meaning mappings, natural languages also take advantage of associations between perception and emotion. Thus, for example, we use curse words like ‘fuck’ that contain higher proportions of fricative and plosive consonants and also prosodic cues that highlight their affective weight, allowing them to hijack the perceptual machinery of their perceiver to increase their salience. The ability of words like ‘fuck’ to induce affective or behavioural changes in the listener (or utterer) demonstrates a third pressure that shapes the structure of languages: functional deployability. This fundamental pressure has

heretofore been largely overlooked because human language is typically characterized as a system for the transfer of propositional content (information) that is largely free of the influence of affective systems and low-level perceptual and motivational biases of the sort that impel many other sorts of behavior. Here, we highlight this pressure as especially interesting because it is evidenced widely in animal communication systems and may represent an important, underappreciated link between the two.

In addition to the pressures for learnability and functional deployability in determining the structure of human languages based on an interaction with perceptuo-cognitive processes, constraints in domain-general processes like memory also have important impacts on language structure (Kirby, Cornish, Smith, 2006). In the terms of iterated learning, languages need to be compressible: that is, languages are easier to learn when they are structured in such a way that storing the rules and representations of the language takes up minimal space. Thus, regular tense marking aids in language learning because it is generalizable and compressible.

At the same time, the pressure for expressivity is at odds with both learnability and compressibility: a perfectly compressed language would have only a single word, and thus would be perfectly learnable, but it would fail outright to be expressive. Thus, human languages need to balance those pressures, optimizing learnability, deployability, and expressivity relative to one another.

In section 1.1, we outline the evidence from human languages that demonstrates the outcomes of these pressures, considering primarily the mechanistic basis for the perceptual and cognitive biases that shape language and their influence on how language is

learned. Much of this evidence is relatively new, based on a resurgence of interest in what we call *motivated* associations between words and meanings, but also on configurations of the language that are *systematic* (Nielsen, 2016).

Subsequent to our discussion of human languages, in section 1.2 we focus on an exploration of whether analogs of the same types of associations can be found in animal communication systems. In English, for example, we see that curse words like ‘fuck’ often take advantage of associations between acoustic harshness and emotional valence. This type of motivated association between signals and meanings can also be seen in animal communication systems, where harsh, spectrally chaotic calls are often given in aggressive contexts and softer more mellifluous ones in affiliative contexts.

In section 1.3, we attempt to bridge the gap between discussions of human language and animal communication systems, suggesting that, if considered carefully, the exploration of one can inform us about the other. We suggest, first, that many discussions of human language and its evolutionary origins have ignored the pressure for functional deployability and thus one of the potentially most crucial evolutionary links between humans and other animals. To this end, we propose a bio-semantic framework, where meaning at the level of the phoneme (rooted in its underlying acoustic structural features) might represent an important contribution to the evolution of the human language faculty and communication systems more generally.

From this, we suggest that to the degree that animal communication systems can be thought of as conveying propositional content, we should look for the fingerprints of functional deployability in establishing this type of reference. We have suggested

elsewhere that animal communication systems become more functional by leveraging motivated signal-meaning mappings, but extend this suggestion here to propose that motivated signal-meaning mapping might also make animal signals more learnable. Finally, we suggest that animal signaling systems might also bear the hallmarks of systematicity.

Ultimately, of course, while we will emphasize the foundational role of a set of systematic, non-arbitrary processes and relationships in the structure, function and deployment of language and communication systems more generally, we also fully acknowledge that the structures of human languages are, in fact, largely arbitrary. Hence, our emphasis on the potential non-arbitrary elements of them recognizes that these will likely represent only a small component of the realized design of languages. Nevertheless, the relationships we emphasize critically allow for an examination of non-arbitrariness that can explain features of both animal and human communication systems and some productive possible links between them which has been a long-time but heretofore largely unfulfilled goal of comparative, evolutionarily oriented research.

1.1 Human language

How do words get their meanings? This question dates back to at least Plato's *Cratylus* dialogue, which is recognized as the first exploration of the issue. Linguistic tradition has been built around the idea that connections between words and meanings are arbitrary and established only by linguistic convention (de Saussure, 1983; Hockett, 1960, but cf. Joseph, 2015). There is, for example, nothing about the word 'dog' that makes it particularly good for describing a species of domesticated canine, nor any cosmic irony for

why, in English, 'god' is just 'dog' backwards: It's arbitrary. The arbitrariness of relationships between words and meanings became one of the central dogmas of linguistics for the majority of the 20th century, being codified by Hockett (1960) as a design feature of human language. Recently, however, the proposal that languages are entirely arbitrary and conventional (Newman, 1933; Newmeyer, 1993) has come under closer scrutiny. The relationship between words and the objects or events that they describe can be non-arbitrary in two ways, and researchers have increasingly recognized that human languages, far from being entirely arbitrary and conventional, contain many non-arbitrary words. Further, researchers have increasingly suggested that these associations are probably important (Nielsen & Rendall, 2012): they might make words more learnable (Nygaard et al., 2009), expressive (Yardy, 2010) or both (Nielsen, 2011).

The relationship between words and meanings can be non-arbitrary in terms of both their motivatedness and their systematicity (Nielsen, 2016; Dingemanse et al., 2015). Motivatedness refers to non-arbitrary associations between words and meanings where a feature of an individual word is mapped onto some feature of its meaning (Figure 1).

Figure 1. A diagrammatic representation of a motivated relationship between a word's form and its meaning. Modified from Gasser (2004).

This type of association is mediated by the perceptual and cognitive organization of the language users such that a dimension of meaning can be mapped onto a dimension of the signal. In some cases, this type of association is imitative or iconic: 'oink' for example is imitative of its meaning (the sound that a pig makes). In other cases, the association can be based on an affective or perceptual feature of meaning: as we discussed above, a swear word like 'fuck' (or e.g. 'tabarnac' in French) has acoustic features that make it particularly evocative for its purpose.

Second, associations between words and meanings can be non-arbitrary by virtue of being systematic (Monaghan et al., 2011). Systematic relationships between words and meanings refer to a configuration where a shared feature of a set of words is mapped onto a shared feature of a set of meanings (Figure 2).

Figure 2. A diagrammatic representation of a systematic association between word forms and meanings. Here, word forms that are similar to each other are mapped onto meanings that are similar to one another, but the specific mapping between the form space and the meaning space is arbitrary.

For example, the ‘gl-’ phonaestheme cluster contains a number of words that share the same initial segment (‘glimmer’, ‘glitter’, ‘glisten’, ‘glint’, etc.) that all have meanings related to vision or light. In the case of the ‘gl-’ cluster, there is nothing that motivates the specific form that the systematic association takes, and the use of ‘gl-’ as a marker for words connoting light is likely a feature of the contingent history of the English language (Cuskley, 2013). However, it bears noting that associations between words and meanings can be both motivated and systematic: the ‘sn-’ phonaestheme cluster, for example, contains a number of words (‘snot’, ‘sniffle’, ‘snout’, etc.) that have to do with the nose. The fact that this cluster of words contains a heavily nasal consonant segment (‘sn-’) suggests that in this case the specific form of the systematic association is likely also motivated (Figure 3), and

thus it is not surprising that this association has been observed across a number of other languages (Blasi et al., 2014).

Figure 3. A diagrammatic representation of the association between word forms and meanings that is both motivated and systematic. In this case, the motivated connection between the form of a set of words and the form of its related set of meanings is based not on individual motivated associations but a motivated mapping of the set of word forms to the set of meanings.

1.1.1 Motivatedness

The acknowledgement that cognitive and perceptual biases have downstream effects on human language has proven to be a rich source of explanatory power. Human language learners share the same basic perceptual and cognitive structures, and thus human languages, despite being different, share some features that reflect the strengths and constraints of human perception and cognition. Languages have a pressure to be learnable (Hockett, 1960; Kirby, Cornish, Smith, 2006), and by taking advantage of motivated associations languages can become easier for their users to learn, which may account for

the ability of humans to learn language easily despite a purportedly impoverished stimulus (Chomsky, 1965).

The motivatedness of associations between words and meanings can vary based on both their modality and transparency. In terms of modality, associations can be unimodal and iconic, or crossmodal and mediated by associations between sensory or affective characteristics that seem otherwise unrelated to one another. The types of associations that are leveraged by languages also vary as a function of their transparency: some are straightforward and iconic, while others are embedded in language systems such that the motivatedness of the association is contingent on knowledge about the rest of the language.

Modality

Unimodal associations between words and meanings are the most straightforwardly understood and thus perhaps the least surprising type of motivated association in language. Onomatopoeia is the most easily recognized example of a unimodal association between words and meanings. In onomatopoeia, the sound of a word is imitative of the sound of the event that it describes, so ‘crash’ for example is imitative of the sound of a collision, while ‘buzz’ is imitative of the sound that a bee makes. Unimodal associations are not limited to imitating the sound of events: in some cases, such as in Japanese mimetics (Kanera et al., 2014), reduplication can be leveraged to convey the temporal patterning of events. Thus, ‘goron’ is the word for a large object rolling, while ‘gorogoro’ is the word for a large object rolling repeatedly (Asano et al., 2015). In this case, the repetition of syllables is imitative of the repeated nature of the event that it describes. Similarly, prosodic cues can leverage unimodal associations, even in words that are already onomatopoeic (Dingemanse

et al., 2016). When saying the word ‘tweet’ for example one might up-modulate their pitch to make the imitative nature of the token more salient. This type of prosodic enhancement is common in both normative speech patterns and in exaggerated forms, such as motherese (Grieser & Kuhl, 1988).

Although unimodal associations are generally straightforward, they are inherently limited in the types of associations that they can leverage. Onomatopoeia has been observed in the majority of languages that have been analysed for its presence (Cuskley, 2013), but reduplicative mimetics are only found in a smaller (but still substantial) portion of the world’s languages (Asano et al., 2015), and there is little if any data examining the use of prosodic cues for establishing unimodal associations (Perniss & Vigliocco, 2014). Even if all of these types of unimodal associations were leveraged heavily by all languages however they would still be limited in their ability to convey meanings beyond a constrained set of possibilities: Many features of meaning do not have unimodal analogs in either the sounds used in languages or the way they are combined to form identifiable words.

Perceptual biases that lead to associations across modalities open up the possibility of expressing a broader range of meanings. A number of studies, for example, have shown that humans demonstrate a persistent bias to associate small objects with higher vocal frequencies, and this is manifest not only linguistically (e.g. Sapir, 1929), but also in expectations about the relationship between speaker body size and voice pitch and resonances or formants (Pisanski & Rendall, 2011). Linguistically, this association can be observed in the frequency with which words connoting small objects contain high front

vowels (with a relatively high 2nd formant frequency) while words connoting large objects contain low back vowels (with a relatively low 2nd formant frequency), and this association has been observed cross-linguistically (e.g., English (Johnson, 1967), but also Chinese, Thai (Huang, 1969), Korean (Kim, 1977), and several other languages (Gebels, 1969; Malmberg, 1964; cf Newman, 1933, Newmeyer, 1993). In the last decade, the empirical investigation of these types of crossmodal biases has experienced a veritable explosion, centered around the classic *bouba-kiki* or *takete-maluma* effect (Kohler, 1947; Ramachandran & Hubbard, 2001; Pexman & Sidhu, 2014), where novel, visually jagged object forms are reliably associated with novel, nonsense words containing strident consonants (e.g. /k/, /p/, and /t/), while curvier object forms are associated with nonsense words containing more mellifluous, sonorant consonants (e.g. /m/, /n/, /l/). The Bouba-Kiki effect has been demonstrated in both children (e.g. Ozturk, Krehm, & Vouloumanos, 2013) and adults, as well as with speakers of multiple languages (Davis, 1961; Bremner et al., 2013; see Figure 4 for sample of original object forms used by Kohler in 1947, and Appendix 1 for audio samples of speech tokens used in more recent experiments).

Figure 4. The original ‘maluma’ (left) and ‘takete’ (right) shapes from Kohler (1947).

The number of reliable crossmodal relationships using nonsense words that have been observed in the psychological literature is staggering, although the degree to which the relationships involved are manifest in the structure of real words is only now emerging as a field of study (Nielsen, 2016). Certainly, the capacity for crossmodal biases functionally related to a broad range of perceptual features have been described (see Figure 5) both among people in the so-called ‘normal’ population and also among synaesthetes who have exaggerated cross-modal perceptual biases that have been proposed to be simply an exaggeration of biases in the normal population (Bankieris & Simner, 2015).

Figure 5. Web diagram of cross-modal connections labeled according to their pervasiveness. Class 1 connections are those which seem mandatory given the laws of physics (such as light fading over distance). Class 2 connections are those which don't seem mandatory, but which otherwise seem aberrant (e.g. the association between taste and smell). Class 3 connections are those which are typically labeled as aberrant and attributed to synesthesia (e.g. between shape and pitch), but have also been observed in non-synaesthetes to some extent.

Transparency

Both unimodal and crossmodal associations can vary in terms of their transparency, that is, how obvious they would be to a naïve language user. The word 'moo' is more similar to the sound that a cow makes than the word 'cock-a-doodle-doo' is to the sound of a rooster, and thus might be more easily recognized. One of the limitations of motivated associations for expressing certain meanings is thus that some words are more amenable to

transmission over certain types of channels. Because English is a spoken language and the call of a rooster is relatively complex, even our onomatopoeic imitation of that sound is constrained. First, human language is unable to perfectly mimic the sounds of some acoustic events because words are composed of strings of speech sounds (i.e. vowels and consonants) that are themselves constrained by the human vocal apparatus. Second, even if phonemes could perfectly mimic environmental sounds, all languages have a constrained set of available phonemes (Assaneo, Nichols, & Trevisan, 2011), so some languages would be more apt than others at imitating environmental sounds. Because of the interaction of these features, the onomatopoeic words for a rooster crowing are quite different across languages: German uses 'kikiriki', where French uses 'cocorico'. As an English speaker, I might suggest that 'cock-a-doodle-doo' is more straightforwardly iconic than the other two, but nevertheless all three are quite different from the actual sound made by a rooster (Perniss, Thompson, & Vigliocco, 2010).

The constrained ability of languages to transparently represent certain types of meanings can also be seen in sign languages, where the communication channel is gestural rather than acoustic. The use of sign affords the possibility of representing a different suite of meanings iconically than does vocal communication (Taub, 2001). Thus, sign languages often iconically represent movement and spatial features in ways that spoken languages simply cannot (Thompson, Vinson, Woll, & Vigliocco, 2012). This is especially true early in the development of those signed languages before signals become smaller, more discrete, and conventionalized (Berent & Goldin-Meadow, 2015). Conversely, because signed languages are non-verbal, they cannot include the acoustic onomatopoeia pervasive in many spoken languages.

Crossmodal associations can also vary in their transparency or saliency: size-sound symbolism has been observed in a number of the world's languages (though experimental evidence isn't very strong cf. Cuskley, 2013), whereas reduplication is not as common, and arguably exhibits secondary iconicity (Ahlner & Zlatev, 2010), where the reduplication of syllables serving to highlight the repetition of an action is only apparent after exposure to an example.

In addition to varying in transparency based on the ability of the language channel to express a given meaning, associations can be motivated only based on their relationship to other words in a language. Dingemanse (2011) outlines one such example in Siwu, where a group of words that varies in terms of their vowel quality ('pɔmbɔlɔɔ', 'pumbuluu', and 'pimbilii') maps to meanings about the protrusion of the belly, with /ɔ/ being mapped to the largest protrusion and /i/ to the smallest. Considered alone, the motivatedness of these associations might not be salient enough to be recognized by a naïve language user, but considered together the crossmodal association between vowel roundedness and roundness (protrusion of the belly) becomes more obvious.

Mechanism

There is converging evidence that the types of motivated biases described above are underpinned by gross structural and anatomical features of the brain. First, in the normal population, the perceptual biases underlying associations like the bouba-kiki effect have been demonstrated to be underpinned by differential neural activation (Lockwood & Dingemanse, 2015; Kanera et al., 2014). Second, the study of synaesthesia, a condition that results in exaggerated connections between unrelated sensory modalities (Ramachandran

& Hubbard, 2001), has demonstrated an increased density of connections between the cortical areas responsible for processing crossmodally associated percepts (Rouw & Scholte, 2007), and that synesthesia appears to be a heritable condition (Asher et al., 2009). Although some have suggested that synesthesia relies on cortical wiring that is not present in the normal population (e.g. Brang, Hubbard, Coulson, Huang, & Ramachandran, 2010), others have provided evidence that at least some forms of synesthesia make use of cross-modal connections that are common in the normal population (e.g. Ward et al., 2006; Revill et al., 2014). Further support for the proposal that synaesthetes and the normal population share the same mechanistic underpinnings is provided by the finding that many, but not all, crossmodal associations observed in synaesthetes have also been demonstrated in the normal population, with synaesthetes showing exaggerated versions of those associations (Bankieris & Simner, 2015).

Taken together, the study of sound-symbolism and crossmodality in the normal population, and the study of synesthesia, thus illuminate a plausible mechanistic account that appears to be a common organizational feature of the nervous system (Rouw & Scholte, 2007). This further suggests a potentially important role for motivated word-meaning associations in language acquisition, transmission, and use. Determining the specific nature of these associations, and whether they reflect a fundamental feature of neural organization (direct connectivity) or are mediated by a central structural circuit is thus critical for an explanation of their importance or evolutionary trajectory.

As we saw above in Figure 5, associations between affect and certain perceptual features are amongst the most common of those reported in the literature, which might suggest that

some crossmodal perceptual biases are mediated by affect (Nielsen, 2010). For example, there are well established associations between color and affect (Valdez & Mehrabian, 1994), and also between pitch and affect (Krumhansl, 2002), which raises the possibility that any one of those three dimensions mediates the connection between the remaining two. For example, if high pitch is associated with bright colors, bright colors with positive affect, and high pitch with positive affect, it is possible that the presence of one of those associations can be explained by one of the others. In this case, we might suggest that high pitch is associated with positive affect, and bright colors are associated with positive affect, and that this creates a third association between high pitch and bright colors.

The possible centrality of affect to motivated associations between words and meanings is further supported by the recognition that language, in addition to being about the transfer of information between conspecifics, is often about influencing the behaviour of others by modulating their affect. Poets and musicians have recognized the importance of sounds and rhythm in inducing affect in their audiences seemingly far longer than the idea has been considered scientifically (Paquette, Peretz, & Belin, 2013; Trost et al., 2015). The central proposal of affective semantics (Rendall & Owren, 2006) recognizes this type of language use as important in its own right, but also important to the evolutionary history of language, as the modulation of affect has clear homologues in animal communication systems and does not require advanced cognition or the transfer of any propositional content (Rendall, Owren, & Ryan, 2009).

Swearing serves as a paradigm example of emotionally valenced language illustrating the principle of affective semantics. Lancker and Cummings (1999; Yardy, 2010) for

example have shown that swear words contain an unusually high number of fricative and plosive consonants. Whether one considers swear words an honest reflection of the underlying emotional or motivational state of utterers (such as when signaling pain), or as being exceptionally effective at grabbing and modulating listener attention and affect (when directed at others), they are undoubtedly effective. By using consonants that are relatively harsh and broadband in their acoustical structure, and also by introducing prosodic cues that accentuate that harshness or amplitude, the use of swear words can hijack the perceptual apparatus of perceivers to produce a desired response.

Gross acoustical characteristics are of course far from the only way in which human language can be modulated. Temporal patterning, pitch, and other aspects of speech prosody are all important for both conveying meaning or emotion and influencing emotions in others. For example, rising or falling pitch can be used to demarcate certain phrase types (e.g. questions from statements; Hirst & Di Cristo, 1998) and also to signal the relative confidence of the speaker (with confident speakers using low or falling pitch and unconfident ones using high or rising pitch; Bolinger, 1978) as well as to modulate the attention and affect of the listener as classically illustrated in the phenomenon of infant-directed-speech or ‘motherese’ (Fernald 1992).

1.1.2 Systematicity

Where motivatedness refers to associations that operate directly between words and their meanings, the second non-arbitrary dimension along which language can be structured (systematicity) operates by mapping features of sets of words to features of sets of meanings. Language is uncontroversially systematic at the level of morphosyntax, and it

has been suggested that this type of systematicity has important implications for learning (Chater & Vityani, 2003; Tamariz & Kirby, 2015). The use of regular suffixes to mark tense, for example, makes a language more compressible and thus easier to learn than if every morpheme was entirely idiosyncratic.

At the level of the lexicon, however, there has been little work exploring the degree to which languages are systematic. Small systematic pockets of language like the ‘gl-’ phonaestheme cluster exist in a number of languages but are typically treated as marginal. However, Monaghan et al. (2014) conducted a broad corpus analysis of a number of languages and found that the lexica of those languages was more systematic than would be expected by chance. That is, words that were similar to one another based on their phonology were more likely to have meanings that were also similar to one another. The level of systematicity of the analysed languages was overall rather modest and statistical in nature, which might explain why the previous assumption had been that such systematic associations were rare or unimportant. However, even previously recognized systematic mappings like phonaestheme clusters are not absolute in their mapping: although words like ‘glimmer’, ‘glitter’, and ‘glisten’ share both the same initial segment and have similar meanings, many words exist that use that same initial segment but have meanings unrelated to light or vision (e.g. ‘glaive’, ‘glove’, ‘glum’, etc.): systematicity in natural languages operates at a statistical level, rather than an absolute one (Reilly et al., 2012).

Crucially, associations between words and meanings can be both systematic and motivated at the same time. Consider, for example, the ‘sn-’ phonaestheme cluster (‘sneeze’, ‘snore’, ‘sniff’, etc.) mentioned above. In this phonaestheme cluster, the use of a word initial

segment that is heavily nasalized is unlikely to be explained by historical accident, and thus a word like ‘sniffle’ has the property of being both systematic and motivated at the same time. In fact, we have suggested elsewhere (Nielsen, 2016) that the leveraging of motivated associations between word forms and meanings can lead towards the establishment of systematic associations between sets of words and sets of meanings, producing what we have called “incidental systematicity”.

Consider again the structure and meaning of swear words, which, to rehearse, include an abnormal proportion of fricative and plosive consonants (in addition to being marked prosodically). In a language with only a single curse word, say ‘shit’, for example, the association between ‘shit’ and its meaning would be motivated, but not systematic. However, in English and most other languages there is a large repertoire of curse words, and insofar as each of those words leverages the spectral harshness and affective salience of the same set of phonemes, the structure of the set of curse words and the structure of the set of their meanings could become aligned and gain the property of being systematic, in addition to being motivated (Figure 6).

Figure 6. A diagrammatic representation of the formation of an incidentally systematic mapping between words and meanings. In this case, individual word forms are mapped to meanings based on a motivated association between the two. Because multiple similar word forms are mapped to multiple similar meanings, the resulting configuration of the language can be recognized as being systematic.

In the remainder of this chapter we will focus on non-arbitrariness at the level of the lexicon, because it has the clearest analogs in animal communication systems: i.e. it's difficult to look for non-arbitrary morphosyntax in animal communication systems that are not generally considered to have either morphology or syntax to begin with (cf. Engesser et al., 2015; Suzuki et al., 2016).

1.1.3 Learnability and Expressivity

The cross-generational transmission of languages is recognized to be subject to a selection process analogous to natural selection, with words or structures that are easier for learners to acquire or retain being passed on more faithfully than other, less suitable

variants (Kirby, Tamariz, Cornish, & Smith, 2015). Crucially, this process does not require intelligent design or deliberate selection by language learners: because of constraints on memory, production, saliency, and fidelity of transmission that are imposed by language learners, some language variants will win out over others and be retained, while others will be outcompeted and thus eliminated. Because the process of language transmission is operating at all times and across many learners simultaneously, languages can adapt to the constraints of their learners much faster than biological evolution can produce adaptations that shape the cognition and perception of learners to the structure of languages (Thompson, Kirby, & Smith, 2016).

In addition to being learnable, languages also need to be expressive. A language with only a single word denoting a single meaning would be perfectly learnable, but wouldn't be sufficiently expressive to facilitate communication. As we have discussed above, exclusive reliance on motivated associations between words and meanings would lead to a language that could only express a relatively small set of meanings. Words like 'lullaby' and 'shit' can be straightforwardly mapped onto the underlying affective dimensions of their meanings, but motivated signal forms for many other words are hard to fathom and quite unlikely.

Nevertheless, the pressure for languages to be learnable should favor both motivatedness and systematicity (Dingemanse et al., 2014). Motivated associations between words and meanings are easier for language learners to acquire because the association between a word and its meaning is, in some sense, natural. In support of this suggestion, researchers have explored the learnability of motivated words, both experimentally and by analyzing the corpora of natural languages. Experimentally,

researchers have demonstrated using both artificial (Nielsen & Rendall, 2012; Aveyard, 2012; Monaghan, 2012) and natural languages (Nygaard, Cook, & Namy, 2009; Yoshida, 2012) that sound-symbolic, or otherwise motivated, associations between words and meaning facilitate learning not only in children (Kantarzis, Imai, & Kita, 2011), but also in adults (Asano et al., 2015). For example, Imai et al. (2008) showed that English-speaking children can learn the meaning of putatively sound-symbolic ideophones in Japanese more easily than non sound-symbolic synonyms in this language. This finding aligns with data from corpus analyses, where researchers have found that the degree of motivatedness of word-meaning associations can be predicted by their age of acquisition (Monaghan et al., 2014): children learn sound-symbolic and other motivated words early before progressing to learn the remainder of the lexicon that is predominantly arbitrary.

Systematicity at the level of the lexicon has been less thoroughly explored than has motivatedness, but preliminary results broadly suggest that systematic mappings between sets of words and sets of meanings facilitate learning, at least in some contexts (Monaghan et al., 2011; Nielsen, 2016). Primarily, researchers have suggested that systematicity facilitates the processes of categorisation and generalisation. Imagine, for example, a language where all words for food ended with the segment ‘-um’: in this language chicken might be called ‘chum’, pork called ‘pum’, bread called ‘brum’, etc. Because the association between ‘-um’ and edibility is not, necessarily, a motivated one, each of these word-meaning pairs might have to be learned individually, but given sufficient exposure to the language a learner would find their ability to divine the meaning of unfamiliar labels enhanced by the systematic structure of the language. If, for example, they were told to grab the ‘bacum’ from the table, they would immediately know that they were being asked

to procure some type of edible substance, even if they were not sure which particular substance was being referenced. By learning the rule of their language by which the segment ‘-um’ was mapped systematically to edible objects, a user of this language would gain the ability to generalize to novel tokens, much in the way that learners rely on generalisation to guess the correct tense marker for unfamiliar verbs in English (e.g. Rumelhart & McClelland, 1986). In addition to aiding in generalisation, systematicity can also aid categorisation. When presented with a novel type of berry along with its name, the learner of this artificial language could immediately determine its suitability for consumption based on the presence or absence of the ‘-um’ segment: ‘strums’ are edible, whereas ‘belladonams’ are not.

The structure of human languages is fundamentally determined by the interaction of the pressures for learnability and expressivity with the perceptual, cognitive, and production machinery of its users, which serve to create a selective bottleneck through which language is filtered and undergoes change (Kirby et al., 2015). Despite the implication that both motivatedness and systematicity enhance learnability, however, at the level of the lexicon languages are curiously largely arbitrary – why is this the case? First, as we have discussed above, motivated associations between words and meanings can only convey a limited number and type of meanings, suggesting that the contribution of motivatedness to the structure of a complete language should be fairly minimal overall (Nielsen, 2016; Lockwood & Dingemanse, 2015). Second, the same features of systematicity that enhance categorisation and generalisation can negatively influence the learnability of individual words, especially as the number of words to be learned increases (Gasser, 2004; Monaghan et al., 2011). In the example we gave earlier, consider the suggestion that an ideal ‘sandum’

is made with two slices of ‘brum’, a smear of ‘mustum’, a few slices of ‘hum’, two slices of creamy ‘havartum’ and a healthy dollop of ‘mayonum’. Even with the added contextual information, this set of directions for constructing a sandwich might be confusing, especially when you take into account the imperfect fidelity of both production and reception. Did your partner ask you to pick up ‘milum’ at the store, or was it ‘malum’? Systematic associations, when applied absolutely, constrain the overall flexibility, and thus the memorability of their language (Gasser, 2004; Nielsen, 2016).

The potential negative influence of systematicity is compounded by the fact that there are so many systematic dimensions along which a language can be divided, and many of those dimensions overlap: kale is green, it is a vegetable, it is edible (arguably), etc. The inability of languages to express a sufficient number of meanings while remaining entirely systematic is best exemplified by Wilkins (1668) attempt to create a “perfect” language that was entirely systematic. First, Wilkins’ perfect language resulted in classifications that were unnatural: the English word salmon, for example was translated as ‘zana’ and meant “a scaled river fish with ruddy meat”. Because Wilkins language was so constrained, it was also easy to confuse similar words. Thus, even Wilkins, who created the language, confused ‘gade’ (barley) with the similar meaning ‘gape’ (tulip). These two outcomes explain the dominance of arbitrary word-meaning mappings in the lexicon, while leaving open the possibility that, at lower levels of saturation, systematic associations can be leveraged without introducing any concomitant learning penalty based on confusability or unnaturalness (Gasser, 2004).

The importance of the pressures for learnability and expressivity and their influence on the structure of language are well established and accepted, but both pressures are based on the notion that the purpose of language is based on the transmission of information between conspecifics. However, as we have suggested above, and elsewhere (Nielsen, 2011; Owren, Rendall, & Ryan, 2010), human language involves more than the exchange of information. Specifically, much of language and communication is about influencing the behaviour of others. In a Machiavellian sense, the behaviour of others can be influenced by sharing or withholding information, but thanks to perceptual biases it is also possible to induce desired affective responses in others separately from the propositional content of a given utterance. Using an affectively valenced word like ‘fuck’ is effective for grabbing attention not only because of its agreed-upon and conventional naughtiness, but also because of its acoustic characteristics (the former stemming in part from the latter). Thus, in addition to pressures for learnability and expressivity shaping the structure of language, here we suggest that an additional pressure for functional deployability based on affect induction, rather than information transmission, can have important effects on the structure of language.

When it comes to fully fledged human languages, we suggest that the strength of this pressure will be rather modest, but the relative weakness of the pressure does not preclude it from having an important influence. Specifically, we suggest that because the types of perceptual biases underpinning motivated associations between sensory and perceptual modalities are broadly conserved across a number of species (see next section: Morton, 1977, 1994), the continuity of those associations might inform our understanding of the evolution of the human language faculty.

1.2 Animal communication

We suggested earlier that the informational model does not capture the entirety of human communication and thus fails to recognize that the structure of language can be shaped by pressures that do not influence the transmission of propositional content. This goes double for animal communication, which displays little evidence of morphology or meaningful syntax (Suzuki, Wheatcroft, & Grieser, 2016, cf: Ouattara, Lemasson, & Zuberbühler, 2009). Animals do use discrete signals that some have considered analogous to the (monomorphemic) words of human languages (Cheney & Seyfarth, 1996; Zuberbühler 2000), but these signals are almost exclusively indexical (Queiroz & Ribeiro, 2002) and the degree to which their production is intentional is highly controversial (Penn & Povinelli, 2007; Tomasello 2008).

Below, we propose that the structure of animal signals is determined by the same pressure for languages to be functionally deployable, namely by being filtered through the perceptuo-cognitive apparatus of the animal.

1.2.1 Motivatedness

Just as associations between words and meanings in human languages can be motivated by links between perception, production, and cognition, so too can animal signals be similarly motivated. Although some early studies in primate communication focused on the possibility that primate vocalizations might be arbitrarily structured, in the main, research on primates (and other animals) has adopted the stance that the particular form that a signal takes is likely to be closely tied to the function it serves. In this, work on animal signaling obeys a broader axiom of evolutionary biology which is that form and

function are intimately connected for most (possibly all) organismal traits. To wit, Morton (1977) was among the first to lay-out some common principles of the form-function fit for animal signals with what he termed Motivation-Structural rules. MS rules captured some very common associations between the form of broad classes of vocal signal and the context in which they are typically produced, and, in particular the motivational state underlying signal production. For example, he observed that harsh, spectrally broadband calls tend to be given in agonistic contexts while more mellifluous calls are used in prosocial affiliative contexts (Morton, 1977, 1994). Sometime later, Owren & Rendall (1997, 2001) elaborated this framework noting that, while such structural features may reliably reflect the underlying affect or emotion of signalers, they likewise can have potential effects on the affect and responses of listeners. Indeed, they argued that the latter effects on listeners might ultimately represent the more salient pressure motivating many of the signal structure patterns first noted by Morton.

For example, across many species, alarm calls produced by animals in the context of encountering dangerous predators are often structured quite similarly and are typically short, high amplitude calls with very abrupt onsets and harsh spectral structures (see Appendix 1 for sample audio files). Not coincidentally, these call features are also exactly those that best elicit a well-documented auditory reflex, termed the acoustic startle reflex (Eaton 1984). This involuntary response involves immediate attentional shifts and the interruption of ongoing activity, and it induces a host of other basic nervous system responses, including stimulating reticular formation nuclei in the brainstem that help to regulate overall brain activation, all preparing the listening organism for immediate, dramatic action highly functional in the context of encountering predators and other

dangers. The phenomenon is thought to occur in every hearing species (Eaton 1984) and clearly demonstrates the way in which sounds can have direct access to low-level nervous system mechanisms that guide functional behaviors in listening animals. In fact, so direct are the effects that they can be quite difficult, or even impossible, to resist or habituate to. Starlings, for example, are unable to habituate to the sound of their species-typical distress call, which will always elicit a startle reaction regardless of the number of previous presentations (Johnson, Cole, & Stroup, 1985).

Other examples of sounds with direct effects on listener behavior are common. For example, both humans and animals are sensitive to signals that incorporate repeated pulses and dramatic frequency sweeps. Frequency upsweeps are especially effective for capturing receiver attention and increasing arousal or motor activity, and this has been observed both in animals and in humans, through both music (Schneider, 1963) and in infant-directed speech (Fernald, 1992; Kaplan & Owren, 1994; Papousek et al., 1991). Both animal and human infants are also known to take advantage of these motivated signal-meaning associations, producing affiliative cooing and babbling or aversive shrieking and wailing to modulate the behaviour of their caregivers to their own ends (Rendall, Notman & Owren, 2009).

Beyond modulating the behaviour of conspecifics, the ability to functionally leverage motivated signal-meaning associations can be observed where calls are directed from one species to another. For instance, handlers and herders of various domesticated animals have long capitalized on the impact of sounds like whistles, tongue clicks, and lip smacks to manage their charges (McConnell 1991). Similarly, many prey species, when captured by a

predator, produce “death screams”, which are often described as sudden, powerful, and piercing and have been suggested to be used as an attempt to startle the predator and allow for a chance for the caller to escape (Driver & Humphries, 1969; cf. Arnal et al., 2015; Belin & Zatorre, 2015 for analysis of the special status of screams for human communication).

In general, then, the signals of primates and other animals are fundamentally motivated and the associations between signals and ‘meanings’ or, more appropriately ‘outcomes’ are typically indexical, and appear to be mediated often by an association between general arousal, or affect, and, for example, gross acoustic features like the spectral density of a signal. This might suggest that animals are able to learn connections between signals and meanings only when those connections are motivated, but we know that this is not the case entirely. For example, the extended history of attempts to teach artificial languages to some species of great ape clearly show that they are capable, when tutored, of learning unmotivated (arbitrary) signal-object associations (Segerdahl, Fields & Savage-Rumbaugh 2005). Instead, we suggest that just as in human languages, the presence of motivated signal-meaning mappings over arbitrary ones might be accounted for by the pressure for those signal-meaning pairs to be learnable and functionally deployable. Below, we discuss the constraints of animal signaling systems that either further bias them towards motivatedness or limit their expressivity.

Modality

Animals, much like humans, seem to share associations between sensory modalities that are not limited to those connecting acoustic and affective dimensions, although to date

there is no evidence that those crossmodal biases (Hanganu-Opatz et al., 2015) are functionally leveraged in their communication systems. For example, chimpanzees have been shown to share the human bias of associating high pitched sounds with perceptually bright objects (Ludwig, Adachi, & Matsuzawa, 2011), but do not have calls that denote the presence of bright objects in their environment.

Similarly, animal signals do not make use of unimodal associations in the same way that human languages do. Even in animal species that are vocal mimics, mimicked signals are either used blindly, as when they are incorporated into mating displays (Higgins, Peter, & Steele, 1990), or used truly imitatively to attract prey (Calleia, Rohe, & Gordo, 2009) or produce a response from conspecifics or another species that is in some way beneficial to the mimic (Flower, 2014). In no case that we know of are mimicked calls used to refer to the presence of the animal, or event, being imitated.

Transparency

Whether animal signals can be meaningfully described as either transparent or opaque is difficult to determine, because transparency is so closely tied to the idea of meaning. If, even without any prior learning, an animal responds “correctly” to an alarm call by becoming startled and surveying their surroundings, for example, should we suggest that the “meaning” of the alarm call is transparent to them? If their startle response is mediated by an unavoidable association between sound and arousal, and that association leads to appropriate behaviour, by what method can we establish that the animal understands anything about the meaning of the call?

In cases of so-called functionally referential vocalizations, such as the classic example of alarm calls given by vervet monkeys (Cheney & Seyfarth, 2006), evaluating transparency is no easier. The alarm calls the vervets produce for different classes of predator certainly share many broad characteristics that are appropriate for eliciting a startle response (Owren & Rendall 2001), but the fact that each call elicits a somewhat different response from listeners suggests that either: a) there is something about the call for one type of predator, say 'leopard' that makes it more appropriate for leopards than for other types of predators such as snakes or hawks; or b) the general structure of each alarm call is motivated by the same sound-affect bias, and specific responses are not transparent but are established (learned) by experience (i.e., following or emulating the responses of others). The fact that different populations of Campbell's monkeys are reported to make use of local "dialects" (Schlenker et al., 2014) suggests that the second possibility is more likely.

Production constraints

One potential explanation for the lack of signals that leverage non-affective perceptual biases to more effectively convey meaning in animals is that the anatomy and operation of the vocal apparatus may be more constrained in the range of sounds produced compared to humans (Fitch, 2000). However, even prodigious vocal mimics among birds who are capable of producing a far broader range of sounds than humans do not take advantage of these perceptual biases, which may point to a general cognitive deficit in the ability to map signals to specific meanings, even when they have the benefit of being motivated.

Mechanism - Affective Semantics

Natural forms of crossmodal association have not been systematically studied in animals. However, the evidence from some of the best documented cases where they are most likely to be found – for example the alarm call system of vervets – points to a mechanism of ‘affective semantics’. As reviewed above, the alarm calls of vervets, and those of many other species, are similar in possessing a common suite of acoustic structural features well suited to stimulating a host of reflexive autonomic, affective responses that immediately prepare listeners for a ‘flight-or-fight’ type of response, which is obviously functional in the context of confronting predators or other dangers. An interesting element of this phenomenon as documented in vervet monkeys is that it takes predator-naïve infants some time to develop adult-like, differentiated escape responses to the alarm calls elicited by different predators (Seyfarth & Cheney 1986). At first, the different alarm calls simply produce a generalized startle response in infants as a result of the common affect-inducing acoustic features of each call. Over time, infants’ responses begin to differentiate into the more adult-like repertoire of different escape options. Although the details of this process remain undocumented, it is well-established that the upregulation of brain activation, glucose metabolism, and stress hormones that accompanies emotion-inducing experiences facilitates learning and memory (McGaugh, 2003). Therefore, the powerful effects that the alarm calls have from the very start on attentional and affective systems likely serve to tag the significance of these events for naïve infants and promote additional learning about the different predators involved and the specific behavioral responses that follow and are appropriate to them. As a result, although predator avoidance is rooted developmentally in the inherent affect-inducing properties the alarm calls have (i.e., inherent sound-affect associations), later as mature responders, vervets may well develop

some sort of representation of the different types of predator they encounter as a result of their accumulated history of experiencing them in association with the alarm calls themselves. Hence, the calls may develop some rudimentary semantic value that is rooted in the original functional perceptual and affective biases that kicked things off.

1.2.2 Systematicity

The question of whether animal signals can be considered systematic in the sense outlined here is an interesting and novel one. For species reported to use signals even semi-referentially in ways suggestive of signal-meaning mappings, the repertoire of such signals is typically quite small, on the order of one to three call types, and this necessarily makes it challenging to evaluate the potential systematicity of the relationships between the sets of signals and the sets of 'meanings' involved. We might suggest that the small suite of alarm calls produced by vervet monkeys has the property of being incidentally systematic, in having a small number of similarly structured calls pointing out a small set of different predators or classes of danger. However, the meaningfulness of this type of systematicity to the animals themselves is entirely unknown. Given experience with their own set of different alarm calls, would vervets be able to generalize to a novel signal and recognize it as an alarm call for a new predator in their environment?

1.2.3 Learnability and Expressivity

Animal signaling systems are generally characterized by relatively small overall repertoires, at least compared to the lexicons of languages. They are unlikely then to be significantly constrained by a pressure for expressivity. However, the fact that animal calls are typically indexical and often leverage sound-affect associations suggests either that the

pressure for those signals to be learnable has influenced their structure, or that the perceptual biases mediating the sound-affect associations actively constrain the possible signals that an animal can produce for a given “meaning”.

The broadly conserved structure of alarm calls across many species seems to be shaped by the pressure for functional deployability, but is the specific detailed form that individual signals take constrained by some need also to be learnable? Put differently, in the absence of a pressure for functional deployability, would a vervet be able to learn that a quite different and mellifluous ‘coo-ing’ sound is a signal for a specific kind of predator, or is the normal, affectively-mediated perceptual bias to harsh calls required as a substrate upon which to establish an element of reference?

1.3 Filling in the blanks

Both animal and human communication are at least partially structured based on the interaction of a pressure for functional deployability with the perceptuocognitive architecture of their users. In a sense, this functional deployability pressure is extra-linguistic, as it deals with the modulation of the behaviour of conspecifics by exploiting associations between perceptual features delivered via the vocal channel and affective and attentional processes. In animal communication systems, the leveraging of affective biases for functional purposes seems to be the only way that signal structures are influenced, but in human language those same affective biases are supplemented by others to influence the learnability and expressivity of the language.

The shared evolutionary history of the perceptual and cognitive apparatus of humans and other animals leads naturally to the suggestion that the pressure for functional

deployability might have served as an initial seed from which more complex associations could be leveraged to convey a growing set of meanings. Animal signals, like the alarm calls of vervet monkeys, that are at least putatively referential seem to suggest exactly this possibility. In the sections below, we suggest a number of ways that these areas can inform one another, as well as surveying a number of open questions about the evolution of communication systems and how they might be approached.

1.3.1 Bio-semantics

The morphemes of human languages are composed of phonemes, the basic building blocks of language that, by themselves, are conventionally held to carry no meaning. As we have seen, however, that is not necessarily true: phonemes are processed both as discrete potentially meaningless units, but also as sounds whose acoustic features can leverage meaning. Thus, phonemes have meaning that is separate from their embeddedness and typical conventionalised use in a language. The ability of sound to carry “meaning” by virtue of affective or perceptual associations is shared with a number of non-human species, but the possibility that the richer semantics of more robust communication systems can be scaffolded on these simple sound-meaning associations is rarely considered.

For example, infants of all species first learn sound-meaning associations that have clear functional biological relevance. For example, they learn to establish the age, sex, body size, and disposition of caregivers and others in their world based on vocal cues. These distinctions are signaled by differences in basic acoustic features like voice pitch, formants and prosodic variation that vary predictably and systematically with consequences of clear

biological relevance and affective salience such as provision of food, comfort and care or danger and threat (Titze, 1989 ; Fitch and Giedd, 1999 ; Rendall et al., 2005). Thus, the first sound-meaning associations that infants acquire are not propositional in nature, but are nonetheless highly functional, predicting not only social distinctions but also their concomitant affective and behavioural consequences. Many animals learn similar types of sound-meaning associations early in their development, yet fail to establish the rich semantics of human language. Why is this the case? And how much of the ‘meaning’ of animal signals is given directly by the leveraging of perceptual bias, or facilitated and scaffolded by those associations?

This is what we’re referring to as Bio-semantics, which could be characterized, a bit awkwardly, as “biologically constrained phonological semantics”. The suggestion is that species typical biological organization acts as a substrate by which phonological or acoustic features of utterances have ‘meaning’, or at the very least proto-semantic meaning. Thus, certain phonetic forms might be biologically motivated, grounded in the broader evolutionary history of the structure and use of similar signal forms in animal signaling systems where they mark distinctions of clear functional, biological relevance (e.g., harsh spectral structures and dangers; low pitch or resonance and large size and social potency). Parsimony suggests that the broadly conserved perceptual and cognitive biases that support this long evolutionary history of functionality in animals need not abruptly end or somehow be abandoned uniquely in the human line. Rather it would be expected to continue and offer communicative possibilities in language as well. By this route, some phonetic forms in language (as reviewed earlier) might thus inherit natural meaning potential based on their specific acoustic structural forms and the conserved history those

may have had in signaling functional distinctions with clear biological relevance in animal communication systems.

The novelty in this approach is in seeking continuity between human and animal communication systems not in the potentially more rarefied features of full-blown language like intentionality, high-level semantics, and syntax but rather at much more fundamental levels, the level of individual sound units, that are indisputably shared; and then seeing the evolutionarily conserved pressure for functional deployability at this level as a potential seed for the evolution of language. The value of this approach may be manifold. First, it may prompt a productive reorientation of analysis in language, where traditionally the assumption has been that linguistic forms are largely arbitrary and constructed from meaningless phonemes. It might also prompt an equally productive reorientation of research in animal communication systems, particularly those of closely related nonhuman primates, away from attempts to find continuity in the more rarefied features of language, where results to date, even on a favorable reading, have been thin. Finally, it might thus allow better integration and comparability between the two programs based on adoption of common constructs and methods of analysis.

To this point, a central problem in research on sound-symbolic phenomena in human language and animal communication is that the features of signals from the two systems are described using non-overlapping jargon, or according to measures that cannot easily be translated between the two. Human perceptual bias, for example, is generally explained in terms of phonology: i.e. aspirated voiceless stop consonants are associated with jagged visual images; or by invoking folk psychological intuitions about sounds: i.e. that 'kiki' is a

“harsher” word than is “bouba”. In contrast, animal signals are typically described based on detailed acoustic measures such as amplitude envelope, harmonics-to-noise ratio, or spectral density that make the differences between signals more explicit and objectively quantifiable.

Because these metrics are not directly comparable, the degree to which human and animal perceptual and affective biases are similar remains unanswered, with few authors (e.g. Owren & Rendall, 1997, 2001) recognizing that the biases are likely to be conserved and underpinned by the same general mechanisms. To explore this possibility, it is first necessary that researchers should explore human affective and perceptual biases like the bouba-kiki effect using stimuli that are characterized based on metrics that can be compared directly to animal signals: i.e. bio-semantic biases should be described based on their acoustic, rather than their phonological, features.

If human and animal affective and perceptual biases are indeed similar to one another, and those biases are leveraged by the requirement in human language for learnability (and thus have downstream effects on the structure of language), then it stands to reason that animal communication systems might similarly be structured around such biases, or that the leveraging of biases might allow animals to learn motivated signal-meaning mappings with increased ease in the same way that humans do. The exploration of this possibility can serve to bridge the gap between human and animal communication based on both structure and function. It might also generate many further testable predictions that address the importance of biosemantic associations for human language and also highlight

the pieces missing in animals that hamper transitioning from a functional leveraging of perceptual and affective biases to a truly semantic leveraging of those same biases.

1.3.2 Human affective semantics

An account of the origins of human language that returns to functional pressures and affective biases as a driving pressure raises important questions concerning both the possible centrality of affect to perceptual biases that are leveraged semantically and also the degree to which the use of language in modern humans is still mediated by those same functional pressures.

In the modern era of human communication, the suggestion that language is primarily about the transfer of information seems unimpeachable. We daily consume massive amounts of information, and generally take in a large proportion of this information in written form, which is not likely to be as appropriate a channel for leveraging perceptual and affective associations. Historically, however, this was not the case, and only half of the world's extant languages have a formal writing system (Paul, Simons, & Fennig, 2015). The informational account of human language also stumbles on questions about its evolutionary trajectory. A fully formed language system is, without a doubt, valuable for transmitting information and doing uniquely human things, but where does that leave the connection between animal and human communication? The recognition that human verbal communication continues to leverage core affective systems and widely conserved perceptual biases embraces the possibility that the arbitrary and conventional semantic components of language, central to its modern functioning in carrying and conveying

information, are likely built on a common framework of affective and perceptual biases shared widely among primates, certainly, and possibly other animal groups.

1.3.3 Systematicity in Animal Communication

The degree to which animal communication systems are systematically structured, or that systematic signal-meaning associations might positively influence learnability in animals as they do in humans, are open empirical questions. Nielsen (2016) has suggested that learning systematic associations between words and meanings might enhance the learnability of later-acquired conventional associations by bootstrapping the acquisition of concepts and categories in human language learners: might animal signaling systems be less complex than human language partially because they do not take advantage of conceptual bootstrapping, or are the “deficiencies” of animal communication systems entirely explained by additional cognitive abilities in humans specifically associated with the elaboration of language?

1.4 Conclusions

The relatively recent recognition that the structure of languages is shaped by the pressures to be both learnable and expressible, and also when filtered through the perceptual and cognitive apparatus of users, has been immensely productive for modern linguistic research. Similarly, research into animal communication has recognized the importance of perceptual, productive, and cognitive processes for shaping the behavioural and signaling repertoires of various species. Here, we have proposed that these two streams of research can be productively combined and can inform each other to develop

not only a better understanding of natural languages but also the evolutionary trajectory of language and communication systems more broadly.

Specifically, we have suggested that in addition to pressures for learnability and expressivity, both human and animal communication systems are sculpted by a pressure for their signals to be functionally deployable. This pressure for functional deployability is not merely a filter through which communication signals must pass but rather is intimately and directly tied to core perceptual and cognitive biases that thus underpin and determine signal effectiveness. Fully embracing and integrating these points into future work promises a host of additional potential insights into the structural and functional organization of communication systems in humans and animals alike, and, importantly, the potential productive links between them.

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Appendix 1. Sample of human and primate sounds.

Human Speech:

This sample provides examples of synthetic speech stimuli used in experiments testing the classic *Bouba-Kiki* effect, wherein nonsense words containing spectrally harsh or strident consonants (such as /k/ or /t/) tend to be matched to unfamiliar objects or images that are *jagged* or *fractured* in appearance, while nonsense words containing more sonorant consonants (such as /b/ but more especially /l/ or /m/) tend to be matched to unfamiliar objects or images that are *smooth* or *rounded* in appearance. The functional argument is that, although formal linguistic theory typically regards these basic differences in spectral structure between strident and sonorant consonants to be meaningless, it is possible that the differences, in fact, carry some natural semantic potential: that is, some ability to convey rudimentary semantic contrasts of the sort just noted. Further, the different consonant forms may inherit their semantic potential from the wider use of sounds typifying these same basic distinctions in other species, such as closing related nonhuman primates.

Primate Vocalizations:

This sample provides examples of typical primate vocalizations given in one of two different contexts. The first context is characterized by high arousal and excitement and is typified by encounters with dangerous predators, or with social agonism involving hostility, aggression or fighting with companions. In either context, typically associated vocalizations are loud, strident *barks* and *screams* which are high-amplitude, abrupt, and spectrally harsh, noisy or chaotic sounds. The second general context, contrasts sharply with the first, and is typified either by

relaxed group movement through the landscape or relatively calm, affiliative social interactions with companions involving friendly contact and grooming. In such situations, typically associated vocalizations are sonorant *grunts* and *coos* which are comparatively low amplitude, with smooth signal onsets and tonal or harmonic spectral structures.