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Developmental plasticity and language: A comparative perspective

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Abstract

The growing field of evo-devo is increasingly demonstrating the complexity of steps involved in genetic, intracellular regulatory, and extracellular environmental control of the development of phenotypes. A key result of such work is an account for the remarkable plasticity of *organismal form* in many species based on relatively minor changes in regulation of highly conserved genes and genetic processes. Accounting for *behavioral* plasticity is of similar potential interest but has received far less attention. Of particular interest is plasticity in communication systems, where human language represents an ultimate target for research. The present paper considers plasticity of language capabilities in a comparative framework, focusing attention on examples of a remarkable fact: Whereas there exist design features of mature human language that have never been observed to occur in nonhumans in the wild, many of these features can be developed to notable extents when nonhumans are enculturated through human training (especially with intensive social interaction). These examples of enculturated developmental plasticity across extremely diverse taxa suggest, consistent with the evo-devo theme of highly conserved processes in evolution, that human language is founded in part on cognitive capabilities that are indeed ancient and that even modern humans show self-organized emergence of many language capabilities in the context of rich enculturation, built on the special social/ecological history of the hominin line. Human culture can thus be seen as a regulatory system encouraging language development in the context of a cognitive background with many highly conserved features.

Evo-devo as a framework for new perspectives on language evolution and development

Evolutionary-developmental biology or evo-devo is not a new field, but rather the elaboration of a long-term trend, increasingly emphasizing that natural selection tends to target developmental processes and that evolutionary change tends to proceed by adjusting intracellular regulatory mechanisms (Carroll, 2005). Another feature of evo-devo is emphasis on “conserved” systems that produce widely different organismal forms through minor regulatory changes (Kirschner & Gerhart, 2005). Thus point mutations, duplications or deletions may change the timing or scope of expression of conserved “toolkit genes”, yielding vastly different phenotypes, often different species. Similarly, organismal form can be affected dramatically by environment, a fact known for over 100 years—e.g., *Bonellia viridis* (green spoonworm) larvae are initially undifferentiated sexually, floating in ocean water. Falling on or near a female spoonworm, they develop into 1-3 mm-long males. Falling on the ocean floor, they develop into ~50-times larger females (Hertwig, 1894). Thus environmental conditions can yield dramatically different organismal forms from one genotype (Newman, 1989).

The evo-devo agenda predicts that environmental conditions can radically modify behavioral phenotypes as well, in relatively short time frames, sometimes with concomitant changes in form. Darwin’s finches provide a good example: both beak type and feeding behavior were modified from a highly conserved background through regulatory changes naturally selected under differing environmental pressures on different islands.

Language also presents an important case of developmental plasticity. Whereas specific human languages differ, humans around the world can be thought to share a phenotype at the level of “infrastructural capabilities” (Oller, 2000) or “design features” (Hockett & Altmann, 1968) of language. In the context of the evo-devo agenda we ask: 1) What design features are essentially unique to humans? And 2) what role might environment, especially human enculturation, play in regulating language-approximating phenotypes across species? We review evidence to illustrate that the evo-devo theme (Figure 1A) can be applied by analogy to language-approximating phenotypes in many human-trained

animals (Figure 1B). In both cases conserved processes regulated by environmental conditions produce significantly modified phenotypes.

Of course, many have argued that human language also depends upon enculturation (e.g., Tomasello, 1996) and that language evolution has involved ratcheting interactions of growth in culture and in inherent capabilities necessary to learn language (Christiansen & Kirby, 2003; Elman et al., 1996). We argue that evidence from nonhumans learning to recognize and use language-like structures offers a unique perspective on conserved cognitive systems shared across many taxa, systems that form a basis for at least minimal command of many language-design features *if* human training and interaction are brought to bear. The arguments are that 1) many nonhumans share critical foundations with humans in language-relevant cognitive systems, and 2) even for humans, enculturation may play a critical role in command of infrastructural features of language. The design features discussed represent a small set that can be addressed with current empirical evidence (for rationale on selection see Supplementary Material 1, SM1). The species to be discussed have been selected primarily on the basis of available data (see SM2) compiled predominantly from peer-reviewed studies (see SM3).

Design features of language and enculturation of non-human learners

Symbolism/semanticity. Whereas animals in the wild use various signals to transmit illocutionary functions (Austin, 1962; Griebel & Oller, 2008), no indisputable report exists of any case of fully referential *symbolism* or *semanticity* in natural animal communication (see SM1). In language, words can refer to anything conceivable (entity, event, being, quality, state...), but animal signals appear predominantly to express states of senders (fearful, angry, solicitous...) and to induce states and action tendencies in receivers rather than to transmit referential/semantic content about the external world. The possibility that animals ever transmit external-world information in their natural signals is in dispute (Stegmann, 2013) in part because animal receivers seem capable of inferring information not actually encoded in signals from correlations between signal occurrence and the external world (Owren & Rendall, 2001) (and see SM1).

In dramatic contrast, nonhumans from a wide variety of taxa have learned to understand and often produce symbols with semantic content *if they experience intensive human training*. As examples, a border collie is reported to have learned to retrieve over 1000 objects on voice command (Pilley & Reid, 2011), chimpanzees and bonobos have been trained to comprehend and produce scores to hundreds of signs or lexigrams (Gardner, Gardner, & Van Cantfort, 1989; Premack, 1971; Savage-Rumbaugh et al., 1993), and Grey parrots have learned to talk, using scores of spoken words and phrases with referential content (Pepperberg, 2010).

Animal referential word learning seems to be dependent on intensive, long-term training, and seems to be facilitated by direct human interaction and/or observation of human interaction. The claim that a border collie could learn words by fast mapping (Kaminski, Call, & Fischer, 2004) has been called into question empirically (Griebel & Oller, 2012), but it is generally agreed now that *semanticity*, with production/comprehension of hundreds of labels, compared to many thousands for humans, can be instilled in many animals with persistent human enculturation.

Displacement. Humans use referential terms in such a way that they are utterly free of the here-and-now, referring to things in the past, future, and in any location, real or imaginary, a capability called *displacement* (see SM1). Such reference has never been observed in nonhumans in the wild although evidence of *displacement* in communication has been suggested, for example, in honeybees (von Frisch, 1967; Riley, Greggers, Smith, Reynolds, & R. Menzel, 2005) and chimpanzees (E. Menzel, 1988). These indications, however, fall far short of referential *displacement* as in human words, if for no other reason, because there is no “lexicon” of semantic items in these animal communications; the system may operate according to simpler routines where receivers derive information from correlations between signaler actions and situations, even without lexically-coded information in signals themselves.

But again, human training can enable such abilities. For example, C. Menzel and colleagues (1999) showed that, when an experimenter hid one of more than 30 objects in a nearby woods, a language-trained chimpanzee could, from her enclosure hours later, touch the appropriate lexigrams to indicate, with extremely high reliability, the identity and location of the object to an uninformed keeper.

This game proved the chimpanzee labeled items using the design feature of *displacement*, as the objects labeled were always displaced in both space and time.

Functional flexibility. Any referential word or sentence in a human language can be used to serve a wide variety of illocutionary functions (Austin, 1962). Thus, we can use the word “pig” to serve an aggressive function (“You pig!”), as a question (“Is this a pig?”), as a statement (“This is a pig.”), as a warning (“Watch out, a pig!”), as an endearment (“My sweet little pig!”), as an example (which we are doing here), etc. In all these cases “pig” refers to a type of mammal with certain characteristics (the semantic content), but the illocutionary force can vary dramatically, with emotional valences ranging from positive, to neutral, to negative (see SM1).

Active investigation exists about the extent to which animal communication in the wild may show flexibility of the relation between signal and function (Crockford & Boesch, 2005; Laporte & Zuberbühler, 2011), a pursuit that is helping to moderate the claim of classical ethology that animal signals have one-to-one mappings between signal and function (Lorenz, 1951). A substantial difference, however, between the extent of *functional flexibility* in animal and human communication is not in dispute—for example, no reports demonstrate that any animal signal in the wild is used with a full range of illocutionary valences from positive (e.g., exultation) to negative (e.g., aggressive). But all normal adult humans can use words these ways, and even three-month-old human infants use several prespeech vocalizations with illocutionary forces ranging from positive, to neutral, to negative (Oller et al., 2013).

The picture can change, however, after intensive human training of animals to use referential labels. The type of training appears important, because one chimpanzee trained in a strict reward/reinforcement paradigm used his acquired vocabulary almost exclusively as requests for food, hugs, or tickling, a single illocutionary function (Terrace, 1979). Other experimental animals raised in human-like social conditions with only intermittent reinforcement have shown much more diverse illocutions. In addition to requests, they could also query What, Who, and Where: e.g., the Grey parrot Alex asked: “What color?” to his reflection. He had been trained to *respond* to that question, but learned to produce it via observation only (Pepperberg, 1999). Human-trained animals could inform their trainers

about novel things, e.g., the chimpanzee Washoe would climb a tree from which she could see who was arriving by car and would sign names of arriving people to trainers and/or other chimps on the ground, thus not just naming, but informing (an additional illocution). Some animals also commented on objects or events (e.g., Washoe, on hearing barking in the neighborhood, signed “dog”, Gardner et al. 1989)

Washoe was reported to use “swear words” appended to her utterances to express the illocution of insult, signing “dirty” before the name of a person with whom she was displeased, although she also could use the term merely as a description. Another insult, or perhaps a dare, was creative use of the signs “you bird”, meaning “you’re chicken”. Washoe interfered in a fight between her adopted son and another juvenile male, whom she slapped, and then she produced the sign “go”, which in other cases she used as a description, but here as a command. The chimpanzee Tatu signed “black” as a description but, for reasons unknown, also to indicate she thought something to be beautiful or “cool” (Gardner et al. 1989). Alex similarly used “wanna go (back, chair, shoulder, etc.)” to request movement or that a trainer leave (“go away”), and also as a descriptive comment (“I’m gonna go away”) as he broke contact with a trainer (Pepperberg, 1999).

Such reports provide evidence for notable diversification of functional usage by nonhumans of human-trained labels. The reports *at least* demonstrate multiple illocutionary uses of the same human-trained label, and at least (in Washoe’s “dirty”) both negative (insult) and neutral (descriptive) types and (in Tatu’s “black”), both positive (adulation) and neutral (descriptive)—a clear step toward *functional flexibility* of the sort found in language. These cases provide much more convincing demonstrations of *functional flexibility* than in cases reported for in-the-wild communication by nonhumans.

Serial ordering/recombination. Human language involves systematic *recombination* of words and morphemes, forming indefinitely long sentences of semantic material (see SM1). Only weak evidence exists for even minimal “syntax” for in-the-wild animal communication, although some have argued that combinations of calls or of calls and gestures such as drumming have effects on receivers that suggest modifications of function by the combinations (e.g., Clay & Zuberbühler, 2011).

Some human-trained animals in contrast—including parrots, dogs, primates, dolphins and pinnipeds—comprehend differences in meaning for at least short human-generated sequences of words or lexical-like symbols presented in different orders (e.g., Gisinger & Schusterman, 1992; Herman, Richards, & Wolz, 1984; Pepperberg, 1999; Savage-Rumbaugh et al., 1993; Pilley, 2013).

Production of serially-ordered lexemes in human-trained animals has been questioned (Terrace, Petitto, Sanders, & Bever, 1979), even though sequences, mostly of 2-4 lexemes, have been reported in at least human-trained parrots and great apes (Gardner et al., 1989; Pepperberg, 2004). Still it is not clear that ordering is itself a systematic indicator of meaning in such cases. In reported cases where lexemes were not used in consistent sequences to indicate meaning, trainers could often interpret by context (e.g. “give orange me” or “me give orange”) and/or accompanying gestures, e.g., a begging hand. Once again human-trained animals, although far from producing language *per se*, appear to have produced much more language-like behavior after intensive human communicative interaction and training. Alex the parrot even engaged in phonemic or phonetic *recombination* (Pepperberg, 1999, 2010), creating novel vocalizations (e.g., “banerry” for apple”) out of parts of existent labels (banana, cherry) or sounds and labels (e.g., “s-none” as a precursor to “seven”) (see SM4).

Cultural transmission. Language is inherently cultural, with semantic elements transmitted across generations. Data on birds suggest *cultural transmission* of signals, though not semantic elements (SM1). A few reports exist of *cultural transmission* of behaviors from one generation to another in great apes (Boesch, 1991; Hannah & McGrew, 1987), but no convincing examples of learned communicative signals thus transmitted. The case of sign-language trained chimpanzees offers, however, one intriguing view of possible *cultural transmission* of learned lexemes in primates. When Washoe was living with a group of sign-trained chimpanzees, who often signed to each other, she was given an adoptive son, Loulis. Human trainers were not allowed to sign in Loulis’ presence. After seven years in the group, Loulis acquired ~70 signs (Fouts et al. 1989). Researchers also observed that Washoe and the other chimpanzees had acquired a few new signs from each other over the same period. A few documented observations also existed of Washoe actively trying to teach Loulis a new sign.

An observational opportunity such as the one Fouts et al. developed is unique. Few language-trained apes have lived together in a socially nurturant environment, and Loulis represents the only case we know of where another ape lacking prior human-training has been allowed to grow up in such an environment. The result suggests that *cultural transmission* of language-approximating lexemes to a second generation individual is possible for chimpanzees trained by humans (SM3 for issues regarding peer-review of this work). We wonder if there will ever be another opportunity to confirm this result.

Why not in the wild?

At this point, we must ask how it is possible for animals in captivity to learn lexemes while not developing such elements in the wild. Clearly, considerable cognitive foundations of minimal lexical learning are in place across many taxa, and given the variety of species capable of learning human labels, we might suspect that with intensive training, similar capacities might be demonstrated in many other mammals and birds, perhaps even in reptiles or fish. Clearly, neither evolutionary distance from humans nor absolute brain size is a major factor here (relative brain size or brain organization could of course be more important predictors) given that a parrot is one of the champions of all nonhuman learners of language-approximating communication skills, even demonstrating capacities such as phonological or phonetic awareness (Pepperberg, 2010, and SM4). Some researchers suggest that label learning is based, at least in part at the very earliest of stages, on very basic associative-learning mechanisms that are shared across species ranging at least from mammals to birds (see SM5).

The simple answer to “why not in the wild” seems to be that no animal society appears to have developed to the point of providing the cultural support necessary to initiate the chain of events that would bring such features as strong *functional flexibility* or *semanticity* into the communicative repertoire. Much speculation exists that the hominin line profited in communicative evolution from increases in social group size and complexity (Dunbar, 1996) and from intensified parental attention to their altricial infants and their signaling behavior (Locke, 2006; Oller & Griebel, 2006, and SM6).

One conclusion from animal language studies is that method is crucial. Best results on all fronts, including spontaneity of communication, number of labels, and usage complexity have been achieved

with total immersion into human culture with nonhumans raised as much as possible like human children, with maximal social interaction. This approach has worked with parrots, dogs, and great apes. For example, the Gardners did not use operant conditioning; signs were learned during daily interactions in the home. Trainers often molded chimpanzees' hands for correct configuration, but reinforcement was merely social attention and the acquisition of a relevant object or pursuance of the relevant action. Trainers prompted chimpanzees in ways teachers commonly prompt human children, and like children, chimpanzees were often denied their requests, and were more likely to get what they wanted if they made themselves understood. Parrots have learned best when trained with interactive social modeling demonstrating the connection between vocal labels and related objects or attributes; they have failed when exposed merely to audio or videotapes of human speech (Pepperberg, 1999). Interactive teaching also evoked spontaneous signing by chimpanzees and vocalizations by parrots, just as seems to occur with human children (and see SM6 on birdsong learning).

The results suggest many animals categorize things and events in ways not unlike those of humans and these shared conceptions allow many nonhumans to associate arbitrary labels with things and events if they experience appropriate interactions with humans. Perhaps given our evolutionary past, this should not be surprising. But it does take us aback to recognize that in *a single generation*, an enculturated cross-fostered ape learned to communicate with language-approximating behavior at a level a lot like that of a 2-year-old human. We have no test yet of how far this kind of language-approximating behavior could go across multiple generations supported by human training and conspecific interaction, but the Loulis result intriguingly suggests there may be considerable room for growth.

The findings reviewed here also support the evo-devo compatible idea that human language may be substantially self-organized under the influence of human culture (see Christiansen & Dale, 2004). Ancient hominins may have experienced multiple rounds of communicative growth, including at each round, expansion in language-learning capabilities through natural selection, as well as advancement in hominin communicative culture that would have placed further selective pressure on learning capabilities (e.g., via Baldwin Effects). If the reasoning is correct, hominins would have progressively distanced

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themselves from their primate background in communication, because at each step, culture would have provided a mechanism of selection for more powerful communication both within and across generations.

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Fig. 1 Conserved evolutionary processes and developmental plasticity

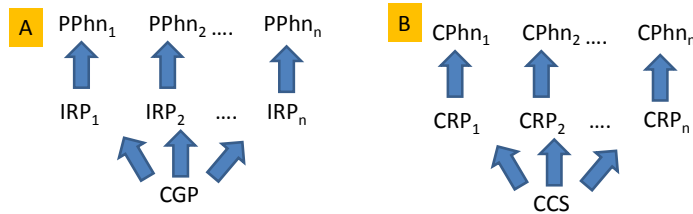


Figure 1 Caption: Conserved evolutionary processes and developmental plasticity

A. Organismal form (PPhn=Physical Phenotypes) can vary dramatically based on minor adjustments in regulatory processes (IRP=Intracellular Regulatory Processes) that determine the expression of protein-coding genes, which are often themselves highly conserved (CGP=Conserved Genetic Processes) as toolkits shared across widely different taxa. Evolution can thus produce vast differences in species in relatively few generations, maintaining a core of conserved genetic processes across all of them.

B. Similarly, we argue, communicative capabilities (CPhn=Communicative Phenotypes) in a variety of non-humans can vary substantially *within generation* based on exposure to differing human training (CRP=Cultural Regulatory Processes), which appears to exploit cognitive systems that are highly conserved across many species (CCS=Conserved Cognitive Systems) to produce a variety of potential “language-approximating” phenotypes. Different modern human languages can also be thought of as different phenotypes, determined by cultural regulation. However, mature languages share a wide variety of “design features” around the world, although these features are not generally shared with nonhumans in the wild. Fig. 2B portrays the phenotypic plasticity seen across many species in response to human enculturation.

Supplementary Material

Developmental plasticity and language: A comparative perspective

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SM1: Rationale for selection of particular language design features, their definitions, and differences from the Hockett scheme

Three primary reasons exist for selecting a small set of design features for focus in this article: 1) these features have been treated as important theoretical characteristics of human language in prior cross-species comparative literature; 2) empirical evidence exists to address these particular features comparatively; and 3) space limitations for the article prevent treatment of a variety of additional possibilities.

A few of the terms describing the features have origins in the work of Hockett and his colleagues (Hockett, 1960; Hockett, 1960; Hockett & Altmann, 1968), who formulated a list of design features that have been widely utilized in comparative research (e.g., Lyons, 1991; Noble & Davidson, 1996; Snowdon, 2004). While the Hockett list continues to have some utility, it needs updating in some ways that Hockett himself acknowledged, and in other ways that have been highlighted by critics including for example von Glaserfeld (1976) and Oller (2000, pp. 224-229). In the cited and in subsequent work, Oller and colleagues have outlined a much more extensive set of features that attempt to remedy some of the limitations of the Hockett scheme. This more extensive set of “infrastructural” characteristics (or design features) of language are organized in a hierarchical scheme ordered in terms of a natural logic of capabilities required for language—Hockett’s features, in contrast, form a flat list with no developmental or naturally-logical implications. Within the newer scheme, language-relevant capabilities are seen to build one upon another in a sequence demanded by their inherent relations. A more current version of the scheme is also outlined in an accompanying paper in this volume (Oller, Griebel, and Warlaumont).

For the present article, five design features are addressed. Two of the terms (*semanticity*, *displacement*) describing these features are drawn from Hockett, but the usages are quite different in both cases from those specified by Hockett (see below). Another feature (*cultural transmission*) appears to be equivalent here and in Hockett’s work (the feature is also called “tradition” in one of the Hockett papers). The terms *Semanticity*, *displacement*, *functional flexibility*, and *serial ordering/recombination* are all used in Oller et al.’s natural logic. The last term (*cultural transmission*) is not mentioned specifically in the natural logic, but at various stages in the natural-logic hierarchy, capabilities exist that imply *cultural transmission* as an aspect of the instantiation of the capabilities.

1) *Semanticity/symbolism*. When we use the term *semanticity*, we imply, in addition to other characteristics to be mentioned below, a learned association between a “symbol/signal” and some “concept”; all referential semantic/symbolic relations must involve a category that can be

jointly referred to by both sender and receiver. Thus *semanticity* requires triadic relations of sender-receiver-entity, along with learning of the relation between the conceptual entity shared between sender and receiver and the shared symbol for that entity. The simplest cases may involve the learning of a name for an object or entity present in the here-and-now, about which both sender and receiver share awareness—e.g., the word “pig” to label a pig present in the situation. This definition of *semanticity* generally corresponds to the intuitive idea that language requires a lexicon, a storehouse of words, each of which is paired with a meaning. Another characteristic of a semantic item (or label) is that it must be functionally flexible (see below), implying that each label can bear multiple illocutionary forces (Austin, 1962; Oller, 2000).

A pure illocutionary signal, such as an aggression call or a pain shriek, does not thus bear *semanticity* in our usage. Yet Hockett included gibbon calls as “semantic” signals even though gibbon calls have never been shown to our knowledge to transmit “information” triadically between sender and receiver about a shared concept or referent. A more conservative view is that gibbon calls transmit emotional states of the sender to the receiver (a dyadic relation), much as the human infant cry transmits the state of the infant to its caregivers without making reference to any shared concept and without showing signs of learning of any relation between any symbol and concept (Owings & Zeifman, 2004; Oller & Griebel, 2014). Hockett and his colleagues did not take into consideration the distinction between dyadic illocutionary forces (such as distress calls, warnings, threats, mating solicitations, etc.) and triadic semantic messages, a distinction that was just coming to be recognized, as a result of the work of Austin (1962) in the era of Hockett’s formulation of the design features.

Interestingly, there exist learned words that under normal circumstances (especially for young children) have a single illocutionary force. Such words are not triadic, bear no reference, and thus do not have full *semanticity*. “Hello” normally has the force of greeting, but makes no triadic reference, and “uhoh” expresses dismay or negative surprise, but again makes no triadic reference, because it does not name a thing or event about which the surprise is expressed. Perhaps predictably these “performatives”, words that perform a particular illocution (we could add “byebye”, “ouch”, “hurray”, and “wow”), are often among the earliest words of children learning to talk. Other words in the earliest vocabulary of children also appear to lack full *semanticity* because they are not truly referential (when they first appear), even though they seem like they should be referential. If a child says “ball” when people are playing a particular game of rolling a ball, s/he may not be aware that the word is intended to name the ball or the class of balls, but instead the child may act as if the word “ball” is merely something to be said in the situation of the game, a part of the performance of the social act of playing. In this sense the word “ball” would function for the child as a kind of performative (with the single illocutionary force of participating in a game), thus lacking full *semanticity*.

An important note here is that there has been an extensive effort to justify the claim that a variety of animals in the wild show the kind of *semanticity* that is implied by our usage. This effort has recently focused on the idea of “functional referentiality”, a weak form of *semanticity*, where information about the world is presumed to be transmitted but where the sender may be unaware of the transmission. The idea that animals transmit functional referentiality continues to be discussed in the animal communication literature after very widespread publicity starting with a study of vervet monkeys (Seyfarth, Cheney, & Marler, 1980), and continuing to much more recent time with studies of other species such as Japanese tits (Suzuki, 2014), but the idea is increasingly treated with skepticism (Oller & Griebel, 2014; Owings & Morton, 1998; Owings & Zeifman, 2004; Owren, Amoss, & Rendall, 2011; Owren & Rendall, 2001; Owren, Rendall, &

Ryan, 2010; Rendall, Owren, & Ryan, 2009; Wheeler & Fischer, 2012). This skepticism has been intensified since the empirical claims of *semanticity* in animal communication have been challenged on the basis of reexamination of the original vervet monkey data about presumed “predator-specific alarm calls” (Seyfarth et al., 1980; Struhsaker, 1967) that were used to advance the functional referentiality argument in the first place and based also on new data collected at the same site from descendants of the original vervet group (Price, 2013). This new evaluation (presented in a full chapter in the Price dissertation, in which Cheney, Seyfarth and Struhsaker are all listed as co-authors of a paper in submission) suggests that neither of the original foundational claims was correct: 1) the presumed predator-specific alarm calls are not apparently predator specific, but instead are used commonly in intra-specific aggression, suggesting they are in fact some sort of fear/aggression state indicators, not predator-specific alarm calls, and 2) the calls are not discrete, but are instead graded among each other, showing no sharp specific-predator associations. Furthermore it should be noted that no one has claimed that alarm calls represent culture-specific pairings of individual predator types with individual signal types in any animal species.

Whereas *semanticity* is thus a disputed, and we think doubtful, characteristic of animal communication in the wild, observations summarized in the main text suggest it is present in a variety of human-trained animals in the form of labels (i.e., words, signs, or lexigrams) with all the characteristics indicated above.

2) *Displacement*. In some ways the idea of *displacement* is similar in our usage and that of Hockett. Both imply that a signal can invoke ideas or referents outside the here-and-now. However, within the Oller scheme of infrastructural natural logic, *displacement* implies (and must be founded upon) *semanticity*. For example, the capability for *displacement* would be revealed by a child asking for someone to find his “blanket” (by saying the word, an apparently semantic act) when the object is not present. But Hockett suggested using the term *displacement* to refer also to cases where an alarm call might be inhibited temporarily while a monkey escapes from a predator. With the escape complete, the production of the alarm call might be viewed, according to Hockett, as a displaced semantic reference to the predator. But of course this reasoning depends on the idea that such an alarm call was indeed semantic in the first place. The citations above suggest it may instead have been an expression of fear with no external reference from the standpoint of the sender, in which case, it was not an example of *displacement* as defined in the natural logic. Examples of *displacement* in word-like communications of human-trained animals in the main text are, we think, more convincing.

3) *Functional flexibility*. The idea of *functional flexibility* (Griebel & Oller, 2008) is based on the Austinian notion of illocutionary force—when a signal can be used with different illocutionary forces on different occasions, it can be said to be functionally flexible. This capability is argued to be a critical foundation for language (all words and sentences of any natural language can be used with different illocutionary forces on different occasions—even performatives pose no problem to this claim in the case of mature speakers of language because they can be produced, for example, in pure practice or in exemplification). Furthermore, recent results illustrate that human infants show *functional flexibility* with prespeech vocalizations by three months of age, long before they show evidence of *semanticity* (Oller et al., 2013). It remains uncertain that *functional flexibility* ever occurs in animals in the wild—the requisite observational research has not been done to determine its existence. So far the best that can be said is that many animals can show usage of the same signal type in different “contexts”, such as travelling, eating, lounging, etc. But situational context bears only an indirect relation to

function, and indeed the very same communicative function can be transmitted in multiple situational contexts (aggression for example can be expressed while traveling, eating, lounging, etc.; Rendall et al., 2009). Context variation in the usage of signals cannot thus illustrate *functional flexibility*, and so far the human infant at not later than three months has shown far greater capability in this domain (with positive, neutral, and negative affect and illocutionary import being transmitted with each of several prespeech vocalizations) than has been reported for any animal in the wild. At the same time, *functional flexibility* appears to occur in label usage of a variety of animals enculturated with humans. In fact, in accord with the natural logic, it is a requirement of semantic lexemes (or labels) that they show *functional flexibility*. If the word “dog” is to be judged a semantic lexeme for a sender, it must be possible for the sender to use it to denominate a dog, to ask for a dog, to deny that a particular animal is a dog, to correct someone who calls a wolf a dog, and so on, all using the word “dog”.

Of course the intended illocutionary force of a word or sentence can be often signaled for the receiver by the sender’s intonation or other prosodic features on different occasions of word or sentence production. Yet while utterances may differ in intonation, they can share the same phonemic sequence in each case, which allows the invocation of the same semantic categories. For example, the word “dog” with different intonations could transmit different illocutions (one an answer, one a question, one a demand, and so on). In addition it is possible to use a word with the same flat prosody on different occasions, and for the illocutionary force to be different under the influence of contextual factors such as previous verbal information and/or situation. For example, suppose one says “what kind of track in the snow is that?” and you respond “dog”. The utterance might be an answer and an act of naming (illocutionary forces). You could use the same intonation when saying “dog” in response to the assertion, “that’s a wolf”, and it would be a correction in addition to being an act of naming (also illocutionary forces). In some southeast Asian restaurants you might point to an item on the menu and say “dog” (again with the same intonation), and you might be ordering your dinner.

4) **Serial ordering, recombination.** There are two ways to view *recombination* in human vocalization and language. On the one hand we recombine syllables or segments of speech *could* form new potential words or sentences—a purely phonological or phonetic act. On the other hand we recombine existing morphemes, words, or phrases (composed of particular combinations of syllables and segments) to form new propositions, sentences, and paragraphs—a semantic act. The latter kind of *recombination* is a requirement of syntax, where meaningful units of language such as words are produced in combinations that can yield different propositional meanings based, for example, on word order. “Dog bite” can mean something different from “bite dog”. In both cases the words have triadic referential content. On the other hand, meaningless combinations of syllables can be recombined as well (ba di gu vs gu di ba), but they do not produce new semantic content unless the community of users begins to attach them systematically to meanings. In the main text, we refer to observations indicating that semantically significant syntactic *recombination* occurs in some human-trained animals, but has not been shown convincingly to occur in animals in the wild (for a contrary argument see Clay and Zuberbühler, 2011).

In contrast, both songbirds (Searcy & Nowicki, 1999; Verner, 1975; Yip, 2013) and humpback whales (Helweg, Frankel, Mobley, & Herman, 1992; Payne & McVay, 1971; Winn & Winn, 1978) in the absence of human training have been shown to produce *recombination* of the phonological or phonetic type. Such sequences of animal syllables sometimes show internal structure and hierarchy (see review in Yip, 2013). The function of the variable sequences of

sounds produced in such cases in the wild appears to be display for both mating and/or territorial marking. We know of no such displays in the wild that, however, involve *semanticity* in the sense defined within the natural logic.

4) *Cultural transmission.* Our definition of *cultural transmission* is similar to that of Hockett. No one doubts of course that human language is culturally transmitted both within and across generations, but questions exist about the nature of *cultural transmission* of communicative signals as it may occur in other animals. In the case of humans, teaching as well as learning and cross-generational transmission are all involved. Birdsong is probably the most well-studied possibility for culturally-transmitted communication in nonhumans. Clearly many birds show vocal learning. Some researchers have pointed out that, like humans, birds have innate predispositions towards species-specific vocalizations, although other vocalizations can be acquired. Both humans and many birds have sensitive phases during which learning proceeds most readily, but again, flexibility exists depending upon the form of input, and some birds, such as parrots, learn throughout their lives, as do humans. Vocal learning requires auditory input for acquisition in both humans and birds, and both have specialized neuroanatomy and genetic bases for their behavior (review in Moorman & Bolhuis, 2013).

As noted earlier, however, there has been no demonstration that avian systems in nature involve *semanticity*—that is, the transmission of referential labels or lexemes—and thus there has also been no demonstration of the ability to transmit such knowledge culturally. One might propose such transmission involving crows in which transmitted recognition of dangerous humans (those wearing a particular mask) via scolding has been shown to progress both vertically (to young) and horizontally (to cohorts) over a 5-year period (Cornell, Marzluff, & Pecoraro, 2012). But as with the attempt to illustrate functional referentiality in monkeys and other animals (see above under *semanticity*), the crow report is subject to a non-semantic interpretation—crows remember dangerous people, produce scolding (an illocutionary force rather than a semantic message) when the dangerous person appears, and other crows learn to scold when seeing that person. This behavior involves learning to whom scolding should be directed, but not learning to name a person (which would be a semantic achievement), or learning a label to represent a person to scold on one occasion but simply to name on another. One clear way to recognize the limits of the report on the crow learning is that after human-trained learning of a label, as has been shown to occur in some animals, the animal should be able to inform someone of the name of the person without scolding. The crow report suggests illocutionarily-bound learning and thus not *semanticity*.

SM2: Species of particular interest in language-approximating behavior

Our selection of species to discuss in the article is based primarily on available relatively well-documented (see SM3) observational and experimental data, especially related to human training of animals raised from early infancy. We have pursued the expressed purpose of evaluating effects of human enculturation. Very few such studies exist because they are expensive, they often have required commitments of many years from the trainers and their families, and because some of the most dedicated human participants have come to feel morally bound either to cease training their animals or to withdraw from attempts to publicize their work in academic venues, because they view the animals as friends with desires and needs that supersede those of the academic community. Both Fouts and Patterson are among the salient

players in this field who have expressed such reservations. Furthermore, animal rights activism and increasing governmental regulation has imposed serious limits on such research.

The most important of the reasons we have only fragmentary data about language-approximating skills in animals is perhaps the demands in cost, time, and dedication to the project. Acquiring evidence for referential labeling in an animal appears to require raising it from infancy—in some instances as a near member of the family—and devoting almost as much attention to it as to a child. Not many scientists are willing to dedicate a good portion of their lives to such training. For these reasons, the kind of research we report on is fragmentary (we are lucky to have the reports we do have), and it appears to be dying out.

Overwhelmingly, then, the reason we primarily report on great apes, dogs, pinnipeds, dolphins, and parrots is that these are the species with which the most intensive language training has been done. One might wonder why, for example, songbirds or humpback whales (who show extensive capabilities for *recombination* of syllable-like elements, see above) have not been extensively included in this sort of work. With songbirds the key reason may be that their lifespans tend to be much shorter than in the case of parrots, yielding less potential learning time. With humpback whales the key issues are obviously the difficulty of observation in the water environment, the sheer size of the animals, and all the problems attendant to captivity for whales of any type.

Additional studies could not be considered in the main text due to space limitations. A few may be worthy of mention here: 1) Sign vocabulary and syntactic recombination in gorillas and orangutans (Patterson, 1978; Patterson & Matevia, 2001; Miles, 1990); these, however, fail our criteria of peer-review and jurying (see below); 2) receptive vocabulary learning in dolphins (Herman & Forestell, 1985); and 3) symbol categorization in pinnipeds (Kastak et al., 2001; Schusterman & Kastak, 1993).

SM3: On the question of reliability of the reported findings: The importance of peer-review and jurying

The research reviewed in our article comes from a variety of sources, some of which were peer-reviewed, juried, and published in respected journals. Others of the sources were not juried, but there are, we think, good reasons for examining those results in any case, as we will explain. Of course every body of research needs to be evaluated for reliability whether it is peer-reviewed or not, because there are numerous well-known cases of peer-reviewed articles that have turned out to be wrong or even fabricated. Still, we agree that it is preferable for all research to be subjected to scrutiny and to jurying when possible.

Why then consider any findings that have not been peer-reviewed and juried? First there is a long tradition of book publication (and articles in such books) where peer-review occurs, but where blind jurying is not involved, a sort of intermediate level of review. Authors of such books have the benefit of commentary from peers, but they usually know who the peers are, and publication may or may not be dependent upon making adjustments to satisfy concerns of reviewers. Very often theoretical articles and interpretive reviews of literature are published in books under just such intermediate peer-review circumstances, and several articles of this sort are cited in our article. There have also been many significant cases of empirical reports occurring primarily in edited volumes, and often it is not clear what the process of review may have been. In particular, we have extensively cited work on chimpanzees from an edited volume

by Gardner, Gardner, and Van Cantfort (1989), and especially articles in the book by the Gardners and by Fouts. Although not juried (and we do not know what, if any, peer review may have occurred), the volume includes extensive descriptive information about the methods and results of the long-term studies (especially with Washoe and her adoptive son Loulis) not available elsewhere. Our decision to discuss this work is prompted in part by the fact that no similar study appears likely ever to be conducted again and, importantly, because much of the work summarized in the edited volume was indeed juried for other publications (B. T. Gardner & Gardner, 1985; R. A. Gardner & Gardner, 1969, 1984; R. A. Gardner, Van Cantfort, & Gardner, 1992; Fouts, 1972, 1973; Fouts, Chown, & Goodin, 1976; Fouts, Fouts, & Schoenfeld, 1984).

Our decision about what to include in the review was measured in each case. We resisted extensive reference to or citation to works of Patterson regarding the gorilla Koko, who may indeed be an important example of animal language learning, precisely because there has been, in our view, too little peer-review of the work. Similarly we feel justified in our emphasis on the importance of the work with Grey parrots in part because of the long-term history right up to present time of juried publications associated with that work (including those cited in the main text and, for example, Pepperberg, 2002; 2006; 2012; Pepperberg and Carey, 2012; and Pepperberg & Hartsfield, 2014). Further, the work on language-training with parrots is ongoing. Work with apes is dying out, as can be seen by noting the years in which publication occurred for the most important items we have cited. Work with dogs is ongoing, but it has the limitation of focus on receptive learning of language-like labels, with no obvious prospect for production learning on the horizon.

SM4: Phonological or phonetic awareness in Alex

The capacity for something akin to phonological or phonetic awareness in the Grey parrot Alex is suggested by two sets of examples. First, significant portions of Alex's solitary practice (in the absence of any humans) involved production of syllables and syllable sequences that appeared to constitute rhyming practice (e.g. "green, cheen, bean"; "mail, banail"). Using the phonologist's terms "onset" and "rime", we could say that, in this rhyming practice, onsets (Alex's versions of initial consonants and consonant clusters) were varied, while rimes (Alex's versions of vowels or diphthongs and their following consonants or consonant clusters) remained stable, those rimes pertaining to the ends of previously learned labels (Pepperberg, Brese, & Harris, 1991). It thus appears that Alex had acquired categorical distinctions along with the ability to construct rhyming minimal pairs based on his human models of words. Second, when deriving new labels (e.g., "spool" and "seven"), he seemed to pull apart and put together previously learned speech-like acoustic segments, and his initial attempts ("s...wool"; "s...one") sometimes employed a pause as a place filler. Later he would insert additional acoustic elements that simulated the sound of labial or labio-dental articulations for the "p" in "spool" or the "v" in "seven", and adapt the vowel-like sounds so that the productions were quite intelligible versions of "spool" and "seven". He thus seemed aware of the need to develop the words to the point where they seemed to have the right number of syllables and an adequate rendering of all the required acoustic segments (Pepperberg, 2010).

SM5: How far back in evolutionary time do conserved cognitive processes relevant to language-approximating behavior go?

One conserved cognitive process relevant to *semanticity* appears to go back at least as far as the connection between mammals and birds. This speculation is based on the evidence reviewed in the main text, and is based on the assumption that *semanticity* requires, at the very least, pairings between word-like symbols and concept-like categories. This presumably ancient foundational association capability, which is necessary though far from sufficient for *semanticity*, has been demonstrated for reception in a variety of species. This most primitive aspect of *semanticity* can be attained with nothing more than learned linking of one object with another object. For example, pigeons in an operant conditioning paradigm learned to peck at 16 arbitrary lexigrams (called “pexigrams”) in the presence of 16 sets of 12 different pictures, each set consisting of entities representing the categories the lexigrams were supposed to symbolize (Wasserman, Brooks, & McMurray, 2015). The findings are intriguing because neural mechanisms of this type of associative learning may be present in a wide variety of animals. It is important, however, to emphasize that although a neurally-based association can be established this way, the contingencies at stake in learning by the pigeons were fundamentally different from the kinds of contingencies we presume to occur in human infant learning of associations between symbols and concepts in the process of language acquisition. Human infants hear language over many months and engage in social interaction about objects and entities with their caregivers, eventually learning that words and the entities they represent constitute referential terms, that is, names for the entities. The pigeons in the research, on the other hand, merely pecked to get a reward and presumably had no sense of the referentiality of the pexigrams. Even humans trained for associative learning in a paradigm of pure operant conditioning may fail to gain any sense of referentiality. Indeed, when Lenneberg taught college students to manipulate plastic chips (lexigrams) with respect to objects via the operant system Premack had used to teach the chimpanzee Sarah, the results suggested that the students did not understand the procedure to be anything but a way to solve a series of problems; they did not seem to conceive of it as referential communication (cited in Nottebohm, 1973).

Semanticity clearly requires more. Consider the fact that in addition to the initial step of association, children must learn that words are not just associated with a class of observations, but that they analytically refer to coherent concepts encompassing the classes of observations (or entities), and that these concepts are invoked any time the words are produced. Children must also learn to *use* the words referring to the concepts productively and to do so with *functionally flexibility*, and not just to serve a single illocutionary function. Savage-Rumbaugh (1986) emphasized that early operant conditioning of great apes to associate lexigrams with pictures had failed to yield flexible usage of the lexigrams. Similarly the learning of pexigram-picture pairings by the pigeons in the Wasserman et al. study meets none of these additional requirements, and so only shows a very preliminary aspect of *semanticity*, that of receptive association.

In contrast, animals from Grey parrots to great apes raised in more natural human-interactive environments appear sometimes to achieve the other requirements of *semanticity*, including learning of symbol-concept pairings, production of the learned symbols in appropriate circumstances, and *functional flexibility* of usage. Thus many such animals have learned to

produce the learned symbols as well as respond appropriately to them, communicating with others through the shared system of symbol-concept pairings.

Because the occurrence of at least limited receptive *semanticity* after human enculturation shows quite a spread among mammalian groups, we tend to consider the occurrence in parrots as homologous rather than analogous. Researchers such as Jarvis et al. (2005) argue that the cortical-like areas responsible for vocal learning in birds derive from the same pallial areas as the cortical areas for language acquisition in humans.

We have not been able to find a simple common denominator among the species that have been trained successfully for receptive *semanticity*. Alex, the Grey parrot, proves that a large brain is not required. The California sea lions show that long-term social bonds are probably not necessary. Is living in a complex 3-D environment (i.e. tree tops, open ocean, etc.) a requirement, or does the animal have to be a versatile generalist or a cunning predator? The answer is no on these issues as well. Examples of receptive label learning in animals with human training seem to be found in a very wide variety of taxa and life styles. That range suggests that with adequate investment in enculturation, we might find that quite a variety of additional species could show the same language-approximating capabilities as the ones about which we know already. The range suggests again that learning referential labeling at the receptive level does not require language-specific evolved mechanisms but is based on general mechanisms that have been found in mammals as well as birds, and may occur in other animal groups as well. So, at this point, we speculate that at least in the case of receptive *semanticity*, the underlying capability that can be activated with human enculturation appears to be homologous rather than analogous.

Similar arguments about conserved cognitive capabilities underlying *displacement*, *functional flexibility*, and *recombination* can be constructed because at least human-trained apes and parrots have been found to show them all. The argument for *cultural transmission* is less well-supported by the evidence, but suggestive empirical support has been reported at least in the case of chimpanzees.

SM6: Interactive learning in the wild

Even in nature, interactive learning can enable acquisition of heterospecific communication. Baptista, Morton, & Pereya (1981) documented a Lincoln sparrow incorporating song elements of neighboring white-crowned sparrows into its repertoire; in contrast, when trained in isolation in laboratory settings with tapes, birds such as white-crowned sparrows consistently ignored all but their species-specific input (Marler, 1970).

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