

Recursion in Fixed Motor Sequences

Towards a Biologically Based Paradigm for Studying Fixed Motor Patterns in Human Speech and Language

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Abstract. It has been argued by prominent linguists that recursion as found in natural language may be reliant on human-specific cognitive and neural mechanisms. In this article, I seek to challenge this notion by comparison between the motor properties of human language and two well-studied cases of fixed action patterns with recursion-like properties, birdsong and rodent grooming behaviour. I outline a compelling case for the profound similarity of these behaviours at a cognitive and motoric level by appealing to comparative neuroanatomical studies and work in behavioural genetics with the goal of providing a common framework for the study of recursion in fixed action patterns.

Keywords. Language, Motor Coordination, Recursion, Fixed Action Patterns, Birdsong, Rodent Grooming, Basal Ganglia

1. Introduction

Fixed action patterns are sequences of stereotyped motor behaviours elicited in response to a stimulus present in an organism's environment. Once initiated, these patterns of motor behaviour progress to completion without reference to feedback from the consequences of the actions' performance [14]. Typically, these behaviours are governed by highly specialised neural structures. A classical example of this physiological scaffolding of an innate behavioural response is present in the escape response in squids. In the case of the squid's escape response, two large neural ganglia near the base of the mantle cavity combined with large tubular unmyelinated axons radiating into the mantle cavity, enable the rapid transmission of electrical impulses in response to a perceived threat in the environment. These structures facilitate a series of quick muscular contractions which expel a jet of the water from the squid, propelling it through the water in a brief burst of rapid movement [15]. While some fixed action patterns can be classed as wholly innate, present in organisms from birth, others are taken on as the result of motor learning and may display complex environ-

mental and developmental substrates. The ethological study of these neurologically scaffolded patterns of action stands to grant insight into the interplay between nature and nurture at the level of neurophysiology.

Though this framework is generally applied in ethological studies of problems such as mating dances, escape responses, hunting behaviours and the like, it is worth considering that the motoric processes of language production share much in common with these behaviours. Language, like any of these triggered responses involves the precise coordination of motor resources. The gestures of speech, like the escape response of the squid, are stereotyped and subject to motoric constraints on the degrees of freedom in their realisation. A phoneme, for example, is constrained to both a specific place and manner of articulation with some limited possibilities of allophonic variation, both of which can be cast in motoric terms as in the gestures of the tongue and the movement of the voice box [22]. Furthermore, the use of fixed action patterns for communicative stuff is not unknown in nature. For example, vervet monkeys make alarm calls in response to the detection of eagles, leopards and snakes in their immediate surroundings for the purpose warning other individuals who might be in the vicinity [8]. In parallel with human language, these calls display a developmental time course in which juveniles' call repertoire comes to mirror those of adults in the individual's locality.

Yet, unlike these very basic communicative capacities, however, human language has an infinite productive capacity as a result of a property known in linguistics as *recursion*, the ability to embed equivalent computational functions within functions of the same type. This incredible capacity has given rise to insistence in linguistics that recursion exists as a human-specific cognitive property [9]. This assertion opens the way for ethology to make a meaningful direct contribution to the study of human language. In this paper, I seek to argue that the property of recursion is neither a human-specific aspect of cognition nor of motor control. In order to accomplish this, I will examine research findings on two compelling examples of fixed action patterns with recursive capacities, birdsong and rodent grooming behaviour, highlighting critical commonalities in their neural underpinnings, developmental time courses and environmental substrates.

2. Recursion in Human Language

Before delving into these cases, it is worth examining what exactly is meant by recursion and why it occupies such a central role within the canon of modern generative linguistics. Recursion at its most essential level can be defined as a computational procedure which either calls itself or an equivalent type of function [6]. Embedding sets within other sets necessitates keeping track of long-distance dependencies between these sets. Within natural language, this capacity manifests in two distinct

ways across all languages, tail embedding and centre embedding. Consider the following examples of each process;

Tail Embedding (1)

“The teacher knows the doctor.”
“The teacher knows the doctor who works with the lawyer.”
“The teacher knows the doctor who works with the lawyer who speaks Hebrew.”

Centre Embedding (2)

“The teacher who the doctor knows plays chess”
“The teacher who the doctor who the child visited knows plays chess”
“The teacher who the doctor who the child who loves books visited knows plays chess”

These are two profoundly similar operations which operate by distinct sets of rules. In the first case, equivalent phrasal components nested within a single phrase head. This pattern could be represented as AABB, in which a single phrase, AA, takes as its argument another equivalent item, BB. In the second case, phrases are nested within another by the pattern ABBA. While this phrase may be awkward on page, it is readily parsed by the listener from reliance on prosodic cues. In this case, complete phrases are embedded within another phrase to which speaker and listener are able to keep track of long distance relationships between the components of the over-arching phrase structure. The ability to parse these computational relationships requires a fit for purpose cognitive architecture. This property of linguistic syntax allows for the infinite productivity of human language, the capacity to produce an infinite number of grammatically correct sentences from a finite set of components. The upper limits of the length of grammatical sentences formed utilising these processes is determined by the working memory of both the speaker and the listener, not by computational constraints. It is generally accepted that this property is present within all natural languages, though some linguists take issue with this assessment [9].

3. Ethological Cases of Recursion in Fixed Action Patterns

Similar processes which require some facility with the same types of long distance relationships and structural hierarchies of computational components may be shown in non-human species. Like language, these behaviours require not only the cognitive capacity to handle computational relationships, but also a high degree of precision motor control to articulate.

The first of these instances I shall consider is the structural properties of birdsong in vocal learning species. Constraints on the structure of learned birdsong have been

likened both to computational, syntactic parameters of human language and to the articulatory constraints on human speech imposed by the speech organs [13]. Furthermore, it has been asserted that birdsong contains a hierarchical scheme for the embedding of elements [12]. As with the sounds of human speech, bird vocalizations, though diverse in nature, are composed of long series of small sets of iterative fixed action patterns producing what might be described as warbles, rattles or whistles [12]. Further reminiscent of the gestures of human speech, these articulatory gestures seem to also vary in place and manner of articulation [7]. Elements of Zebra Finch song, for example, can be voiceless producing rhythmic percussion while others can be voiced and result in melodious tunes [3]. Beak gape and expansion or contraction of the oropharyngeal-oesophageal cavity can further alter the iterations of these motifs [3]. Therefore, there exist meaningful comparisons with human speech both at a syntactic level and at an articulatory level.

Seminal work in this regard has centred around the training of captive birds to learn novel lengthy songs comprised of these discrete, iterative motifs. For example, it has been demonstrated that European Starlings are able to acquire syntactically well-formed strings including patterns which include centre embedding [12]. This was attested to with the training of birds to recognise finite-state like constructions, such as AB, and context-free like strings, such as ABBA, of articulatory gestures through operant conditioning. In this manner, birds learned the underlying organising principles of the two types of constructions [12]. One might object to these conclusions on the grounds that the birds may have been reliant on other strategies such as rote memorisation in order to classify these probes. However, doubt is cast upon this potential analysis as birds were shown to be significantly less proficient in correct classification of agrammatical strings.

Compounding these observations of structure in birdsong, rodent facial grooming exhibits distinct structural properties similar to those of human language which have been likened explicitly to the syntax of natural language [16]. Robust rules of sequential and hierarchical organisation of gestures have been attested in ways which mirror the syntax of natural language [16]. These rules include formulae for how individual paw strokes can be combined into larger units of stroke patterns and how these larger units of pattern can follow each other in sequence [4].

4. A Comparison of Relevant Neural Resources

As I have begun to outline the case for the potential similarity of the fixed action patterns found within rodent grooming, birdsong and human speech; all are constrained and governed by hierarchical structures of articulation of formation, all include a developmental time course in which juveniles acquire mature adult characteristics and all are presumably constrained by some species-specific genetic component; it stands

to reason that these items might have similar neurological underpinnings. In examining such fixed action patterns, it has been established that the basal ganglia have some role to play in their control [21]. After all, disorders of the basal ganglia result in profoundly impaired motor coordination as in Parkinson's Disease, Huntington's Disease, Cerebral Palsy and Tardive Dyskinesia. Within patients suffering from Parkinson's disease, there is a body of evidence which suggests that motor sequencing is more impaired than the elemental constituents of movement themselves [1]. Furthermore, the role of the basal ganglia may be underscored by the temporal disorganisation of speech often observed in patients suffering from disorders affecting them [2].

To clarify the relationship between these behaviours, it might be advantageous to compare disruption of mouse facial grooming patterns with stuttering, both of which can result from damage to the basal ganglia. In cases of stuttering, there is strong evidence to suggest that the mechanism involved is the inability of the basal ganglia to produce timing cues for the initiation of each sequential motor segment in speech [2]. This can be the result of damage due to trauma, pathological degeneration associated with ageing and by a variety of drugs [2]. In mice, grooming patterns can be similarly disturbed by the surgical lesioning of the same structure within the brain [1]. Such lesions result in prolongation of strokes, repetitions of previously preformed movements, premature termination of individual strokes and periods of inactivity within strings, highly reminiscent of the presentation of neurogenic stutter and stammer [1,2].

For these purposes, comparative anatomical investigation of these structures within humans, songbirds and rodents may also be especially beneficial. The basal ganglia are evolutionarily fundamental components of the cerebrum, the forebrain, and are recognisable in all vertebrate species [24, 25]. These structures are readily visible in the brains of the lampreys, the most phylogenetically ancient of vertebrate species alive today [24, 25]. They, together with the Thalamus, have significant afferent projections to and efferent projections from the cerebellum, a structure which has been implicated in motor control; in fine movement, in posture and in motor learning [5], [18] [24]. As such, these regions considered as a circuit likely have significant implications for the control of fixed action patterns [5], [24]. Within all vertebrate species, these systems are not only present, but well-developed. Therefore, comparison of the neurobiology of these fixed action patterns is a meaningful exercise at a neurological level in addition to the behavioural level.

It has been claimed that these circuits are specified in a gene called Forkhead box protein P2 or FOXP2 though this has not been well established [29]. This gene was once billed as a 'language gene' in the popular press after the examination of the KE family from England, a family with a heritable mutation in this gene and impaired linguistic ability [29]. The shape of the resulting speech deficit was made manifest in both grammatical and articulatory impairments, including difficulties with plosive

consonant and consonant cluster production and difficulty in syntactic comprehension and production [29]. However, the case for the FOXP2 gene being involved exclusively in grammar specific processes has been challenged as the gene mutation might also be tied to lower IQ scores as well [29].

Literature from ethological studies, however, contribute to a different picture of the gene's function. Orthologs of FOXP2 are well preserved across vertebrate species enabling knock-out studies of the gene's role [27]. Knock-out studies of FOXP2 in mice, for example, indicate that there exists some role for the gene in vocalisation, as the frequency of calls made by mice were reduced in individuals with gene knock-outs as compared to the normal population although structure of the mouse vocalisations was preserved in both groups [27]. Similar studies with Zebra Finches have resulted in observable differences in production of songs in male individuals with gene knock-outs, with observable deficits in song production when the birds were alone though not when singing to females, two similar motor behaviours with profoundly different social implications [28]). Though in these animal analogues there is little evidence to suggest impaired performance of the patterns of grooming and song, there is a case for the study of articulatory processes at the genetic level in FOXP2.

5. Vocal Sequence Learning in Rodents and Songbirds

The previous sections have pointed to some meaningful areas of comparison between the processes of human speech and these well-documented patterns of action at the level of motor control. However, a case still needs to be presented for the profound similarity of these phenomena at a cognitive level. Evidence to bolster such a claim might become available from a study of the learning of recursive patterns in each of the examined cases. To this end, a study of the relatively rare trait of vocal learning may be beneficial to our understanding of the issues at hand.

Vocal learning is the ability to learn to produce and modify sequences of sounds produced by the use of the vocal organs such as the mammalian larynx and the avian syrinx [28]. It is a fairly rare trait, attested within a small subset of closely evolutionarily related species, arising seemingly independently within the mammalian and avian phylogenetic classes. It is worth noting that vocal learning is entirely distinct from auditory learning, the ability to distinguish between perceptible sounds, a trait present in most hearing species [20], [28].

Examining the instances of avian vocal learning, it appears that vocal learning must have evolved at least two times or perhaps three times: within the *passeriformes* the oscine songbirds, the psittaciformes or parrots and in the trochiliformes or the hummingbirds [20]. A number of mutually-exclusive hypotheses have been proposed to explain these observations. Firstly, it is possible that the vocal learning trait evolved three independent times within the avian lineage [20], [28]. Another pos-

sible alternative is the gain and subsequent loss of the trait within the lineage on either four or nine occasions [20]. A final possibility is that all subsequent avian species from a common ancestor have the vocal learning trait to some reduced extent, neatly removing the necessity to explain independent trait losses [20], [28]. It is worth noting that independent gains and losses imply an absolute distinction between learning and non-learning. This reduction in trait capacity implies a spectrum of trait phenotypes.

On the other hand, within the mammalian phylogenetic lineage, complex vocal learning is known to have arisen three times, amongst cetaceans, humans and in bats [20]. However, limited learning capacities are far more widely distributed. Many species, such as non-human primates, are able to produce learned vocalisations as warning calls [28]. Cross-fostering experiments also confirm that mammals are able to acquire new sounds from their environmental peers [28]. However, unlike complex vocal learners, they are unable to modify these sequences.

The presence of vocal learning within rodent species is much more controversial, however. Adult rodents have been observed to produce ultrasonic songs as part of courtship sequences [17]. Juvenile rodents have been seen to produce similar ultrasonic calls when in distress from isolation or from coldness [17]. As seen in the patterns of vocal learning in other mammals and in birds, these songs follow a developmental time course. Isolation calls disappear in adolescent mice suggesting some degree of hormonal control. Adult vocalisations are only present within males and typically occur as a response to detection of female pheromones [17]. Recall that vocal learning in songbirds, a well-attested group of complex vocal learners, is only present within male birds and utilised as a courting mechanism. The degree to which learning plays a role within the development of vocalisations is also controversial. Deafened mice, for example, produce significantly louder vocalisations than their litter mates implying a degree of feedback within normal development of vocalisation. By contrast, within deafening studies of vocal non-learners, innate vocalisations appear far more similar to non-deafened peers. Interestingly, it has been demonstrated that mice lacking a cerebral cortex are able to exhibit normal vocal learning implying a significant degree of innateness in vocalisations [17].

For the purposes of this paper, however, it is worth highlighting the similarities between the rodent vocal learning and the ontogeny of grooming behaviour. The presence of some degree of vocal learning traits imply some common neural architecture and thus perhaps a reasonable grounds for comparisons with humans. These neural resources may be involved in the processes of grooming and may facilitate the degrees of complexity within.

6. Developmental and Environmental Substrates

A characteristic feature of human language is its complex developmental time course, characterised by the gradual acquisition of adult linguistic competence over a critical period spanning the early years of a child's life. Critical periods can be defined as an identifiable phase within an individual's lifespan in which there exists heightened sensitivity to the presence or absence of an experience [21]. Current consensus in the sciences of language asserts that language acquisition after puberty is qualitatively different to childhood language acquisition [26]. This claim is bolstered by evidence taken from three primary sources; cases of severely hampered language development in children who have been socially isolated throughout the pro-ported critical period, examination of adult second-language acquisition which suggest differences in accuracy and in rate of acquisition during adulthood and childhood and from studies of neurogenic language impairment which suggest greater potential for recovery during childhood than later in life. Interestingly, this manner of developmental time course is mirrored in the ontogenies of both rodent grooming and birdsong, perhaps bolstering the case for a degree neurological similarity between these processes and human speech at a motor level.

Songbirds appear to have a critical period which mirrors that of human language acquisition in more than a few aspects. It has been attested, for example, that during the first fifty days of life, white-crowned sparrows are far better at acquisition of tutored songs [23]. However, this trend is not present across all species with some, such as the canaries, maintaining plasticity across their entire lifespans and others, such as the starlings, being demonstrably better at song acquisition depending on season, perhaps in response to migratory patterns [19]. It remains unclear what the mechanism for the opening and closing of these windows of plasticity might be though perhaps comparative neuroanatomy might provide some clues [19], [21]. Plasticity also appears to be under the influence of androgens during the birds' lifespans. Juvenile male sparrows, for example, when castrated have been shown to develop song along a normal developmental time-course when observing tutors yet fail to crystallise song as adults [7]. However, when the same individuals are given testosterone, they readily make the transition from plastic to stereotyped song, suggesting the critical period is a function of physiological development [7]. These findings have been robustly replicated in chaffinches [7]. These findings are perhaps more understandable when acknowledging the profound differences in the teleology of birdsong and human speech; attraction and courtship of mates as compared to expression and communication. Highlighting this disparity is not to assert that there exist no meaningful grounds for comparison nor downplay the role of physiological development in human language acquisition, but to suggest that we are dealing with fundamentally unlike things.

Given these factors, it is also worth considering yet another parallel between birdsong and human language, namely the development of group-level dialects. The constituents of the mature form of any individual's song are limited to a subset of all possible articulatory features [3]. The particular incarnation of the mature form is dependant on birds which are highly dependant on the individual adults or tutors present within the juvenile's developmental environment. This conclusion is evident in the observation that birds of one species raised by another will acquire the songs of that species demonstrating further that mature song has a high degree of independence from any genetic constraints and is the result of a cognitive architecture [3].

These critical periods in rodent grooming patterns are not present in the same manner as in birdsong. In direct contrast to the trends observed in songbirds and in humans, rats raised in isolation will execute the same grooming patterns as their socialised peers[16]. Nonetheless, an interesting developmental time course is present in grooming ontogeny from which meaningful comparisons might be made with human language development.

Within the first two to three weeks of life, individual patterns change on a day to day basis and thus it is impossible to establish fixed categories of behaviour within this time frame [10], [16]. However, after this period, patterns emerge in two distinct trajectories. Firstly, the fine motor coordination improves; paw strokes which overreach the rodent's face are gradually decreased and strokes following incomplete contact paths are eliminated. Within the first few weeks, strokes are also localised exclusively to the face, gradually becoming extended to the rest of the head, neck and finally to the trunk [16], [21]. However, there are also seen changes which undergo a dramatic reversal in trend. There is observed, for example, a gradual restriction of forepaws contact paths followed by their re-emergence. The same trend can be observed in asymmetric grooming paths and in groupings of strokes in rapid succession [11], [16].

The simultaneous occurrence of these two disparate trends presents quite a puzzle in that, the classical view of development is gradual marked progress towards a particular goal. However, one might find a developmental linguistic parallel in humans by considering the period of over-generalisation during human language development during which children, having acquired the rules for verb formation, apply them superfluously to the formation of the past tense [26].

7. Concluding Remarks

Reviewing these parallel developments in neuroethology and in speech science, the case builds against the faculty of recursion as a human-specific property of cognition and motor control. Instead, we are left with a picture of a faculty shaped by the course of evolution which is expressed across species reliant on similar neural and de-

developmental substrates. Within this light, it is important for linguists to take these two distinct fixed action patterns seriously in order to better understand the neurological. When positing claims about the uniqueness of a faculty of human language. However, the question remains as to why humans alone have been able to harness recursion in order to build such a powerful communicative system as language. Such questions can provide fertile ground for a mutually enriching and productive interaction between the behavioural and biological sciences in the future. More broadly, the comparative study of fixed action patterns stands to provide an interesting object of study for the scientist of language as they provide a unique insight into the interaction between genes and environment, between neurophysiology and social structures.

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