Structured sequence learning across sensory modalities in humans and nonhuman primates

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Highlights

- Sequence processing probes cognitive abilities that are relevant to language
- In humans these abilities are subject to stimulus and modality-specific constraints
- Comparative work is starting to provide evolutionary insights into these processes
- Research in humans can guide future sequence processing work in nonhuman primates
- Understanding these abilities requires a cross-species and cross-modal approach

Abstract [120 words]

Structured sequence processing tasks inform us about statistical learning abilities that are relevant to many areas of cognition, including language. Despite the ubiquity of these abilities across different tasks and cognitive domains, recent research in humans has demonstrated that these cognitive capacities do not represent a single, domain-general system, but are subject to modality- and stimulus-specific constraints. Sequence processing studies in nonhuman primates have provided initial insights into the evolution of these abilities. However, few studies have examined similarities and/or differences in sequence learning across sensory modalities. We review how behavioural and neuroimaging experiments assess sequence processing abilities across sensory modalities, and how these tasks could be implemented in nonhuman primates to better understand the evolution of these cognitive systems.

Introduction

The ability to recognise and learn predictive dependencies between environmental events is critical to an animal's survival and is central to a wide range of behaviours. For example, statistical learning—the development of sensitivity to distributional regularities in an input—appears to be important for processes as diverse as linguistic processing [1] visual scene analysis [2], motor learning [3] and many other behaviours that require the prediction of future events [4]. An early suggestion was therefore that a single cognitive system for extracting statistical regularities might operate over a number of different domains [5]. In humans, however, direct comparisons across sensory modalities, or between different types of stimuli, suggest clear modality- and stimulus-specific constraints on how information is processed [6–8], pointing to differences in the neural systems that underpin these apparently similar behaviours ([9] and see Fig. 1).

Statistical learning experiments, including structured sequence processing tasks and artificial grammar learning paradigms, can be used to explore the ability to extract order-based regularities from sequentially-presented stimuli [10,11], (see [12] for a historical review). This approach has demonstrated that statistical learning abilities likely play a role in language acquisition [1,11] and syntactic processing [13–15]. Furthermore, comparative experiments have identified similarities in structured sequence learning across a wide range of nonhuman animals, providing insights into the types of sequence processing abilities that may have been evolutionary conserved and those which may have adapted to support language in humans (for reviews, see [16–18]). However, while both auditory and visual sequence processing have been studied in nonhuman animals, direct comparisons across modalities are lacking. Such comparisons will be critical in determining how closely the cognitive systems supporting auditory and visual sequence processing in nonhuman primates resemble those present in humans.

Understanding differences both between the species and across modalities can provide important insights about potential cognitive specialisations that occurred during more recent human evolution, and their contributions to the emergence of language. For example, while we might observe striking similarities in the responses of humans and monkeys using certain stimuli and particular tasks, it remains possible that very different patterns of learning may be observed across the species using different stimuli in another modality. Such differences would highlight not only those abilities that appear to be evolutionarily conserved in nonhuman primates, but might point to behavioural abilities and the underlying neural substrates which have functionally differentiated in more recent evolution, and their possible role in language. Identifying such potentially human-unique adaptations will be critical in understanding how humans diverged from other primates, and how language might be supported by the human brain [19].

In this paper, we summarise how sequence learning has been assessed across sensory modalities in humans, consider how data from nonhuman animals might be compared in similar ways,

and discuss how similarities and differences, across sensory modalities and species, might inform us about the cognitive and neural systems that support statistical sequence learning.

Constraints on sequence processing in humans

A wide range of studies using different stimuli and tasks have shown that humans can extract statistical regularities from a wide range of sequentially presented auditory or visual stimuli (summarised in Table 1). These tasks vary in complexity, from learning relatively simple predictive relationships between adjacent sequence elements, to more nonadjacent or long-distance dependencies between stimuli, or embedded patterns involving multiple overlapping nonadjacent dependencies (for reviews see [17,20,21]). However, there is some debate regarding whether statistical learning across sensory modalities is supported by a single amodal system or by multiple sub-systems that are subject to stimulus- and modality-specific constraints [9]. While some studies show similar sensitivity to transitional probabilities between stimuli on matched auditory and visual tasks [22] (see Box 1, Point 1), others report substantial differences. Similarly, although early work identified transfer of learning from one modality to another [5] (Box 1, Point 2) subsequent studies have suggested that transfer may be task and structure dependent [23]. In particular, where tasks are based on learning specific relationships between individual stimuli (e.g. the nonsense word 'biff' predicts 'cav'), transferring the relationships to a new modality requires learning the mappings between these two stimulus sets, and therefore is unlikely to occur easily or implicitly. By contrast, more abstract representations or rules could be more easily transferred between stimuli or modalities as learning is not linked to any specific stimulus [24], but instead relates to patterns of stimuli (for example element repetitions [23,25]). Nonetheless in certain tasks information from one modality can influence learning in another (Box 1, Point 3). For instance, the addition of auditory cues can aid visual sequence learning [26], and bimodal audio-visual presentation of the same sequence structure results in better performance than unimodal presentation [27]. However, in humans there is little evidence that individuals' sequence learning abilities are correlated across modalities or perceptual domains, further highlighting stimulus-specific constraints on sequence processing [9,28,29] (Box 1, Point 4). Finally, neuroimaging work (Box 1, Point 5) can investigate whether the same brain regions are recruited for sequence learning across modalities. Current evidence paints a complex picture of sequence processing in the brain (Fig. 1) and is therefore considered in more detail in subsequent sections of this review. Taken together, this data suggests that there is unlikely to be a unitary sequence processing mechanism that is tied, for example to general cognitive abilities (for a review see [30]).

Sequence learning in primates

In humans, sequence learning is observed reliably across a wide range of tasks and sensory modalities, albeit with input-related constraints. It is therefore unsurprising that similar learning is also observed in other species. The study of nonhuman animals, particularly nonhuman primates, has become a valuable way to investigate the evolutionary origins of cognitive and neural systems that might be related to those that support language in humans [31]. Nonhuman primates have been tested

with a wide variety of different sequence processing tasks [32–37]. Cross-species studies can inform us about unique adaptations, including specialisations that have been recruited for language in humans [38], as well as similarities between humans and other primates (see Table 1) [16,22,33,39,40]. Behavioural and neurobiological similarities in sequence learning abilities between humans and other primate species, suggest that certain sequence processing abilities appear to be evolutionarily conserved [40–42]. However, there is a lack of evidence about how similarly these systems might operate across different inputs or sensory modalities, and thus little information as to whether the variability observed in human sequence learning across different modalities is conserved in nonhuman animals.

In a recent experiment, we directly compared auditory and visual sequence learning in humans and monkeys [22] (see Box 1, Point 1). This study found similar patterns of responses to a range of sequences of auditory and visual stimuli, suggesting these processes might be supported by similar computations [22]. In humans, further insights into the domain-general nature of sequence processing have been provided by assessing whether learning about one set of stimuli can be transferred or generalised to novel stimuli or to a different modality (Box 1, Point 2; Table 1). However, similar experiments have rarely been performed in nonhuman primates. Some studies have shown that nonhuman primates generalise learning to previously unheard, novel sequences comprised of familiar stimulus elements [16,32,43], but to date no studies have tested transfer to new stimulus sets or across modalities. There is some evidence of cross-modal influences, whereby the presentation of sequences of auditory stimuli might have an impact on visual sequence processing (Box 1, Point 3) in chimpanzees. In a two-alternative forced-choice experiment, chimpanzees were trained to select symmetrical rather than asymmetrical sequences of shapes (i.e., XYX vs XYY) [35]. In testing, the presentation of the visual stimuli was preceded by a previously unheard auditory tone sequence that was either congruent (symmetrical) or incongruent (asymmetrical) with the visual sequence the animals were trained to select. The presentation of incongruent auditory stimuli caused an increase in reaction times, delaying their selection of the appropriate visual sequence [44]. This demonstrates that properties of the auditory stimuli (i.e., the presence or absence of element repetitions) produced some interference in visual sequence processing, suggesting at least some cross-modal interactions in great apes. However, the ability to generalise or transfer statistical regularities has yet to be fully established in nonhuman primates.

In humans there is growing interest in assessing the patterns of individual performance across sequence learning tasks (Box 1, Point 4; for discussion see [9] and [30]). However, this line of enquiry has yet to be studied it nonhuman primates. Most primate studies use small sample sizes or use methods that are hard to replicate in the visual modality [37] - though also see [45]. Although, an opportunity could be provided by recent work in baboons in which voluntary engagement systems have been shown to produce thousands of trials worth of a data from many animals [46,47].

Nonhuman primate research can provide invaluable insights into the evolution and neurobiology of the systems that support sequence processing. However, in comparative research

there are often unavoidable methodological and cognitive differences between the species which must be considered [38]. For example, nonhuman primates (and human infants) are often passively exposed to sequences, while adult humans may be asked to attend to the stimuli, possibly resulting in different patterns of learning. Similarly, humans can be instructed how to respond, while it is often more practical to rely on animals' natural orienting responses. Alternatively, animals might be trained using an operant task for tens of thousands of trials [46,47], making direct comparisons to humans difficult. There are also unavoidable cognitive differences between humans and other species. Humans may verbalise or label stimuli, using language to help process stimuli in ways unavailable to nonhuman primates. They may also try and infer the goal of implicit learning experiments, and respond in the manner that they think the experimenter desires, which is less likely in nonhuman animals. These differences must be considered when designing comparative experiments and interpreting their results, particularly when cross species differences are observed.

Nevertheless, the existing behavioural evidence from nonhuman primates indicates that, as in humans, sequence learning can occur in the auditory and visual modalities, and in primates we observe similar responses across different types of input [22] as well as some interactions across the modalities [44]. However, initial human studies also focused on general similarities in statistical learning. It was only when these capacities were probed in more detail that evidence of modality-specific constraints on processing emerged. As such, the evidence suggests that humans do not possess a single, domain-general system that operates identically over all auditory and visual sequences. Rather the system appears to be more complex and operates under modality and stimulus-specific constraints. If we are to compare humans and monkeys to draw evolutionary inferences, we must be careful to compare like to like and not to over-extrapolate from one modality, task, or type of stimulus to all others. Additional evidence is required to understand if nonhuman primates, like humans, show sequence learning abilities that vary both qualitatively and quantitatively across modalities [6], and if these differences were important for the evolution of language.

Sequence learning in the brain: across modalities and species

Human neuroimaging experiments using sequence learning and artificial grammar paradigms have identified a broad network of regions involved in sequence processing (see Fig. 1). Some of these regions are primarily engaged in only the auditory or visual modality, while other areas are involved in sequence processing regardless of stimulus modality. In particular, a number of regions such as the inferior frontal gyrus including the frontal operculum [20] and Broca's territory tend to be engaged by sequence processing tasks in both the auditory [42,48] and visual modality [49,50] (see Fig. 1 and Table 2). This evidence suggests that overlapping areas are involved in structured sequence learning across modalities, at least for certain tasks. Importantly, though, some of this overlap might be attributed to similarities in task demands and response types [20]. For example, comparisons across tasks that require identification of a violation to the sequence structure (see final column, Table 2)

could reflect similarities in general error detection mechanisms rather than just those which relate to the extraction of sequence-based regularities.

Recently, comparative fMRI experiments using auditory sequence processing tasks in both humans and macaques [42,43] have demonstrated that sequence violations produced activity in certain homologous frontal, temporal and parietal regions, particularly inferior frontal regions including the frontal operculum [43] (see Fig. 1). In this study, activity was also observed in the homologue of Broca's area in macaques, but not in humans, suggesting potential differentiation of this region [43] (for a review see [17] and also [42,51]). Visual experiments and direct comparisons across modalities have yet to be performed using primate neuroimaging, but these will be critical to fully understand the evolution of the neurobiological systems that support sequence processing (see Fig. 1).

While these fMRI studies can provide valuable insights into the neural substrates responsible for detecting sequence violations, it is also important consider other brain areas within the neural network involved in sequence processing. Primarily unisensory areas, such as primary auditory and visual cortex are also likely to play important role in these tasks (Fig. 1 and [2]) and processing that occurs within these regions is likely to have implications for operations that occur upstream, in higher cortical areas (see [9] for a review). In both humans and monkeys, direct recordings of neuronal responses have highlighted the role of auditory cortex during sequence processing [52]. This study identified both neurons that showed a preferential response to sequence violations, and others that responded to sequences that do not contain a violation [52]. These results indicate that even the earliest cortical regions are sensitive to the order of elements in a sequence (see also [53]). Although some studies have assessed processing in early visual cortex [2,54], as yet no study has directly compared how primary auditory and visual cortex respond to identically structured sequences. Experiments carefully considering the role of sensory cortices and their interactions with other brain areas including inferior frontal gyrus, either using direct recordings or neuroimaging techniques, are critical for understanding how different brain regions contribute to the processing of sequence information, and how this might vary across different stimuli or modalities (Fig. 1).

Conclusions

Understanding how the brain supports complex cognitive operations, like those involved in sequence processing, requires rigorous research to differentiate the mechanisms that have been conserved since our last common ancestor with nonhuman primates from those that have diverged. It is initially tempting to assume that similar patterns in behavioural data point to the presence of a single, domain-general cognitive or neurobiological system. However, in humans there is little evidence to support such a conclusion [9]. In primates, there is initial evidence for similar sequence processing abilities, both between humans and monkeys, and between auditory and visual modalities [22]. However, we should learn from the human work and not assume that identical processes are at play until we probe

exactly how (and how similarly) auditory and visual sequences are processed, both behaviourally and in the brain. Another key missing element is the potential role of development in the emergence of sequence processing skills in nonhuman primates. Our understanding of cross-sensory sequence processing in nonhuman primates is in its infancy, but by learning from work done in humans, future research may provide insights that are not possible in humans. These would not only improve our understanding of how sequence learning abilities evolved, but also the core neuronal computations and mechanisms which support them.

Box 1: Methods of assessing sequence processing across modalities

A number of approaches have been used to assess how sequence processing operates across different types of stimuli or sensory modalities, to provide insight into the nature of the cognitive and neural systems involved. These include:

1. Directly comparing learning of identically structured sequences across different stimuli or modalities.
2. Assessing generalisation of learning to new stimuli or transfer to another modality.
3. Investigating cross-modal influences, such as inhibition or facilitation of the learning of artificial grammars presented in different modalities.
4. Exploring correlations in individual performance across statistical learning tasks.
5. Studying the brain areas and networks engaged in processing sequences presented in different modalities.

Evidence from each of these different approaches can provide important insights into the system(s) that support sequence learning (see Table 1). However, the data must be carefully considered. For example, similar patterns of behavioural responses across modalities (e.g., [22]) might be suggestive of a single, domain-general system. Yet, it is also possible that this result arises from similar computational principles that are applied in different cognitive or neural systems [9]. Similarly, while a lack of transfer between modalities suggests some separation in auditory and visual sequence processing (e.g., [7]), humans may be able to generalise certain stimulus properties (e.g., presence or absence of repetitions) to novel stimuli, independent of the sequence structure. Evidence of activation in different brain regions across modalities (e.g., in auditory and visual cortex) can inform us about the (potentially modality specific) role of initial sensory processing on sequence learning. However, in cases where both auditory and visual stimuli engage the same brain areas, it is important to rule out other explanations, such as task-specific effects, before drawing conclusions about the domain-generality of the functions of these regions. For example, comparison across tasks that require identification of a violation to the sequence structure could reflect similarities in general error detection mechanisms rather than just those which relate to sequence processing. Relatedly, whether learning and testing occurs in an implicit or explicit paradigm is likely to impact how different neural systems are engaged [20,55]. Overall, sequence processing is likely supported by complex cognitive and neurobiological systems (Fig. 1). Understanding the nature of these systems requires us to carefully consider and interpret the data from several different sources to appreciate how stimulus- and modality-specific constraints might interact with more domain-general neural substrates or cognitive computations.

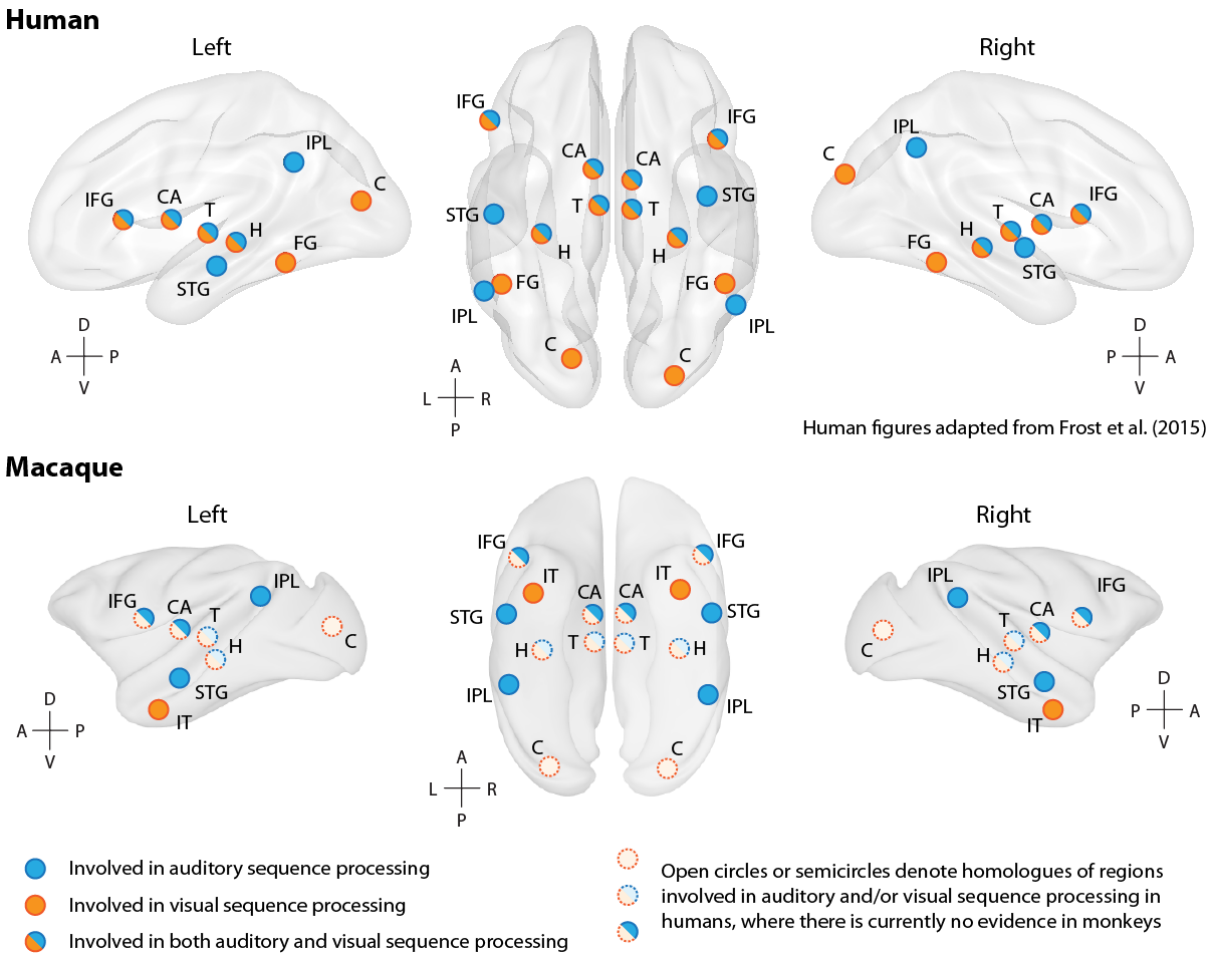

Figure 1. Brain areas involved in auditory and visual sequence processing in humans and macaques. Upper panel (adapted from [9]), shows key brain areas involved in auditory and visual sequence processing. Brain areas associated with modality-specific auditory and visual processing are shown in blue and orange circles respectively, and areas involved in domain-general processes in combined blue and orange circles. These tasks engage a broad network of areas, including areas that are both primarily unisensory, and those which are involved in both auditory and visual processing. It may be important to consider the contribution of each of these nodes to fully understand how sequence processing operates across modalities. This panel illustrates that a broad set of regions are involved in sequence processing tasks, but that these are not identical across modalities, challenging the idea of a "domain-general" sequence processing network in the brain. The lower panel shows the location of anatomical homologues of those regions identified in humans in [9]. Brain areas involved in auditory [42,43] and visual [56,57]sequence processing tasks in nonhuman primates are shown in filled blue circles. This highlights that, in the auditory modality similar activation is observed in humans and monkeys in a number of homologous regions (compare filled and half-filled blue circles in upper and lower panel), including IFG, STG, IPL and caudate. In monkeys, visual sequence processing has been measured in inferotemporal cortex using electrophysiological recordings [56,58] , although other regions are undoubtedly also involved. Therefore, homologues of the regions seen in visual tasks in humans are denoted by open circles with dashed lines, highlighting the need for further research into the role of these regions in the visual modality. The depicted regions are not intended to constitute an exhaustive set of brain regions sub-serving each domain in either species. Abbreviations: C, cuneus; CA, caudate; FG, fusiform gyrus; H, hippocampus; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; IT, inferotemporal cortex; STG, superior temporal gyrus; T, thalamus; A, anterior; P, posterior; D, dorsal; V, ventral; L, left; R, right.

	Experiment	Auditory Stimuli	Visual Stimuli	Artificial Grammar (AG)	Key Results
Humans					
Effects across modalities	**Conway and Christiansen, 2005 [6]**	Tones	Location	Two Reber-style AGs with probabilistic relationships between adjacent elements	Auditory > visual
	Conway & Christiansen, 2009 [59]	Tones	Textured squares	Reber-style AG with probabilistic relationships between adjacent elements	Fast presentation: Auditory > visual; Slow presentation: Visual > auditory
	Emberson et al., 2011 [8]	Nonsense words	Abstract shapes	Stream segmentation: high probabilities between elements that form 'words' (i.e. triplets of elements), with low probabilities between words	Fast presentation: Auditory > visual; Slow presentation: Visual > auditory
	Walk & Conway, 2016 [29]	Tones/ nonsense words	Abstract shapes / colour	Sequences consisting of both auditory and visual stimuli, in which each element could only be followed by one auditory or one visual element	No evidence of cross-modal learning or learning of cross-category dependencies
	Milne et al., 2017 [22]	Sound effects	Abstract shapes	Simplified Reber-style AG with probabilistic relationships between adjacent elements.	Similar patterns of learning across modalities. Visual performance > auditory performance
	Zimmerer et al., 2011 [60]	Syllables	Abstract shapes	A^nB^n AG with nonadjacent, embedded relationships between two perceptual classes of stimuli	No significant difference between modalities
Transfer between modalities	**Conway and Christiansen, 2006 [7]**	Tones	Colours / shapes	Two Reber-style AGs with probabilistic relationships between adjacent elements	Multiple AGs were learned simultaneously if presented in different modalities (no transfer occurred)
	Durrant et al., 2016 [61]	Tones	Location	Deterministic sequences with non-variable relationships between elements	After 24 hours consolidation, deterministic pattern in tones transferred to location of shapes
	Altmann, Dienes & Goode, 1995 [5]	Tones/syllables /nonsense words	Letters/ syllables	Two Reber-style AGs with probabilistic relationships between adjacent elements	Transfer from auditory stimuli to visual stimuli, and vice versa.
Cross-modal influences	**Mitchel and Weiss, 2011** [62]	Tones	Abstract shapes	Stream segmentation: high probabilities between elements that form 'words' (i.e. triplets of elements), with low probabilities between words	Simultaneous auditory and visual presentation. Learning only occurred in both modalities when statistical boundaries corresponded across modalities
	Mitchel et al., 2014 [63]	Syllables	Abstract shapes	Two Reber-style AGs with probabilistic relationships between adjacent elements	Automatic integration of visual information during auditory statistical learning
	Onnis and Thiessen, 2013 [26]	Italian syllables/tones	Letters	Stream segmentation: high probabilities between elements that form 'words' (i.e. triplets of elements), with low probabilities between words	Visual learning aided by auditory stimuli
	Robinson and Sloutsky, 2007 [64]	Syllables	Shapes and colour	Stream segmentation: high probabilities between elements that form 'words' (i.e. triplets of elements), with low probabilities between words	Statistical information in auditory stream influenced visual learning
	Seitz et al., 2007 [27]	Abstract sounds	Abstract shapes	Stream segmentation: high probabilities between elements that form 'words' (i.e. triplets of elements), with low probabilities between words	Audio-visual sequence learning better than unimodal learning
	van den Bos et al., 2012 [65]	Nonsenses words	Abstract shapes	Probabilistic nonadjacent dependencies	Nonadjacent sequence learning aided by cue from second modality

Correlations across tasks	**Siegelman & Frost, 2015 [9]**	Syllables/ computerised sounds	Abstract shapes	Either deterministic or probabilistic nonadjacent relationships in triplets of elements	No correlations between modalities
Nonhuman primates					
Effects across modalities	**Milne et al., 2017 [22]**	Sounds effects	Abstract shapes	Simplified Reber-style AG with probabilistic relationships between adjacent elements.	Similar responses across modalities
Transfer between modalities	**-**	-	-		-
Cross-modal influences	**Ravignani & Sonnweber, 2017 [44]**	Tones	Shapes	Symmetrical vs asymmetrical triplets of elements	Auditory pattern influences visual sequence processing
Correlations across tasks	-	-	-		-

Table 1. A number of behavioural approaches have been used to access sequence learning across modalities in humans (top panels) and these are outlined in Box 1 (Points 1 to 4). These include a range of different tasks and the stimuli sequences vary in complexity, assessing the learning of different types of sequencing relationships (for recent reviews, see [17,20]). In humans, these studies provide little evidence for the existence of a single 'domain general' sequence processing system, and instead highlight clear stimulus- and modality- specific constraints [9]. Moreover, there does not appear to be a clear link between the types of stimuli or the complexity of the sequences, and cross-modal effects or transfer across modalities. Fewer studies have assessed structured sequence learning across modalities in nonhuman primates (bottom panels). Initial results suggest some similarities across modalities. However, implementing some of the approaches used in human studies in nonhuman primate research will allow us to better understand the constraints under which the sequence processing system(s) operate across modalities and tasks, and how these compare to those observed in humans. This has the potential to provide valuable insights into the evolution of sequence processing abilities, highlighting both those specific abilities and cognitive processes that are evolutionarily conserved, and those which might have diverged and specialised more recently in human evolution.

Modality	Experiment	Stimuli	Artificial grammar	IFG activity	Contrast
Linguistic					
Auditory	**Cunillera et al., 2009** [66]	Syllables	Stream segmentation	Left	Sequences/random vs rest
	Goranskaya et al., 2016 [67]	Syllables	A^nB^n	None	Learners vs non-learners
	Karuza et al., 2013 [68]	Syllables	Nonadjacent	Left	Forward vs backward order
	Wilson et al., 2015 [43]	Nonsense words	Simplified Reber-style	Bilateral	Violation vs consistent
Visual	**Bahlmann et al., 2008** [69]	Syllables	A^nB^n vs $(AB)^n$	Left	Hierarchical vs adjacent
	Bahlmann et al., 2012 [70]	Syllables	A^nB^n	Left	Sequence vs counting
	Folia & Petersson, 2014 [55]	Letters	Reber-style	Bilateral	Violation vs consistent
	Forkstam et al., 2006 [71]	Letters	Reber-style	Left	Classification vs sensorimotor
	Friederici et al., 2006 [49]	Syllables	A^nB^n vs $(AB)^n$	Left	Violation vs consistent
	Hauser et al. 2012 [72]	Nonsense words	BROCANTO	Right	Consistent vs violation
	Kepinska et al., 2016 [73]	Nonsense words	BROCANTO	Left	Violation vs consistent
	Lieberman et al., 2004 [54]	Letters	Reber-style	Left	Consistent vs violation
Non-Linguistic					
Auditory	**Bekinstein et al., 2009 [48]**	Tones	Local Global	Bilateral	Global - local violation
	Wang et al., 2015 [42]	Tones	Local Global	Bilateral	Violation vs consistent
Visual	**Aizenstein et al., 2004** [74]	Shapes/ colours	Transitional probabilities	Bilateral	Pattern vs no pattern
	Bahlmann et al., 2009 [75]	Abstract shapes	A^nB^n vs $(AB)^n$	Left	Hierarchical vs adjacent
	Thiel et al., 2003 [76]	Symbols	Bigrams	Bilateral	New vs Old
	van Opstal et al., 2009 [77]	Symbols	Deterministic sequence	Left	Pre-learning vs post-learning

Table 2. Summary of fMRI sequence learning studies involving linguistic auditory and visual, and non-linguistic auditory and visual stimuli. Most, but not all, studies showed activity in inferior frontal gyrus (IFG), in Broca's territory and/or the frontal operculum. However, the same artificial grammars are rarely used across modalities, and studies frequently use different contrasts to measure different effects. Futhermore there are relatively few studies that use non-linguistic materials. Direct comparisons using the same artificial grammars across modalities are needed to better understand the neurobiological system that

supports sequence processing. Although a recent meta-analysis highlights the frontal operculum as the region most consistently implicated across artificial grammar learning studies [20].

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Annotations:

***Christiansen and Chater, 2015.** Suggest that the ability to process recursive structures in language derives from complex sequence learning skills evolved in the human lineage. Constraints on sequence learning is argues to have played an important role in the cultural evolution of linguistic structure, including the limited ability to process recursive constructions.

***Durrant et al., 2016.** Using a simple statistical learning task with deterministic sequences, transfer was observed from the auditory to the visual modality but only after a 24-hour consolidation period. Initial evidence is provided showing the relevance of consolidation for cross-modal transfer that requires further investigation using probabilistically structured sequences.

***Milne et al., 2017.** In the first study to directly test structure sequence learning abilities across species (human vs. macaque) and modalities (auditory vs. visual), the same artificial grammar was used to generate sequences of computer-generated sound effects or abstract shapes. Both species were sensitive to violations of the artificial grammar and showed patterns of responses were highly consistent across the two modalities. These data suggest that similar computations are likely to occur across modalities in the both human and nonhuman primates.

***Siegelman & Frost, 2015.** Human participants were tested on a range of statistical learning tasks using auditory and visual, verbal and non-verbal stimuli. The results found that performance was not correlated across the tasks showing that at an individual level statistical sequence learning abilities do not reflect a unified capacity.

***Walk and Conway, 2016.** In a multimodal sequence learning experiment subjects could not learn relationships between items of different perceptual categories or perceptual modalities. This study demonstrates that statistical learning can operate within but not across domains.

***Wilson et al., 2015.** Comparative fMRI was used to identify key brain areas in ventral frontal cortex which are similarly involved in auditory sequence processing in both macaque monkeys and human participants. In humans, this region is plays a role in syntactic processing. These results identify evolutionarily conserved neural substrates that are involved in sequence processing.