

PhD students doing a cumulative thesis have to publish 2–4 papers within 3 to 4 years. I have witnessed several cases where this has led to a clash of interest between the young PI, who wants the ‘important’ paper, and the PhD student, who needs those three publications to finish their thesis. I don’t know a perfect solution, but my advice to PhD students is to make sure that your supervisor knows what you want and that you have a thesis committee that can help in case of conflicts.

And concerning another development, I think that open access is a really good idea from the point of view that publicly funded science should be freely accessible. But I’m not sure that it’s good for the quality of published science. The strictness of peer review depends also on the economic interest of the publisher behind it, and it’s pretty clear that open access journals need to publish many papers, and this might compromise quality. Thus, I’m afraid that open access might in fact make a lot of low-quality science openly accessible.

What are your thoughts on crossing the boundaries between disciplines?

Well, as scientists, we usually think that what we’re doing is the only way to attain knowledge and insight (I prefer the German term ‘Erkenntnis’, which embraces the two terms and perhaps goes even further). But I have always been convinced that the arts provide an alternative that is equally well suited for this endeavor — a sort of complementary approach. For me, the work of Marcel Duchamp is a good example: it was a revolution that redefined what art is all about and, in my opinion, it was as important as the scientific revolutions of the time in turning traditional thinking upside down. But he also seems to have committed fraud for the sake of his own myth and claimed someone else’s work as his: the famous *Fountain* is very likely a work of Elsa von Freytag-Loringhoven. Still, his work is a good example of productive art–science: being influenced by mathematician Henri Poincaré, Duchamp’s work is often akin to a scientific experiment (or suggests to be in its title) but then reverts to something different. Just look at the 3 *stoppages étalon*

(1913–1953). For me, this work is artistic research — an experiment on chance and geometry — that mimics the scientific experimental approach and at the same time questions and criticizes it, somehow turning it into absurdity. And this brings me back to crossing the boundaries: on multiple occasions during the last few years I’ve tried to contribute to artistic research by collaborating with artists and participating in conferences that are not strictly scientific, such as those run by ISEA International, or in art–science events, for example, at Ars Electronica 2017. In June of this year I also took part in an Exchange event at London’s Tate Modern art gallery.

And do you have a scientific hero?

I’m a bit skeptical of heroes; I’d say that I don’t have any. I would rather give you an example of important work that is really groundbreaking. Hermann von Helmholtz’s chapter on perception — titled ‘Von den Wahrnehmungen im Allgemeinen’ and published in 1867 in the book *Handbuch der physiologischen Optik* — is absolutely incredible. When I read it for the first time — and that was much too late in my career — I almost couldn’t believe how much he had anticipated of what are currently our best ideas about how perception works, not just the famous ‘unconscious inference’ but also so many other insights, such as anticipating the reafference principle and realizing that perception is not passive but that we actively ‘observe’. Despite using mathematics in most other aspects of his work, he did not translate his ideas about perception into a theoretical, math-based framework. That’s what we’re doing nowadays by using probabilistic modeling, Bayesian statistics, and optimal control. And it turns out that our models, based on these concepts, can very often astonishingly accurately explain experimental results, even results that have puzzled researchers for a long time, such as the systematic biases in time perception discovered 150 years ago.

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Quick guide

Animal syntax

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What is syntax? Etymologically, ‘syntax’ is derived from ancient Greek σύν (together) and τάσσειν (to arrange), hence ‘to arrange together’. In linguistics, the standard definition of syntax is something like a set of principles by which words can be combined into phrases and well-formed sentences. Syntax thus determines the grammar of a language, in addition to phonology and morphology. For evolutionary research, however, definitions that presuppose language are of little use, requiring syntax to be redefined in functional terms, such as a set of principles by which meaning-bearing units can be combined into well-formed complexes.

Do animals have syntax? The notion of syntax has a long history in animal communication research, albeit typically to describe cases of ordered signals. Prominent examples are the songs of humpback whales, gibbons or songbirds. Although undoubtedly interesting, these phenomena are not encompassed by the standard syntax definition, because the song components are meaningless units, while the combined complexes function to advertise features relating to the signaler, such as identity or quality, with no reference to actions or external events. More recently, there has been evidence for animal syntax. For example, Campbell’s monkeys (*Cercopithecus campbelli*) produce ‘hok’ alarms to eagles and ‘krak’ alarms to leopards, but both calls can adopt an acoustically invariable ‘oo’ suffix to form ‘hok-oo’ and ‘krak-oo’. Unsuffixed calls are given to imminent danger, while suffixed calls are given when dangers are less threatening (Figure 1). Although this qualifies as combinations of ‘meaning-bearing units’, the link is stronger to morphology than to syntax because the suffix ‘-oo’ is not an independent unit. Better evidence for syntax-like structure is provided by studies of bird calls. In Japanese tits (*Parus minor*), for example, ‘alert’ calls warn conspecifics



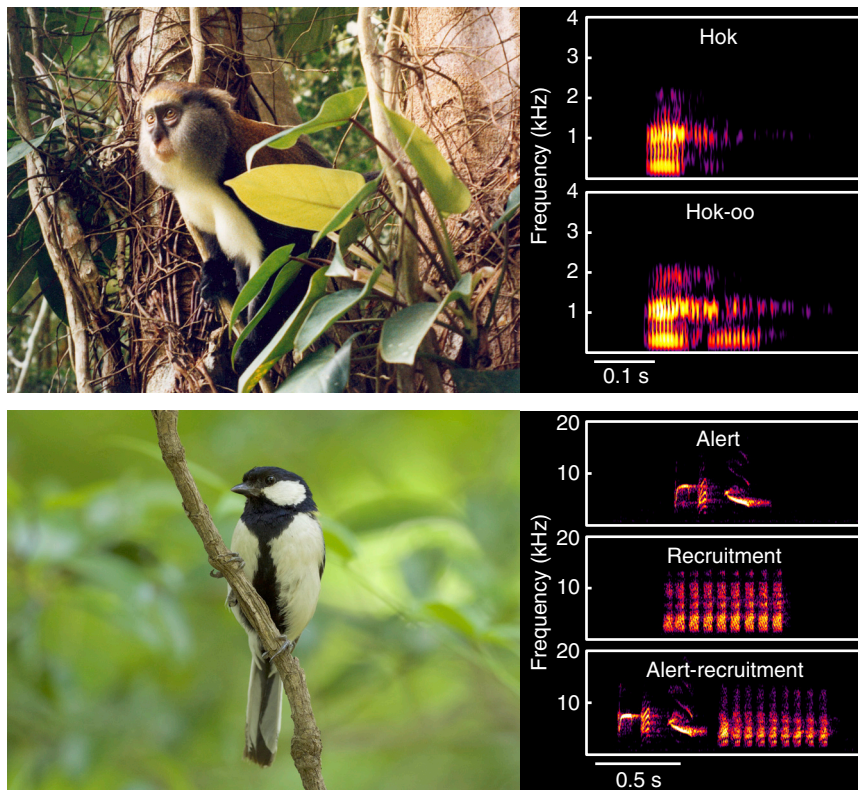


Figure 1. Call combinations in animals.

Campbell's monkeys add 'oo' suffixes to 'hok' alarm calls when perceiving non-urgent danger (top; photo: Eugen Zuberbühler). Japanese tits combine alert and recruitment calls when attracting other individuals to mobbing a predator (bottom; photo Toshitaka Suzuki).

about a predator, while 'recruitment' calls attract conspecifics to non-dangerous situations, such as a nest and a food source. Interestingly, tits combine these two meaning-bearing units into 'alert-recruitment' sequences when recruiting conspecifics to mob stationary predators (Figure 1). The 'alert-recruitment' sequence could be considered as a 'well-formed complex' because artificially reversed sequences ('recruitment-alert') did not elicit mobbing behavior. A similar case of call combinations has been documented for another bird, the southern pied babbler (*Turdoides bicolor*), suggesting that this kind of syntax has evolved independently.

Is animal syntax compositional? Much of the expressive power of language emerges from compositionality, a process by which meaning is determined by the meanings of the constituent parts and the rule that combines them. In human language, compositionality can be found both

at the morphological and syntactic levels, as in the examples above. However, syntax does not need to be compositional. Idiomatic expressions, such as 'kick the bucket', are an example because they consist of meaningful units ("kick", "bucket"), although the combined meaning ("to die") cannot be derived from the constituent parts. An analogy in animal communication are the alarm call combinations of putty-nosed monkeys (*Cercopithecus nictitans*). Here, males produce acoustically distinct alarms for eagles ('hacks') and terrestrial threats ('pyows'), as well as combined 'pyow-hack' sequences. Pyow-hack sequences can be elicited by both predators and trigger group movements regardless of the threat, suggesting that the sequence carries a meaning that is independent of the meaning of the constituent parts.

What do linguists say about animal syntax? There has been a lively, cross-disciplinary debate. Some linguists have

applied their methodology to investigate animal syntax, while others perceive this as an inadmissible transgression. For example, one group has repeatedly argued that the key property of human syntax is a highly specific mental operation, 'merge', which is beyond animal cognitive skills. An interesting amendment to this position is that 'merge' may come in different varieties. According to this theory, 0-merge systems operate with meaning-bearing units, although they do not combine. 1-merge systems, in contrast, have combinatorial properties and can form simple complexes, but without recursive properties. All known cases of animal syntax appear to fall into this group. 2-merge systems go a step further by allowing recursion of units with previously merged complexes. 3-merge systems, finally, allow merges of two already merged complexes. Animal and human syntax, in this view, differ in terms of the complexity of their merge operations, but not in kind, which may simply be linked to memory constraints.

How did syntax evolve? A prominent argument is that syntax evolves as soon as the lexicon (i.e., the number of meaning-bearing units) reaches a threshold, for example due to limitations in vocal production. Although intuitively compelling, the hypothesis is difficult to test because there is no theory of how to determine the maximal lexicon size for each species. Empirically more accessible is the hypothesis that human syntax is a by-product of increased computational power. This has been investigated with artificial grammar research, with the conclusion that humans may be the only species capable of mastering computationally complex grammars. A third hypothesis is that human syntax has evolved continuously at the surface level along increasingly complex signal structures. The hypothesis has been investigated in natural animal communication systems, which has resulted in a bewildering diversity of combinatorial systems with, so far, no apparent evolutionary trends or phylogenetic patterns. Finally, syntax may have evolved from increasingly complex event perception. There is a curious correspondence between how humans categorize natural events and the main grammatical classes in language (actor, action, patient, etc.)

that determine the argument structure. According to this hypothesis, syntax has evolved in response to the ability to categorize and externalize the main components of events, rather than to communicate them as holistic entities. Indeed, some animal signals appear to refer to external objects (e.g. predator classes), while other signals have more emotional properties (e.g. fear) or they refer to entire events.

What's next? More research is needed on the natural surface structures in animal communication, particularly in great apes. If there is a phylogenetic history of the relation between signal combinations and compositionality, then there should be evidence for this in our closest living relatives. Research is also needed on the mental operations underlying syntax. Of particular relevance is how animals mentally represent and structure external events, whether these mental entities correspond to the main grammatical classes of language and whether such entities are communicated in combinatorial and intentional ways. Another largely unexplored problem is how animals acquire the syntactic principles underlying their own communication systems by social learning, in particular whether syntactic competence is homologous, i.e. inherited by common descent, or analogous, i.e. due to socio-ecological adaptation.

Where can I find out more?

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Primer Autophagy

Thomas Wollert

In 1955, the biologist and Nobel Prize laureate Christian de Duve discovered that cells possess specialized organelles filled with hydrolytic enzymes and he called these organelles lysosomes. At the same time, electron microscopy studies by Novikoff and colleagues showed that intracellular dense bodies, which later turned out to be lysosomes, contain cytoplasmic components. Together, these groundbreaking observations revealed that cells can deliver cytoplasmic components to lysosomes for degradation. The hallmark of this degradative process, which de Duve called autophagy, is the formation of double-membrane-limited vesicles. Further morphological characterization of these vesicles (autophagosomes) revealed that they mainly contain bulk cytoplasm. Although this suggested that autophagy leads to a non-selective degradation of cytoplasmic material, de Duve anticipated that a regulated and selective type of this pathway must also exist. Today we know that, under normal conditions, macroautophagy is a highly selective pathway that sequesters damaged or superfluous material from the cytoplasm through the formation of double-membrane-limited autophagosomes. Upon fusion with lysosomes, the content of autophagosomes is degraded and the resulting building blocks are released into the cytoplasm. However, in response to cytotoxic stress or starvation, cells start to produce autophagosomes that capture bulk cytoplasm non-selectively. This stress response is essential for cells to survive adverse environmental conditions, whereas the selective sequestration of cargo is important to maintain cellular homeostasis.

In general, the term autophagy describes an ensemble of pathways that deliver cytoplasmic components to lysosomes. Morphologically, these pathways are remarkably diverse, including not only the generation of autophagosomes in a process referred

to as macroautophagy, but also direct uptake of cytoplasm or cytoplasmic components by lysosomal membrane invaginations in a process termed microautophagy. Moreover, lysosomal channels import a dedicated set of proteins into the lumen of lysosomes in a process that requires assistance by chaperones and has thus been termed chaperone-mediated autophagy. Here, I will focus on macroautophagy (termed autophagy from now on), owing to its versatile nature and its essential contribution to cellular survival and homeostasis.

Identification of the autophagy machinery in yeast

The morphological characterization of autophagy by electron microscopy established general properties of the pathway, but until the 1990s mechanistic or even molecular insights into the biogenesis of autophagosomes as well as its regulation remained uncharacterized. Maybe inspired by genetic screens that Randy Schekman and colleagues developed to identify genes that regulate protein secretion in yeast, Yoshinori Ohsumi and coworkers established a genetic screen to identify autophagy-defective mutants in *Saccharomyces cerevisiae*. The groundbreaking discoveries of both researchers were honored with the Nobel Prize in Physiology or Medicine, first for Schekman in 2013 followed by Ohsumi in 2016, for their characterization of fundamental cellular transport processes. The set of autophagy-deficient mutants that Ohsumi's group identified in their screen comprised 15 *apg* (for autophagy) genes. Similar screens were subsequently employed to expand the repertoire of autophagy genes. However, these studies were based on defects in selective autophagy, leading to the discovery of the cytoplasm to vacuole targeting (Cvt) pathway, which delivers vacuolar hydrolases to the vacuole, and pathways that direct peroxisomes (pexophagy) or mitochondria (mitophagy) to vacuoles for degradation. Selective and non-selective autophagy pathways were initially thought to be distinct and the corresponding genes received pathway-specific names, including *apg* and *aut* (for non-selective and selective autophagy, respectively) as well as

