dots the authors were also able to estimate the number of elongating Pol II complexes along the length of the MS2/lacZ transgene. These calculations suggest that there are approximately 30 elongating Pol II complexes distributed along the length of the transgene at maximal induction. This corresponds to a density of one Pol II complex every 150 basepairs, or one Pol II released from the promoter every six seconds. This is quite a high rate of RNA synthesis, given that the theoretical limit is approximately one Pol II complex every 70–80 basepairs due to the large size of the Pol II footprint.

These studies are the harbingers of things to come: the visualization of time. We are getting the first glimpses into the dynamic activation of gene expression during development. There is no going back, and there is little doubt that these studies are ushering in a new era for the elucidation of temporal control, comparable to the insights gained into the spatial regulation of gene expression provided by the fixed *in situ* hybridization methods first introduced around 30 years ago [14–16]. At long last, the dynamic developing embryo is ready for its close-up.

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Animal Communication: Hidden Complexity

A hallmark of human communication is vocal turn taking. Until recently, turn taking was thought to be unique to humans but new data indicate that marmosets, a new world monkey, take turns when vocalizing too.

Jessica C. Flack

Communication allows individuals to coordinate their behavior and can therefore facilitate cooperation. This effect can be amplified when the communication itself is cooperative, with individuals working together to make sure their messages get transmitted and properly decoded. Despite its obvious advantages, cooperative communication is rare in nature. And, cooperative vocal exchange, in which individuals take turns signaling over an extended sequence of exchanges and control the properties of their utterances, like timing, has been observed only in humans [1]. Results of a new study by Takahashi, Narayanan, and Ghazanfar [2] reported in this issue of *Current Biology* suggest, however, that the common marmoset (*Callithrix jacchus*; Figure 1) also exhibits this kind of cooperative communication.

Takahashi *et al.* [2] found that pairs of marmosets coordinate their vocal exchanges over extended periods, such that the monkeys' call timing is periodically coupled, with the receiver waiting for approximately 5 seconds before responding to the call of its partner and both individuals speeding up or slowing down their calls as necessary to maintain the coupling. The study also suggests that the mechanism underlying the turn taking is mutual entrainment with dynamics characteristic of coupled oscillators.

This is an important study for a number of reasons. It demonstrates that interlocution — like many other traits, including tool making [3], mirror self-recognition [4], and naming of individuals as recently shown in dolphins [5] — can no longer be used as a trump card by proponents of human exceptionalism. More profoundly, the Takahashi *et al.* [2] study raises the question of whether the evolution of turn taking is a signaling innovation that paved the way for finely tuned coordination even when signals themselves are relatively simple. This possibility, as I discuss, injects new energy into the flagging debate in animal communication about how signal–channel design effects signal decoding and, ultimately, what can be communicated.

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Figure 1. A pair of common marmosets (*Callithrix jacchus*). (Photo: copyright Manfred Werner/Tsui/Wikimedia Commons.)

Uncertainty Reduction and Signal–Channel Design

The basis for the proposal that turn taking is a signal–channel design innovation becomes apparent if we recast communication as an information theory problem. A central issue in the evolution of communication is how senders reduce receiver uncertainty about the referent — or meaning — of a signal [6]. Signal referents can include: the internal state of the sender; objects and events in the environment coincident with the signal; objects and events spatially and temporally divorced from the signal, like 'what happened yesterday'; and relational states, like subordination. The question of how senders reduce receiver uncertainty applies whether the underlying nature of the interaction is competitive or cooperative [7] because the basic question, stated in anthropomorphic terms, is how the sender convinces for better or worse the receiver that the signal stands for *X*. The channel capacity, cognitive sophistication of sender and receiver, context of signal exchange, and the structure of the sender–receiver interaction influence the maximum possible uncertainty reduction and hence the scope and content of the communication — in other words, the particular messages that can be transmitted.

Many mechanisms for reducing uncertainty about signal referents have been proposed over the years. One of the most basic is to direct the intended receiver's attention towards the referent. Mechanisms of joint attention [8] include manipulating gaze [9] as well as literally pointing to the signal referent while vocalizing or gesturing [10]. Senders can also manipulate the context in which a signal is emitted to limit the number or type of referents the receiver might associate with the signal. This pragmatic mechanism is particularly useful when pointing will not work because the referent cannot be directly observed, as would be the case if the referent is a relational concept or is spatially or temporally divorced from the signal [11].

In the cases discussed so far, the communication is 'one way'. The sender is emitting a signal that a receiver decodes. Of course, both sender and receiver may have messages to transmit, as is implied by turn taking. This two-way communication can be problematic if both interlocutors are using the same channel [12]. As Takahashi *et al.* [2] discuss, the marmosets' coordinated call timing keeps calls non-overlapping, thereby reducing noise in the channel that might impede decoding.

Turn taking may also play an important role in knowledge generation. The philosopher Paul Grice pointed out that, when communication is cooperative, turn taking facilitates the inference of meanings not explicitly encoded by either sender or receiver [13]. For example, Sally says to Jack, "Little Joey is sick." Jack replies, "Joey was caught in the rain yesterday without his coat." The implication is that Joey got sick because he got wet. Neither speaker actually said anything about the cause of Joey being sick. We, and the speakers, are able to infer the cause because the sequential presentation of facts through a turn-taking mechanism gives the signal exchange an if–then structure.

What is essentially happening in the little Joey example is that each speaker is contributing bits to a message that both are decoding. This induces (presumably) in both a new, shared state (knowledge of the cause of Joey's illness). In our example, this new state corresponds to an increase in the mutual information between the speakers with respect to the state of a third variable exogenous to them

both (little Joey) [14] and is the outcome of decoding an elaborate sequence of signals with complex semantics.

In principle, the new, shared state could be induced by exchanging relatively simple signals in turn, with an increase in the mutual information between the speakers only with respect to their own internal states. Here, as in the more complicated example, the if–then structure intrinsic to turn taking creates an effective grammar at the level of the signal exchange, scaffolding the communication. This kind of explanation may explain the function of turn taking in marmosets. As Takahashi *et al.* [2] suggest, turn taking may serve a coordination function, allowing sender and receiver to finely co-tune their affective states. When affective states predict behavior, turn taking could facilitate tightly coordinated behavior that might otherwise require a semantically richer signaling system.

Evolution of Cooperative Vocal Exchange

Although both humans and marmosets are primates, they are on different branches of the primate family tree, diverging from their common ancestor around 40 million years ago [15]. This observation, coupled to the fact that many primates, including macaques, baboons, and the great apes, are highly social [16] and hence would benefit from cooperative vocal exchange, makes it unlikely that cooperative vocal exchange existed in the common ancestor but was lost in most descendants. Rather cooperative vocal exchange is more likely to have evolved at least twice through convergent evolution.

The possibility of convergent evolution of vocal turn taking in humans and marmosets is interesting because the underlying mechanism — mutual entrainment through coupled oscillators — also appears to be shared [2]. Does this suggest anything about the accessibility of vocal turn taking as a communication strategy — for example, does it initially depend on social structures in which individuals are often in close proximity so that the entrainment can develop? Could evolving the cognitive mechanisms supporting mutual entrainment have increased the accessibility of other strategies observed in cooperative vocal communication in humans?

If so, do we also observe these strategies in marmosets?

Exploration of these issues could provide a way to investigate whether turn taking is in fact a signaling innovation that opens the door for the evolution of the fully fledged phenomenon of cooperative communication, as Takahashi et al. [2] argue. An interesting possibility is that turn taking can also scaffold the evolution of finely tuned cooperative behavior and language, as has been proposed for gesture [17,18] and multimodal communication [19]. At the very least, the Takahashi study suggests it would be worth thinking more creatively about animal communication. It may be that the complexity of animal communication lies in unconventional grammars and pragmatics rather than in the signals themselves.

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Mitochondria: Organization of Respiratory Chain Complexes Becomes Cristae-lized

For over 100 years mitochondria have been known for their distinctive morphology featuring elaborately folded cristae, and their role as 'the powerhouse of the cell'. New research shows that these two characteristics are more dependent on each other than previously thought.

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Mitochondria are double membrane organelles that generate the bulk of cellular ATP through oxidative phosphorylation. Mitochondria contain a series of discrete subcompartments that house subsets of the ~1000 different proteins that make up this organelle — the outer membrane, intermembrane space, inner membrane and the protein dense matrix. Additional complexity exists with the close apposition between the inner and outer membranes termed the inner boundary membrane, and the folds of the inner membrane making up the cristae. The groups of

Scorrano and Enriquez [1] have now revealed a close connection between cristae shape and the activity and assembly of oxidative phosphorylation complexes.

While many textbook depictions show that mitochondrial cristae form regular folds or baffles, electron tomographic imaging has revealed that cristae actually form diverse shapes that are connected to the intermembrane space through small tubular structures termed crista junctions of approximately 30 nm in diameter [2]. Cristae are known to house the respiratory chain complexes, along with cytochrome c and ATP synthase [3] (Figure 1A). Following his

invention of blue native PAGE for the separation of membrane protein complexes, Herman Schägger [4] found that respiratory chain complexes assemble into higher ordered supercomplexes. The composition of these complexes varies and is dependent on the relative stoichiometries — predominantly these consist of complex I with a dimer of complex III and a monomer of complex IV, or complex I with the complex III dimer alone (Figure 1B). Complex II is not found in supercomplex form, while complex V can exist in a dimeric form.

While some argued that these complexes were merely post-lysis artefacts, Schägger's findings have stood the test of time and have been supported by a number of additional discoveries, including roles of complex III and IV in stabilizing complex I; a role for the mitochondrial lipid cardiolipin in stabilizing supercomplexes; and the presence of key proteins that stabilize inter-complex contacts between complex III and IV. Schägger [4] postulated that supercomplexes enable efficient substrate channeling and enhance the catalytic activities