

consideration of the consequences of the next choice: “If I do *this*, will I get my next reward?” (Note that these processes may or may not be ‘conscious’ and indeed probably are not.)

The switch between reverse and forward replays constitutes a segmentation of the replay event; this segmentation was also evident in the observation that ripple events were entirely composed of within-arm sequences and did not straddle the choice point, even though the place field representation was equally strong there. Thus, joint replays seem to be formed by discrete sub-events, with each sub-event representing a spatial unit spanning the entire length of a single arm. The question arises as to why replays did not arise in the middle of an arm and run to the middle of the adjoining arm — sequences appeared to start and stop at nodal points in the maze structure. The reason for this is unknown, but nodes might perhaps

be places where place field sequences during behaviour were interrupted, either by stopping (at the end of an arm) or by divergence (at the fork). Why these nodes should be anchor points for ripple sequences remains an interesting question for future investigation, as is the question of what (mechanistically) determines the start points, stop points and directionality of the sequence segments.

This new study [7] adds to the growing weight of evidence that the hippocampus engages in active, offline construction and consolidation of internal environmental representations. More than this, however, it reinforces the venerable but much disputed idea, first advanced by Tolman [8], that this internal representation mirrors the real world in a truly map-like way.

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Ape Gestures: Interpreting Chimpanzee and Bonobo Minds

Improving methods for studying primate interaction are providing new insights into the relationship between gesture and meaning in chimpanzee and bonobo communication.

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The philosopher Donald Davidson posed the following puzzle [1]. For the most part we understand what others are thinking because we understand the words and sentences that they utter; but we understand what they say only because we know which thoughts their utterances typically express. That makes knowing others’ minds and knowing the meanings of their words and sentences co-dependent. Without knowing both, one cannot grasp either. Davidson called this the problem of *radical interpretation*. How, he asked, could one overcome this interdependence, to come to know the minds of those whose language one did not speak? Two papers in this issue of *Current Biology*, by Hobaiter and Byrne [2] and Genty and Zuberbühler [3], help to answer this question by providing new insights into the relationship of

gesture and meaning in chimpanzee and bonobo communication.

The problem of radical interpretation is particularly acute when trying to interpret the minds of non-human animals. In the case of humans, we can be relatively confident that their thoughts about the world will be similar to our own, and so use our impressions of a scene as a guide to what they might be saying about it. However, this approach is unreliable where cognitive similarity cannot be assumed. We know that all species of great ape use gestures to communicate with one another, and that these gestures are — as in human language — produced intentionally, causally inefficacious, and addressed to audiences with particular communicative intentions [4] (Figure 1). Because these features are central characteristics of human utterances [5], ape gestures are meaningful in

ways analogous to our own. However, knowing *that* ape gestures are meaningful is very different from knowing *what* those gestures mean.

The two new papers [2,3] provide valuable new insights into the question of what apes mean when they gesture to one another. Hobaiter and Byrne [2] produce a partial lexicon of the gestural vocabulary of the Sonso community of chimpanzees in Uganda’s Budongo forest. They identify nineteen meanings distributed over 66 gestures — thereby elaborating the closest thing we have to a chimpanzee gesture phrasebook. Genty and Zuberbühler [3] document a single gesture used by bonobos at the Lola Ya Bonobo sanctuary in the Democratic Republic of Congo. This gesture is particularly striking because of its similarity to one that we use and recognise ourselves — making for an intuitive interpretation of its content that a more careful analysis subsequently confirms.

In the ‘beckoning’ gesture that Genty and Zuberbühler describe [3], one bonobo extends a hand in the direction of a peer before turning and pulling away, while sweeping the outstretched hand back towards them and in the direction of the turn — as if to say “Follow me!” or “Come here!”. This



Figure 1. Two infant chimpanzees use gestures in play. (Photo: copyright Catherine Hobaiter.)

gesture is typically performed by males, to initiate a discreet sexual encounter with a female peer.

Interpretation of this gesture is intuitive, not only because we do something similar, but because the form of the gesture visually resembles its apparent content. This leads Genty and Zuberbühler [3] to conclude that it may be a rare case of iconic gesturing in the *Pan* genus. This is important because iconic gestures are thought to have figured heavily in the communication of our early hominin ancestors [6,7]. Such gestures would have enabled them to compose potentially complex messages by visually recreating actions and events, without possessing the skills for high-fidelity imitation that greatly facilitate conventional communication [8].

Insofar as the beckoning gesture suggests the possibility of iconic communication in our last common ancestor, it is a potentially important insight into the evolution of human communication. At the same time, the finding should be treated with caution. True iconic communication would

require that bonobos choose this gesture because they recognise that its form visually resembles the message they intend to communicate, and that this resemblance should facilitate interpretation. Otherwise the resemblance of content and form might just be a coincidence, unnoticed by the gesturing individuals. We cannot know from observation alone that bonobos act with this insight. Nonetheless, the beckoning gesture is an important candidate for a phylogenetically early form of iconicity. It is a compelling case of a gesture that might be used with the same underlying mental states by human and non-human great apes alike.

In the gestures described by Hobaiter and Byrne [2], visual similarity between gesture and content is less evident — making the route to interpretation less intuitive. Nonetheless, it is shown that at least some chimpanzee gestures are used with stable semantic properties, in the manner of human language.

Since the work of Paul Grice [5] in the 1950s, it has been accepted that the meanings of utterances can be

specified in terms closely related to the intentions with which communicators act. For words or gestures to have established meanings is just for them to be used consistently to express particular communicative intentions. These insights provide support for a method of interpretation that has previously been used to assign meanings to the gestures of gorillas [9] and orang-utans [10] in captivity, and that has now been applied by Hobaiter and Byrne [2] to a population of wild chimpanzees. A gesturer's communicative goal is inferred by observation of the outcomes that seemingly satisfy its act of gesturing, and contrasted with outcomes where goals are not fulfilled. Where the gesturer is satisfied with the outcome, her intention was likely realised — making this 'apparently satisfactory outcome' (ASO) a good approximation of the content of her message.

Hobaiter and Byrne [2] use this method to map gestures to the social functions with which they are used — and so identify which gestures are used to initiate travel, to discourage irritating behaviour, and so on. These findings are exciting because of the answer they hold out to Davidson's question. They constitute our best guide yet to understanding the utterances — and so in some respects, the minds — of our nearest cousins. At the same time, the lexicon is a work-in-progress; an important advance in a still-unfinished project.

Some of the reported gestures are used with several different functions. In some cases this may be because — like the English word 'bank' — they are polysemous (that is, have multiple meanings). In other cases, the intention with which the gesture was produced may be modelled only imperfectly by the ASO method, because a gesture produced with the same intended meaning could be satisfied by more than one response. Attention to this possibility might help resolve some troubling ambiguities. For example, the 'arm swing', 'foot stomp', and 'hand on' gestures described by Hobaiter and Byrne [2] are said to possess two primary meanings — to get another to move closer (as if to say "Move closer!"), or further away ("Move away!"). Were these gestures genuinely polysemous, then these apparently contradictory functions might be problematic. A word that

means both one thing and its opposite ought not to be a stable tool for communication, since it would be an unreliable indicator of its utterer's intention.

It may be that appearances here are deceptive. In the case just described, the gestures might have a single, perhaps more general meaning than is revealed by the range of its ASOs — for example, “Move!”. Precisely how the addressee should move would need to be inferred not just from the gesture but from further contextual elements too, like the nature of social interaction in which the gesture was produced (for example, friendly *versus* antagonistic interactions). In other cases, social relationships may determine which responses are satisfactory. For example, the ‘reach’ gesture is used to solicit climbing, proximity, or closer contact. It may be that the gesture is really used as a general request for physical contact (analogous to “Hold me!”) that is satisfied differently depending upon the individuals involved. Such a request might be satisfied by climbing from an infant, but by a gentle touch from an adult male.

With more exhaustive analysis of the context of gesture production, ambiguities in the current lexicon might be identified and resolved. It

may be that utterances of “Move!” are accompanied by facial expressions or vocalisations containing further information about the gesturer's intentions [11,12], or that satisfactory responses to contact solicitations vary with age and rank. Context-driven analysis of the variance between gestures and ASOs might therefore reveal more univocal intentions underlying different patterns of response. Alternatively, it might not support assignment to gestures of more precise meanings. Here we might conclude that gestures are only general attention-soliciting devices, with meanings analogous to “Hey!” or “Oi!” — as others have supposed [4,7].

The gestural lexicon outlined by Hobaiter and Byrne [2] is a huge achievement for primate science. It provides the most detailed answer yet given to Davidson's question with respect to our nearest living relatives, and the refinements suggested here would not be possible without the valuable dataset presented. At the same time, radical interpretation can be a momentous project, and the process of interpreting chimpanzee minds will not be accomplished quickly. Research into the context-variant elements of great ape gestural communication will be especially valuable in the completion of this task.

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Docking Interactions: Cell-Cycle Regulation and Beyond

In budding yeast, the mating pathway activates Far1 to inhibit G1 cyclins in complex with the cyclin-dependent kinase (Cln-Cdk). Yet, the molecular mechanism has remained largely unclear for over 20 years. A recent report helps shed light on this regulation.

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Progression through the cell cycle is controlled by cyclin-dependent kinases (Cdk) in complex with cyclin regulatory subunits. Cyclins accumulate in distinct cell-cycle phases to drive specific events. To a first approximation, cyclin activity increases as the cell progresses through the cell cycle until plummeting in anaphase upon activation of the

APC E3 ubiquitin ligase, which targets many cyclins for destruction. Interestingly, the cell cycles of fission yeast and frog embryo extracts can be driven by a single, highly active mitotic cyclin [1,2]. In these single cyclin models, it is presumed that distinct cell-cycle events are initiated at specific Cdk activity thresholds. However, all organisms whose cell cycles have been investigated have many cyclins, which must have important functions since they

have not been lost through neutral mutation.

The importance of cyclin specificity for cell-cycle control was first revealed by genetic studies [3]. For example, the S-phase cyclins in yeast and animals, Clb5 and cyclin A, respectively, use a hydrophobic patch to dock substrates and target Cdk activity to initiate DNA replication [4]. It is now appreciated that all early cyclins in yeast likely have docking sites to recognize specific partners. This increased specificity compensates for the fact that the early cyclin-Cdk complexes are less active when examined on model substrates such as histone H1 peptide. This new quantitative model, based mostly on *in vitro* biochemistry, proposes that there is a handoff from more specific, but less active kinase complexes to less specific, but more