

brain regions, and how does their existence inform our understanding of neural networks involved in memory? In rodents, the occurrence of ripples in the hippocampus and association cortex is correlated (14). Similarly, Vaz *et al.* found that ripples in the MTL were significantly coupled to ripples in the temporal association cortex (a region involved in language and multisensory integration), but not primary cortices. These results suggest that dynamic high-frequency oscillatory coupling may establish specific time windows for preferential communication between the MTL and association cortices, enabling these brain regions to effectively cooperate in information processing.

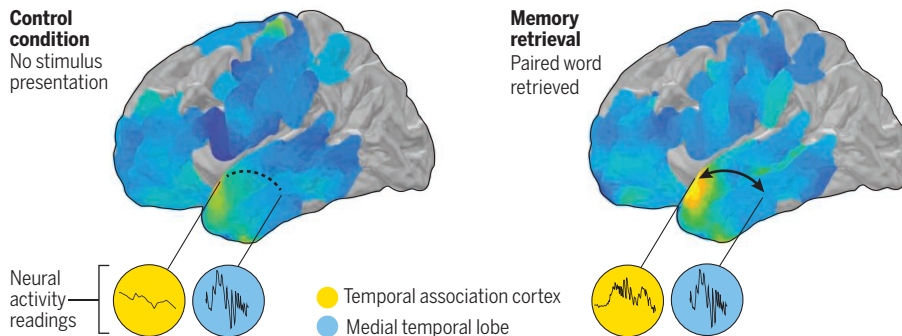
Vaz *et al.* establish the functional importance of this interregional ripple coupling

pass on any given trial. They found that increases in ripple occurrence and coupling occurred during successful memory retrieval, but not during pass or incorrect trials or during encoding (when the memory is first established). Coupled ripples were also associated with a reinstatement of cortical activity patterns that were present during encoding of the word pair to be remembered, offering the possibility that the ripples may “prime” the network for the subsequent conscious process of recollection in this task.

Coupled ripples may serve as a biomarker for the “when” and “where” of memory retrieval in the brain, but the neural spiking sequences embedded in their oscillatory cycles define “what” is being retrieved (see

## Biomarker for memory retrieval

Ripples are synchronized between the medial temporal lobe and temporal association cortex during successful memory retrieval, but not during baseline conditions.



during a memory task wherein human participants recall new associations between pairs of words. They find that both the occurrence rate and degree of MTL–temporal association cortex ripple coupling increase selectively during trials with successful memory performance. These effects were not observed in other association cortices (such as prefrontal or parietal cortices), which were presumably not required for the performance of this language-based task. The demonstration that ripple coupling between the MTL and different association cortices can be driven by varying task requirements would further strengthen the mechanistic interpretation of this phenomenon.

The study of Vaz *et al.* with human participants also permits key insight into the neural mechanisms specifically involved in memory retrieval (accessing a previously stored memory), rather than memory consolidation (strengthening a memory for long-term storage), which has been well studied in animal models (15). The memory task employed by Vaz *et al.* involved acquiring a timed verbal response or a

the figure). Further investigation into these neural signals will help us to understand the syntax (4) that forms the basis of our experiential memories, and perhaps lay the foundation for interventions aimed at improving memory function. ■

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## GEOLOGY

# How high were these mountains?

An iterative approach is needed to constrain the past elevation of mountain belts

By Douwe J. J. van Hinsbergen and Lydian M. Boschman

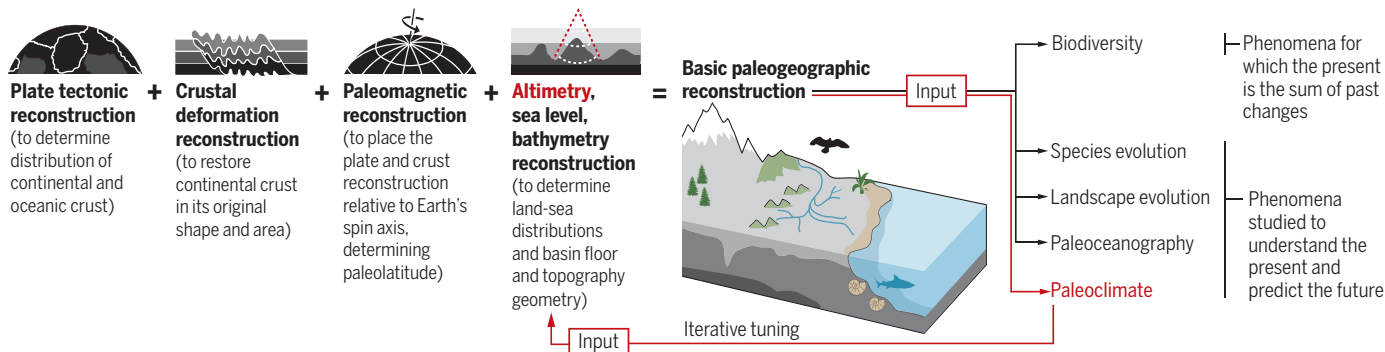
Paleoaltimetry—the quantitative estimate of the past elevation of land surfaces such as mountain belts—is notoriously difficult to constrain. To estimate past elevation, geologists study sedimentary rocks that accumulated in freshwater lakes in ancient mountain belts. They compare fossils or oxygen stable isotopes (the ratio of which is elevation-dependent) from these rocks with present-day records from elevated areas (1). One region where paleoaltimetry studies are widely conducted is the Tibetan Plateau, which owes its extreme elevation to intense deformation that started at least 70 million years ago during subduction of the Indian plate below Asia. However, elevation estimates for the region—for example, for the Eocene (~40 million years ago)—based on either fossils or stable isotopes differ by kilometers (2, 3). On page 946 of this issue, Botsyun *et al.* (4) provide an explanation for this discrepancy and bring the two types of estimate nearer to agreement.

The authors used a numerical model that couples stable isotopes with atmospheric circulation (5). They show that changes in past atmospheric circulation can dramatically affect the relationship between oxygen isotope ratios and elevation. Using their circulation model, they recalibrated the oxygen-isotope paleoaltimeter for Eocene Tibet, using a set of paleogeographic scenarios as input, and brought the isotope-based estimates of Eocene Tibetan elevation down by several kilometers to arguably within the range of fossil-based estimates. This result implies that much of the surface elevation of the Tibetan Plateau was acquired after much of the crustal deformation took place, suggesting that processes in the underlying mantle may have played a key role in the uplift.

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## How to reconstruct past geography

Paleogeographic reconstructions form input for studies aiming to understand complex geological, geophysical, climatic, or biological systems. Botsyun *et al.* show that paleoaltimetry in paleogeographic reconstructions depends on paleoclimate and requires an iterative tuning. Thus, other fields that use paleogeography also become dependent on interpretations and modeling of paleoclimate.



To understand the wider implication of these results, it is important to realize that paleoaltimetry is one of the ingredients of global paleogeography models, alongside the distribution of land and sea and seafloor topography. Changes in paleogeography primarily result from dynamics of Earth's mantle, plate tectonics, deformation of Earth's crust, and absolute sea level changes. Paleogeography models are not only used as input for paleocirculation and paleoclimate modeling but are also essential in the study of many other processes that occurred in the geological past, such as paleoceanographic circulation (6), landscape evolution, and the evolution of life (7). Furthermore, the modern state of, for example, biodiversity is the result of a long history of evolution and extinction, in which paleogeographic changes played a crucial role (8).

Ideally, paleogeography models should be independent from any of the fields that use them as a starting point or model input. Botsyun *et al.* (4) show, however, that quantitative estimates of paleoaltimetry from stable isotopes depend on the outcome of a paleoatmospheric circulation model, which in turn used paleogeographic distribution of land and sea, paleoaltimetry, and the paleolatitude of topographic barriers (the edges of the Tibetan Plateau, including the Himalaya mountain belt in the south) as input. In other words, paleoaltimetry estimates depend on paleoclimate models that require paleoaltimetry as input. This means that paleoaltimetry and paleoclimate models need to be iteratively tuned until the input elevation and the output relations between isotopic ratio and elevation are mutually consistent (see the figure). Furthermore, neighboring scientific fields that use paleogeographic evolution as input, such as biodiversity studies, now become dependent on paleoclimate models. Last, uncertainties in paleogeography models, which influence paleocirculation pat-

terns, may affect paleoaltimetry estimates.

By using different paleogeography models for the Himalaya and the Tibetan Plateau, Botsyun *et al.* illustrate the effect of such uncertainties in paleogeography on paleocirculation models. In particular, they show that the paleolatitude of the Tibetan Plateau and Himalaya in the Eocene strongly affects atmospheric circulation patterns and the altimetry–isotope ratio relationship. Uncertainties in paleogeography models should thus be quantified so that these uncertainties can be taken into account in other models that use paleogeographic information as input.

However, estimating uncertainties in paleogeography is challenging, and currently, paleogeography models generally do not contain quantitative uncertainty. The reason for this is the multilayered nature of paleogeography models (see the figure). The base layer consists of a reconstruction of the major tectonic plates (9). This provides the distribution of oceanic and continental crust in the geological past. Second, intense crustal deformation, which is especially important in plate boundary zones and mountain belts, is reconstructed based on geological and geophysical observations. Third, paleolatitudinal position of the reconstructed continents, oceans, and mountain belts is constrained through paleomagnetic data (10). Last, estimates of sea level, paleoaltimetry, and paleobathymetry (past water depth) are added (11). This provides a paleogeographic base model that is used by other fields of study as input (see the figure).

Uncertainties are now well quantified for the first and third step (12) but are poorly constrained for the other two. The main reason for this is the qualitative nature of geology: To estimate, for example, crustal deformation or paleobathymetry, a succession of rocks must be translated into a quantitative estimate of plate motion or water depth. The resulting estimates are inevitably crude, and because

the rock record is rarely complete, extra- and interpolation in space and time are inevitable. Reconstructing crustal deformation is key in determining where steep topography was located in the past. The paleogeography community therefore needs to develop uncertainty quantifications for crustal deformation reconstructions. The climate modeling/paleoaltimetry community must then propagate these uncertainties in their models for a balanced view on paleoaltimetry.

Botsyun *et al.*'s work shows that estimating paleoaltimetry requires iterative tuning with paleoclimate models, in which uncertainties in paleogeography influence the outcome. This finding means that modeling climate dynamics requires even more computer power than previously realized. Furthermore, it opens opportunities for cross-disciplinary work by geologists, biologists, physicists, statisticians, and computer scientists. This work is needed to understand paleoclimate evolution as a proxy for the future effects of human-induced climate change. It is also crucial for comprehending biodiversity and the fundamental workings of our planet's interior, fields for which knowledge of paleoaltimetry is essential. ■

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