complex with the finding that Rho kinase could also directly phosphorylate myosin light chains, potentially usurping the role of MLCK (*5*). It is clear that myosin light chain phosphorylation is elevated in vivo in response to RhoA activation, but whether this is due primarily to inhibition of the myosin phosphatase or to direct phosphorylation of light chain, or to a combination of both, has not yet been established.

In previous work, PAK was shown to promote the disassembly of stress fibers and focal adhesions (*5–7*). Sanders *et al.* now demonstrate that MLCK is a substrate for PAK. Phosphorylation of MLCK by PAK decreases its activity, which in turn results in decreased myosin light chain phosphorylation and a decrease in actin-myosin filament assembly (see the figure). Just as elevated myosin activity promotes the assembly of stress fibers, it has been shown that inhibiting actin-myosin interactions with pharmacological reagents causes the disassembly of these structures (*3*). Consequently, PAK's ability to inhibit myosin light chain phosphorylation accounts for the disassembly of stress fibers and focal adhesions observed in cells overexpressing activated PAK.

Most of the kinases stimulated by Rac, Cdc42, or RhoA have multiple targets, and so it is likely that there are additional ways in which PAK opposes or modifies the actions of RhoA. Indeed, the cytoskeletal rearrangements induced by activated PAK are dramatic (*6–8*)—reminiscent of those seen in cells treated with the actin filament–disrupting drug cytochalasin D—suggesting that cytoskeletal proteins as well as MLCK are targets for PAK.

The observations of Sanders *et al.* are important for understanding cell motility. During this complex process, protrusive and contractile forces must be coordinated. Prominent focal adhesions and stress fibers are associated with cells that do not move. Rac and Cdc42 stimulate cell movement, and to be effective these proteins must not only stimulate protrusion, but must also promote disassembly and turnover of focal adhesions and stress fibers. The current work is important because it suggests how contractile forces in the cell can be restrained by Rac and Cdc42, and how stress fibers and focal adhesions may be disassembled through the action of PAK on MLCK.

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PERSPECTIVES: MODERN HUMAN ORIGINS

Highly Visible, Curiously Intangible

G. A. Clark

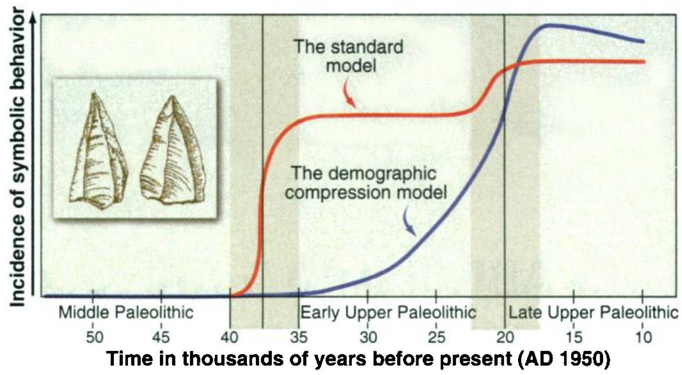
Scientists have been trying to arrive at a consensus about modern human origins (MHO) for more than a century. How is it then that key questions such as whether modern humans evolved only in Africa and migrated from there or evolved in other regions across the world from local archaic ancestors remain unanswered? Many would say that we simply do not have enough data to answer the question of our origins and that with the eventual accumulation of more data, many MHO issues will be resolved. Insufficient data is only part of the answer, however. MHO researchers come from various research traditions. In each of these traditions, different assumptions about the remote human past determine what is considered relevant data, which questions are asked of the data, and how the data are interpreted. More data do not remove the paradigmatic bias implicit within each research tradition, and in consequence people from different fields fail to communicate effectively.

The geneticist Henry Harpending once expressed this problem succinctly when he described MHO research as "a highly visible, yet intangible field" (*1*). The disciplines that contribute to the field (archaeology, human paleontology, and molecular biology) tend to be discovery-driven and focused on methodology. Following a strictly empirical approach ("the facts speak for themselves"), they often have little concern for the logic of inference underlying knowledge claims.

Although these observations apply to all aspects of MHO research, MHO archaeology in Europe is a particularly good example of such epistemological naïvete. Like the larger debate of which it is a part, it can be summarized in terms of two competing models: the continuity model, which contends that modern humans in Europe and elsewhere evolved from their local archaic predecessors, and the replacement model, in which modern humans evolved only in Africa, migrated out of Africa, and replaced other hominids that were the products of earlier, similar radiations (*2, 3*).

Each of these models is based on a set of assumptions that favors some groups of variables at the expense of others, and both define and weight variables thought to be held in common differently (*4*). By making the tenets of the replacement and continuity paradigms explicit, it should in principle be possible to develop tests for their validity—patterns in the archaeological and paleontological records that should hold if in fact the paradigm is an accurate descriptor of reality (*5*). However, such a critically self-conscious approach is often lacking.

According to conventional archaeological systematics, the transition between neandertals and modern humans in Europe coincides with the Middle-Upper Paleolithic transition, 35,000 to 45,000 years ago (see the figure). Although consensus has remained elusive, a dominant "re-



A matter of timing. Comparison of the standard and the demographic compression models for the appearance of symbolic behavior in Europe between 50,000 and 10,000 years before present (yr B.P.). The standard model argues for an "explosion" of evidence for symbolism coincident with the Middle-Upper Paleolithic transition, 40,000 to 35,000 yr B.P. The demographic compression model sees change as much more gradual, with the sharp increase in evidence for symbolism occurring only after 20,000 yr B.P., caused by demographic changes and mainly confined to southern France and northern coastal Spain (*12*).

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placement" view of the European archaeological transition is embodied in textbook generalizations (see the table). The adequacy of the systematics underlying these generalizations needs to be evaluated.

The European approach to paleolithic archaeology originated in France almost a century ago. It is based heavily on a typological systematics that emphasizes retouched stone tools. A cultural transition is usually demarcated by changes in the retouched tool components of archaeological assemblages, that is, the totality of archaeological remains contained in a site. The tacit assumption is made that these tools represent the remains of stylistic microtraditions akin to those produced by more recent ethnic or linguistic units like tribes, peoples, or nations, transmitted from one generation to the next through the medium of culture. Modes of tool fabrication are equated with social learning, and it is assumed that distributions of particular types of stone tools in time and space, to a degree, also define the boundaries of identity-conscious social units analogous to the peoples and cultures of history. This reasoning is then extended to modes in the frequency of entire assemblages of artifacts. However, both the spatial extent and the temporal persistence of these hypothetical entities would have been enormous, orders of magnitude beyond those of any known or imaginable social unit at the time in question.

Changes in the character of retouched stone tools over the Middle-Upper Paleolithic transition have been interpreted in three ways. Some workers see the transition as an in situ phenomenon with clear evidence of continuity between late Middle Paleolithic (LMP) and early Upper Paleolithic (EUP) assemblages. Others argue that certain EUP industries such as the Châtelperronian and the Szeletian are "adaptive responses" by neandertals to the arrival of modern humans making Aurignacian industries. Although it is by no means clear what an adaptive response is, this scenario implies that neandertals modified their existing Mousterian technologies because of contact with modern humans and produced assemblages with mixed Middle and Upper Paleolithic characteristics. A third hypothesis is that no such intermediate industries existed. Contemporaneous LMP and EUP assemblages in the same site or region are taken to imply that the EUP must have been intrusive; that is, modern humans migrated into Europe and replaced existing hominid groups. This scenario implies that the creators of LMP and EUP industries can be known with certainty (they cannot) and that archaic and modern groups coexisted for extended periods of time but did not interact with one another to any substantial extent (*6*).

These different perspectives are inextricably entangled with the classifications for Middle and Upper Paleolithic retouched stone tools. Empirical support for replacement of neandertals by modern humans rests on the notion that Middle Paleolithic stone tools do not exhibit "imposed form" and "morphological standardization" whereas Upper Paleolithic stone tools do (*7*). However, quite distinct and incompatible typological systems are used to characterize these assemblages. Discontinuity is thus "built into" the interpretation right from the start. Harold Dibble showed successfully for Middle Paleolithic stone artifacts that the size and shape of the starting flake (called blank) determine the form of the resulting tool and that tools previously classified as distinct types were simply part of a few, generalized lithic reduction sequence (*8*). The same arguments can and have been made about Upper and even Epipaleolithic artifacts (*9*). If we do not abandon typological systematics altogether, we should at least uncouple them from the historicist biases that are invoked to explain them.

A shift in stone tool technology from predominantly "flake" technologies to "blade" technologies, achieved by means of more economic techniques of core preparation.
A simultaneous increase in the variety and complexity of stone tools involving more standardization of shape and a higher degree of "imposed form" in the various stages of production.
The appearance of relatively complex and extensively shaped bone, antler, and ivory artifacts.
An increase in the rate of technological change accompanied by increased regional diversification of tool forms.
The appearance of beads, pendants, and other personal ornaments made from teeth, shell, bone, stone, and ivory blanks.
The appearance of sophisticated and highly complex forms of representational or "naturalistic" art.
Associated changes in the socioeconomic organization of human groups, marked by (i) a more specialized pattern of animal exploitation, based on systematic hunting, (ii) a sharp increase in the overall density of human population, (iii) an increase in the maximum size of local residential groups, and (iv) the appearance of more highly "structured" sites, including more evidence for hearths, pits, huts, tents, and other habitations.

A time of transition. Problematic generalizations that supposedly mark the Middle-Upper Paleolithic transition in Europe [see for example (*13*)].

The archaeological aspects of the MHO debate turn on the expected behavior and adaptations of two different hominids occupying Europe over tens of thousands of years. Differences in adaptation would clearly be expected under all replacement scenarios published so far. But the common archaeological monitors of adaptation do not show such differences. Patterns in stone tool technology, typology, raw material variability, lithic reduction strategies, blank frequencies, bone and antler technologies, paleolithic art (see the figure), and subsistence strategies change at different rates in different places over the entire transition interval, in a manner that cannot be reconciled with biological replacement (*10*).

In this context, some recent approaches are noteworthy. Since the late 1980s, some researchers have used a community ecology approach to understanding ancient forager adaptations. Grounded in evolutionary ecology, these workers reject ethnographic models, study paleolithic foragers as members of guilds of social carnivores (like wolves and hyenas today), and use ecological niche theory to analyze and interpret prehistoric hunting, scavenging, and foraging behaviors, which are then contrasted and compared with those of other large predators living in the region at the time (*11*).

Paleolithic adaptations almost certainly constituted a range of options very broadly distributed in space and time, held in common by all circum-Mediterranean hominids and invoked differentially according to context. The challenge is to determine the factors that may have constrained choice among these options. Such factors probably included access to raw materials, distribution of food resources, forager mobility strategies, anticipated tasks, group size and composition, changes in occupation of a site during an annual round, and, more generally, duration of site occupation.

On the surface, the voluminous literature on the MHO debate paints a picture of informed and sophisticated interdisciplinary research in which data are absorbed and digested, arguments assimilated, and methodologies understood, compared, and evaluated. I suggest, however, that this is a gross oversimplification of a much more complex reality. We are, in effect, consumers of one another's research conclusions, but we select among alternative sets of research conclusions in accordance with our biases and preconceptions. These biases and preconceptions must be subjected to critical scrutiny. As long as there is no explicit concern with the logic of inference—how we know what we think we know about the past—there can be no consensus.

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PERSPECTIVES: EARTHQUAKE GROUND MOTION

How Does the Ground Shake?

Arthur D. Frankel

When a multistory building is subjected to ground shaking from an earthquake, elastic waves travel up the structure, with some of the energy reflected at each floor and the remainder reflected from the top of the building. As the shaking continues, the structure begins to vibrate at various frequencies. Earthquakes generate ground motions over a wide range of frequencies, from static offsets to tens of cycles per second [hertz (Hz)]. Most man-made structures have natural frequencies of vibration between about 0.1 and 20 Hz; a typical 10-story building has a natural frequency around 1 Hz. Each structure is most sensitive to ground motions with frequencies near its natural frequency. Damage to a building thus depends on its properties and on the character of the earthquake ground motions, such as peak acceleration and velocity, duration, frequency content, kinetic energy, and phasing and coherence.

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One of the major goals of modern seismology is the prediction of the time series (or "time histories") of the ground motions at specific locations when a large earthquake occurs on a particular fault. These artificial time histories are then used to model the response and improve the resistance of structures such as buildings, bridges, or power plants to damage from ground shaking. Many time histories have been recorded at sites near earthquakes in the western United States and elsewhere, although these are mostly for earthquakes with magnitudes (**M**) ≤ 7. In producing artificial time histories for engineering applications, the most attention has been paid to simulating horizontal shear-wave motion (where ground motion is perpendicular to the direction of wave propagation), because it is most damaging to structures. On page 2045, O'Connell (*1*) considers an inherent property of Earth's crust that is often overlooked when ground motions are simulated: its randomness.

Predicting earthquake ground motions requires a detailed description of the source, that is, the slip between opposite sides of the fault during the earthquake rupture process, and of the path along which the seismic waves propagate from the fault to the site of interest. Variations of material properties and stress in the crust occur over a wide range of spatial scales, from the small-scale variety of minerals in a rock to the large-scale complexity of a geologic map, affecting both source and path of the seismic waves.

Earthquakes nucleate when the slip between sides of a fault accelerates in a small patch. The interaction of the resulting propagating rupture with the stress and strength variations on the fault generates seismic waves over a broad frequency range. A fractal distribution of stress release on a fault, with stress release independent of scale, can explain the white spectrum of ground accelerations commonly observed above about 1 Hz for large earthquakes (*2*).

Once generated, seismic waves are refracted and reflected by approximately horizontal boundaries in the crust. At shallow depth, seismic velocities under a site can often be approximated by horizontal layers of soil over bedrock. Multiple reflections within soil layers can cause resonances of ground motions. Superimposed on this structure variation with depth are lateral variations in rock type and composition, fractures, and fluid pressure. Variations in seismic velocity and density on a scale of tens to hundreds of meters scatter seismic waves with frequencies above about 0.5 Hz, producing much of the tail of energy observed after the arrival of shear waves traveling directly from the source. Such scattering can lower the coherence of the shear-wave motion over the dimensions of the foundation of a building, which can affect building response.

At frequencies below about 1 Hz, relatively simple deterministic models (*3*) can reproduce the strong pulse of coherent ground motion observed at locations in the direction of rupture propagation. At high frequencies above about 5 Hz, the small-scale variation of stress on the fault and scatterers in the crust affects the generation and propagation of seismic waves substantially, and stochastic approaches (*4*) are used to match the duration or envelope (or both) of the ground motion and its spectrum, rather than attempting a "wiggle for wiggle" match to observed seismograms.

In the important frequency range of 0.5 to 5 Hz, where many buildings have their natural frequencies, the deterministic and stochastic approaches need to be combined to achieve a reasonable match to observed seismograms and to produce synthetic time histories suitable for use in engineering design (*5*). It is this problematic frequency range that O'Connell addresses in his research article.

It is of particular importance to building codes and engineering design to establish what happens to seismic waves as they propagate through the unconsolidated material at shallow depths beneath a site. Soil sites amplify ground motions more than rock sites, at least at frequencies of about 2 Hz and lower, because of the lower rigidity of soils. However, laboratory experiments have demonstrated that soil behavior becomes nonlinear at the high strains achieved near large earthquakes. Such nonlinear behavior would reduce the amplitude of seismic waves at frequencies above about 2 Hz and lower resonant frequencies caused by the soil. Modern building codes such as the Uniform Building Code in the United States include nonlinear soil behavior in their amplification factors.

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