and could include inorganic and organic species. In addition, the protein cage could be easily and routinely modified by design. The electrostatic environment within the cavity could be altered by site-directed mutagenesis to induce additional specific interactions, and the outer surface of the protein could be modified to facilitate specific biological targeting and surface interaction. The demonstration of gating illustrates a mechanism for molecular capture and release not previously exploited.

**Methods**

**Self assembly of virions and purification.** Empty virions were assembled from purified coat protein as previously described[1]. The empty virus particles were assembled by dialysis of a 1.0 mg ml

**Mineralization of the virion**

**Paratungstate.** Empty virions (50 µg) were incubated with inorganic precursor ions (75 mM NaH2WO4, 50 mM NH4Cl, pH 6.5) for 48 h at 6°C. Under these conditions the virus retains its open (swollen) form and allows all ions access to the central cavity. After incubation the virus solution was concentrated using ultracentrifugation membrane with a relative molecular mass cut-off of 100K, and extensively washed with acetate buffer (0.1 M) at pH 5.0. The mineralized virion was purified by ultracentrifugation on a 10–40% sucrose gradient. Bulk crystallization (in the absence of virion) was induced by slow evaporation of solvent at 6°C and yielded plate-like crystals. X-ray powder diffraction was measured on a Rigaku D/MAX diffractometer.

**Polyanetholesulfonic acid.** Empty virions (100 µg) were incubated in a 20 mg ml

**Transmission electron microscopy.** Liquid samples were placed on TEM grids (carbon-coated, formvar-covered, Cu) and excess solution removed with filter paper. Samples were imaged at 80 kV using a Zeiss EM 10CA or a Philips 400T and high-resolution electron microscopy was performed on a JEOL 4000EX operating at 400 kV. Virions were negatively stained using uranyl acetate.

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**Possibility of**

**Possible triggering of Heinrich events by ice-load-induced earthquakes**

A. G. Hunt & P. E. Malin

**Results**

North Atlantic sediments dating from the last ice age contain layers of rock fragments from northeastern Canada (so-called Heinrich layers)1. Like modern iceberg-borne sediments from Greenland, these layers have been attributed to ice-rafting episodes2–4. Six Heinrich layers have been documented and correlated with climate changes5–8. The layers, which are several centimetres thick, contain negligible amounts of foraminifera (which accumulate at a few millimetres per century), implying that they were deposited over just a few years. These ice-rafting Heinrich events are separated by progressively shorter intervals from about 40 to 6 kyr (ref. 9), and it has been suggested[9] that they are related to the Milankovitch cycles in the Earth’s orbital


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Correspondence and requests for materials should be addressed to T.D. (e-mail: idsglass@stanbus.scs.uc.edu) or M.Y. (e-mail: uplym@gemi.oscs.montana.edu).

North Atlantic sediments dating from the last ice age contain layers of rock fragments from northeastern Canada (so-called Heinrich layers)1. Like modern iceberg-borne sediments from Greenland, these layers have been attributed to ice-rafting episodes2–4. Six Heinrich layers have been documented and correlated with climate changes5–8. The layers, which are several centimetres thick, contain negligible amounts of foraminifera (which accumulate at a few millimetres per century), implying that they were deposited over just a few years. These ice-rafting Heinrich events are separated by progressively shorter intervals from about 40 to 6 kyr (ref. 9), and it has been suggested[9] that they are related to the Milankovitch cycles in the Earth’s orbital
parameters\textsuperscript{11}. Alternatively, they may be generated by forcing mechanisms arising from the internal dynamics of the Laurentide ice sheet\textsuperscript{12}. Here we suggest the possibility that the Heinrich events were precipitated by ice-load-induced earthquakes, analogous to those produced by reservoir water loads\textsuperscript{11}. We suggest that near its edge, the Laurentide ice sheet sheared the Earth's crust, inducing repeated failure that released the ice rafts. This region (along Canada's northeastern seaboard) shows evidence of both current\textsuperscript{14,15} and past seismic activity owing to postglacial rebound. Our model accounts for the intervals between both the Heinrich events and the evidence of palaeoseismicity, and can be tested by studying local sedimentary relationships.

That changing ice loads can cause crustal failures not related to plate tectonics is supported by recently discovered postglacial earthquake faulting in Fennoscandia\textsuperscript{14-17}. As direct evidence for similar postglacial earthquake activity in northeastern Canada, we cite uplifted shorelines on Baffin Island and Newfoundland\textsuperscript{18,19}. These shorelines lie near offshore belts of seismicity that do not coincide with plate boundaries\textsuperscript{14,15} (Fig. 1). Instead, the seismicity lies along the edges of the former Laurentide ice sheet, in the areas where the Heinrich events originated (Fig. 2).

Using a simple model of the crust and mantle beneath the expanding and contracting ice sheet (Fig. 2), we show that the strains and strain rates around the sheet's edges match those of tectonic crustal failure, resulting in massive elastic rebound and ice-sheet damage there\textsuperscript{20}. By using these strains and strain rates, it seems possible to explain the time intervals of both the Heinrich events and the uplifted postglacial shorelines in terms of earthquake recurrence intervals (Fig. 3; Table 1). We note that our model can be tested, for example, by palaeoseismic and dating studies near the edges of the ice.

![Figure 1 Map of modern seismic hazard in eastern Canada and the site of the 1929 M = 7.2 earthquake, which destroyed structures in Newfoundland\textsuperscript{21}](image1)

Numbered H1 to H6 with increasing age, Heinrich layers extend from the Labrador Sea to France and thin from west to east\textsuperscript{1}. Except for their far northern and eastern edges, significant fractions of events H1, H2, H4 and H5 are composed of carbonate materials originating from the Churchill Province in the region of northern Hudson Bay–Baffin Island\textsuperscript{22}. The materials in events H3 and H6, in contrast, are predominantly quartz and feldspar, suggesting that these two events have sediment and ice sources different from the other four. Heinrich events also seem to coincide with vegetation changes in Florida\textsuperscript{4}, increased ice storage in the Andes\textsuperscript{5}, and rises in sea level recorded in the Caribbean\textsuperscript{6}.

The main clue to the origin of Heinrich events is found by comparing total ice storage, as revealed by changes in the abundance of oxygen isotope 18 relative to isotope 16 ($\delta^{18}O$%\textsubscript{o}) with the aperiodicity of the time intervals between Heinrich events\textsuperscript{7}. From 110 to 112 kyr BP forwards, the average shape of the $\delta^{18}O$ curve with time is ramp-like, with an approximately linear increase in inferred ice volume. Placement of Heinrich event times on this ramp divides its underlying area into approximately equal parts (Fig. 3).

Because the area under a linear curve grows quadratically, differences between the squares of the Heinrich event times are nearly constant. Measuring from 110 BP, these differences for the first four events are within 20% of each other (Table 1). The differences for the last two events seem to be related to the large increase in the inferred rate of ice loading at the end of the glacial period\textsuperscript{2}, particularly for the interval between H2 and H3 (Fig. 3). Adjusting for the observed 50% increase in accumulation rate in the latter interval gives differences similar to the earlier events.

The mechanical response of cratonic crust and viscous mantle to ice loading\textsuperscript{23} can account for this nonlinear regularity in the time intervals of Heinrich events (Fig. 2). The flow of the mantle from...
load, \( x(t) \), and isostatic reaction, \( \lambda z \), can be found from the relation

\[
d\mathbf{v}/dt + \mathbf{v} = x(t) - \lambda z
\]

where \( \lambda \), \( \kappa \), and \( \lambda \) are constants and \( z \) is vertical displacement. This is a simple one-dimensional dashpot/spring model of mantle flow under a linearly increasing load. When the position of the load is far from isostatic compensation (which occurs for a depression of 900 m deep for an ice sheet 3,000 m thick), \( \lambda z \) can be neglected. The relaxation time, \( \tau \), is inversely proportional to the mantle viscosity, \( \lambda = 1/\mu \). If \( \mathbf{v} = 0 \) (that is, steady state), then a constant load results in a constant velocity, \( \mathbf{v} = 1/\mu \). With no external forcing, \( \kappa = 0 \) (for example, isostatic rebound after glaciation), equation (1) yields exponential relaxation of the velocity, vertical displacement, and associated strain rates, all involving the time constant \( \tau \). On the basis of rebound data, \( \lambda = 3 \) kyr (refs 14, 22). Under uniformly increasing force without compensation, the flow velocity is given by

\[
\mathbf{v} = \kappa (\mathbf{t} - \mathbf{t}^*) + (\kappa \tau) \exp(-\mathbf{t}/\tau)
\]

For \( \mathbf{t} \gg \mathbf{t}^* \), as would be true of recurrence intervals of 10 kyr, \( \mathbf{v} \propto \mathbf{t} \). Because the rate of crustal shearing is proportional to \( \mathbf{v} \), then \( \mathbf{d}/\mathbf{t} \propto \mathbf{t} \). Thus, the accumulated strain in a given interval must be proportional to \( \mathbf{t}^2 \); e.g., \( \mathbf{t}^2 \mathbf{d} \mathbf{t} \propto \mathbf{t}^3 \), where \( \mathbf{t}^* \) and \( \mathbf{t} \) are the final and initial times of the interval. By analogy with tectonic earthquake recurrence intervals, we expect ice-loading earthquakes to occur at intervals separated by 10\(^2\) increments in elastic strain. Under this assumption, the intervals between \( \mathbf{t}^* \) and \( \mathbf{t} \) must decrease with time. In isostatic rebound after glaciation, the earthquake strain increments remain the same, but the intervals between earthquakes increase as the strain rate decays.

Earthquakes imply faults; one may therefore ask: where are the faults responsible for the ice-loading earthquakes and why have they not been recognized as such? We expect that the greatest deformation, and hence the largest faults, occurred under the edge of the ice sheet, which was on the continental shelf (Fig. 2). To some degree the growth and flow of the ice sheet might have obliterated any associated surface rupture, making them hard to recognize directly, even if they are not underwater. Their existence, however, can be inferred from the seismicity of northeastern Canada, which includes

### Table 1 Heinrich event and shoreline uplift

<table>
<thead>
<tr>
<th>Event</th>
<th>Date (kyr BP)</th>
<th>Time intervals from ( \mathbf{t} = 110 ) kyr BP</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \text{Heinrich}^7 )</td>
<td>H6 ( 70 )</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>H5 ( 54 )</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>H4 ( 40 )</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>H3 ( 28 )</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>H2 ( 21 )</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>H1 ( 14 )</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>( \text{H}0 )(^\dagger)</td>
<td>-</td>
</tr>
<tr>
<td>( \text{Shoreline}^2 )</td>
<td>Baffin East</td>
<td>( \text{BE9} ) ( 8.6 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE8} ) ( 8 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE7} ) ( 7.5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE6} ) ( 6.8 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE5} ) ( 6 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE4} ) ( 5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE3} ) ( 4 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE2} ) ( 2.8 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BE1} ) ( 2 )</td>
</tr>
<tr>
<td>( \text{Baffin West} )</td>
<td>( \text{BW8} ) ( 6.7 )</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BW7} ) ( 6.0 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BW6} ) ( 5.8 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BW5} ) ( 5.5 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BW4} ) ( 5.2 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BW3} ) ( 4.7 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BW2} ) ( 4.2 )</td>
</tr>
<tr>
<td></td>
<td></td>
<td>( \text{BW1} ) ( 3.7 )</td>
</tr>
</tbody>
</table>

\( \dagger \) Takes into account the 50% increase in rate of ice loading between H3 and H2 (ref. 9).

\( \text{\dagger\dagger} \) Includes the Younger Dryas event as also triggered by an ice-load-induced earthquake.

\( \delta \text{O}^18 \) in benthic foraminifera as a function of time before present in thousands of years (\( \delta \text{O}^18 \) against time); \( \delta \text{O}^18 \) is the \( \delta \text{O}^18 \) differences. In a similar way, the \( \delta \text{O}^18 \) differences imply. In the times of the six Heinrich events H1 and H6 are indicated by arrows (see also Table 1; the time of the Younger Dryas event is indicated as H0). In b the ice thickness against time is approximated by three line segments of slopes \( \gamma \), \( \alpha \), and \( \varepsilon \). The segment with slope \( \gamma \) takes into account the 50% greater rate of ice accumulation between H3 and H2. As indicated by the vertical strip pattern, starting at 110 kyr BP the Heinrich events divide the area under the line segments into equal parts. Thus, the differences in the squares of the event times stays nearly constant.

![Figure 3](image-url)
earthquakes 30 km deep (Fig. 1), and from the presence of incrementally raised shorelines (Table 1). Both the earthquakes and stranded shorelines occur near the former edges of the ice sheet. Although only minor raised shorelines have been reported in Hudson Bay13, Baffin Island seems to have eight on its western coast and nine on its eastern coast18 (Table 1). On both coasts the stranded shorelines can be correlated over distances of 70 km, have vertical separations of ~13 m, and were created between 2,000 and 9,000 years ago. Uplifted shorelines are also found in southern Newfoundland, where as many as five strands separated by an average of 12 m can be found at one location19. In this case, the strands can be correlated over tens of kilometres, but they have not been accurately dated. The erosion surfaces behind all these shorelines are not raised in a block-like fashion by elastic rebound instead of on a doming isostatic adjustment.

The raised shorelines lie along the edges of eastern Canada's most seismically active zone, a mostly offshore belt running from the Great Lakes to Newfoundland and Baffin Island. This belt includes the 1929 Grandbanks M = 7.2 earthquake on the seaward-sloping continental shelf of Newfoundland, an event that produced a tsunami that killed 27 people and cut the first transatlantic telephone cable. As Fig. 1 shows, the belt includes zones where there is roughly a 1% chance per decade of horizontal accelerations exceeding 0.3 g (ref. 15). As in 1929, such rapid movements are enough to level unreinforced buildings.

Both the stranded shorelines and seismicity are consistent with our ice-loading strain model. First, the loading and unloading of the crust seems to produce roughly the same number of events: six Heinrich events and seven or eight shoreline uplifts. Second, the strain rates and recurrence intervals scale with each other: the crust was unloaded one-and-a-half orders of magnitude faster than it was loaded. The resulting earthquake recurrence times would also be much shorter, on the order of 102–103 yr. Further, the intervals between the shoreline events increases with time (Table 1).

Studies of ice dynamics have led to the suggestion that the large volume of sediments associated with Heinrich events can be accounted for by a 'binge–purge' cycle in the ice cap12. This cycle begins with ice-sheet thickening, with consequent sub-ice melting and higher seaward flow rates, which in turn produces ice-sheet thinning, slowing down and atachment of saturated subglacial regolith by freezing. The binge is estimated to take ~8 kyr and the purge ~750 yr. This mechanism has been shown to be compatible with the Heinrich event sediment volumes, but it predicts that the event intervals would be uniform and sedimentation rates slow enough to include foraminifera. Our model can account for the rapid purge by nearly instantaneous shaking and failure of the edge of the ice load—in effect, the earthquakes removed the resisting toes of the glacial ice slides. The inherent spatial variability of earthquake epicentres is also consistent with the differences in the Heinrich layer sediments and ice sources.

In addition to searching for and dating the faults implied by our model for the Heinrich events, it can also be tested by studies of sedimentary structures, relations and ages near their origins. If, for example, undisturbed Heinrich layers immediately overlie slumped or otherwise seismic disturbed sediments, our case would be stronger. Such features might be recognized and mapped with reflection profiling. The model could also be strengthened by further dating and palaeoecological studies of the raised shorelines, as well as a complete three-dimensional numerical simulation of the coupled ice dynamics and ice-load-induced failures.

We conclude by suggesting that if it is true that the Heinrich events were driven primarily by crustal, as opposed to orbital, mechanics, then so were their associated climate variations. It may be found that some ice-age climatic variations were feedback effects produced by earthquake-related unloading of the ice sheet. Such a finding would lead to a much simplified interpretation of the timescales of ice-age climate changes.

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Sphenoid shortening and the evolution of modern human cranial shape

Daniel E. Lieberman

Department of Anthropology, Rutgers University, New Brunswick, New Jersey 08903-0270, USA

Crania of ‘anatomically modern’ Homo sapiens from the Holocene and Upper Pleistocene epochs differ from those of other Homo taxa, including Neanderthals, by only a few features. These include a globular braincase, a vertical forehead, a dimunitive browridge, a canine fossa and a pronounced chin1–4. Humans are also unique among mammals in lacking facial projection: the face of the adult H. sapiens lies almost entirely beneath the anterior cranial fossa, whereas the face in all other adult mammals, including Neanderthals, projects to some extent in front of the braincase. Here I use radiographs and computed tomography to show that many of these unique human features stem partly from a single, ontogenetically early reduction in the length of the sphenoid, the central bone of the cranial base from which the face grows forward. Sphenoid reduction, through its effects on facial projection and cranial shape, may account for the appar-