

GEOPHYSICS

Conditions within Earth's crust determine whether human subsurface activities lead to earthquakes

Since 2009, the midwestern United States has seen a dramatic rise in earthquakes induced by human activities. Most of these events were caused by massive reinjection of wastewater produced during oil and

gas extraction (1, 2). In February 2016, regulators in Oklahoma called for an injection rate reduction after several major events up to moment magnitude 5.8 (M_w 5.8) occurred. On the other side of the Atlantic, an unprecedented number of earthquakes has followed gas extraction from the Groningen field in the Netherlands (3). The Dutch government imposed production cuts after

Fifty years ago, Healy *et al.* determined that fluid injection at depth causes the pore pressure to rise in a preexisting fault, reducing its strength and potentially leading to its failure (4). In contrast, fluid extraction at depth reduces the pore pressure, leading to compaction of the rock mass; the increased

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An evacuated house shows damage by depletion-induced earthquakes in Bedum near Groningen.

rock stress can drive a preexisting fault to failure. In both settings, the two factors that control induced earthquakes are operational parameters, such as the volume that is injected or produced, and natural conditions, such as the presence of preexisting faults and their ambient stress level. Operational parameters are often assumed to dominate, but that notion may reflect limited knowledge of the locations of preexisting faults and their ambient stress level. For regulatory measures to be effective in mitigating induced seismicity, it is crucial to understand the role of the natural conditions that existed before human activities.

Recent studies have started to collect measurements that help to validate hydromechanical modeling results of changes in pore pressure and stresses after fluid injection or production. For example, time-lapse shear-wave anisotropy analysis has provided direct evidence linking earthquake occurrences to pore pressure increase in the midwestern United States (5). Measurements of surface deformation derived from InSAR (Interferometric Synthetic Aperture Radar) have linked swarms of induced events 10 to 30 kilometers from the injection well to pore pressure increases of only ~0.1 MPa, even though pore pressure increases are predicted to be higher close to the well (2).

These data point to a mechanism through which wastewater injection induces seismicity (see the figure). During wastewater injection, the pore pressure front diffuses away from the injection wells along highly permeable channels in the disposal aquifers. Once the pressure front reaches large faults that intersect the basement below the reservoir and that are close to their point of tectonic reactivation, even a small pressure increase can trigger earthquakes. In support of this conceptual model, statistical assessment has shown that seismic activity is more highly correlated with the distance between the injection point and the basement than with the net injected volume (6). For mitigation of induced earthquakes, knowledge about the presence of faults and their ambient stress level is thus crucial.

At the Groningen gas field, subsidence measurements are now routinely used to calibrate modeled reservoir compaction (3). Subsidence measurements show that the observed seismicity is concentrated in areas of high compaction and subsidence, confirming the causal relationship between compaction and seismicity (3, 7). However, besides reservoir compaction, an optimal match between model predictions and observations can only be achieved if faults are

included (3, 7). Whereas earthquake-prone faults in the midwestern United States are often unmapped before injection activities, detailed subsurface information is available for the Groningen gas field, which includes more than 600 preexisting faults.

These studies suggest that gas production at the Groningen field induces seismicity through the following mechanism (see the figure). During gas production, the reservoir compacts, resulting in stress buildup along faults. Due to their preexisting offsets, reservoir compartments with different compaction levels are in contact along the faults. This differential compaction can magnify the amount of fault stress that builds up, speeding up the occurrence of earthquakes.

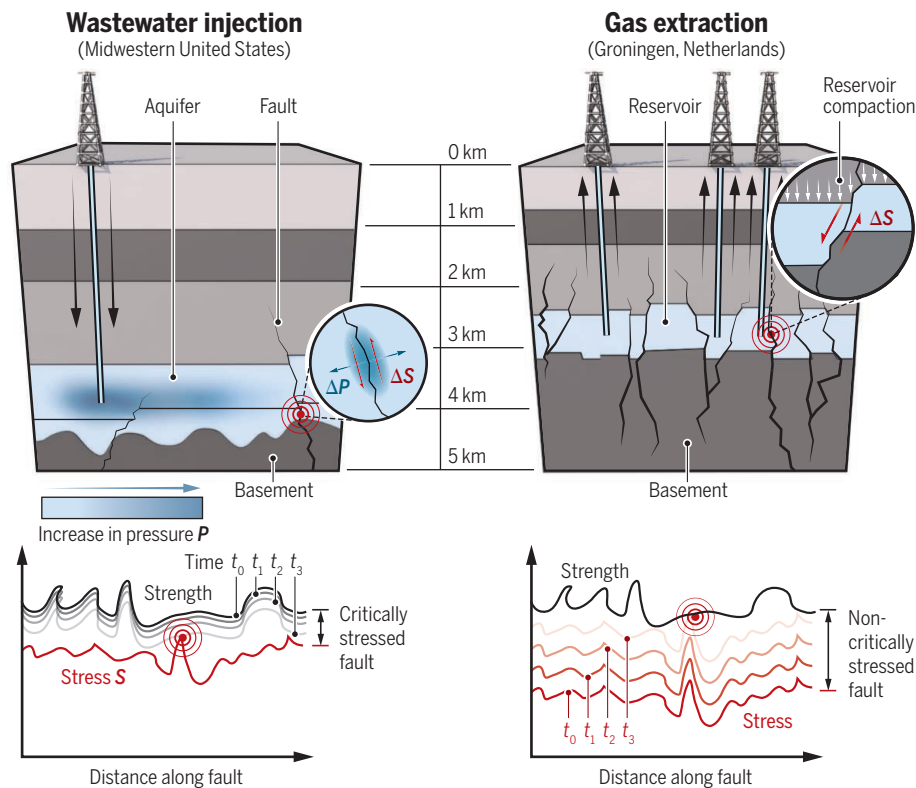
Induced events in the Groningen area have been recorded only after a reduction of the reservoir pore pressure by ~10 MPa, which results in a rock stress increase of similar magnitude. This is generally taken as evidence that before production, most Groningen faults were far from tectonic reactivation (3, 7, 8). This observation is in

contrast with the situation in Oklahoma, where pressure perturbations of ~0.1 MPa can trigger earthquakes. This suggests that the crust there is critically stressed, that is, it contains a subset of faults that are close to failure and that can be reactivated by a slight stress perturbation (9).

Comparison of the two cases leads to the conclusion that the timing and location of induced earthquakes are controlled by the spatial distribution and geometry of preexisting faults and ambient stress conditions before subsurface activities. But what about the size of these induced events? A working assumption is that induced ruptures remain confined to the rock volume affected by fluid pressure or stress changes (10). Recent studies challenge this assumption and reveal that induced earthquakes might potentially rupture outside of the affected volume (11–14). In this case, the maximum size of induced earthquakes might be controlled by natural preexisting fluctuations of the stress along the fault, in the same way as natural events.

Mechanisms of induced seismicity

Both wastewater injection and gas extraction can cause induced earthquakes. Detailed observations from the midwestern United States and Groningen, Netherlands, show that in both cases, preexisting conditions in Earth's crust are of central importance.



Injection of wastewater leads to a nonuniform pressure front. When the pressure front hits a critically stressed fault, an earthquake is triggered. Only a small strength decrease is needed to trigger an event.

Gas extraction leads to rock compaction, causing a buildup of stress. Sufficient shear stress is necessary to cause the initially noncritically stressed fault to fail, causing an earthquake.

Both for fluid injection in the midwestern United States and for gas extraction at the Groningen field, a spectrum of evidence underscores the central role of preexisting faults and their stress level before subsurface human activities. Mitigation strategies to limit induced earthquakes that solely rely on operational parameters, such as the injected or produced volume, can be used as a first approximation, but much added value lies in subsurface characterization of fault populations and ambient stress. In the case of poor prior knowledge of the subsurface, continuous monitoring of seismicity can help illuminate unmapped faults. For this exercise, recent advances in artificial intelligence should be key to optimize real-time earthquake detection and location during operations (15). The state of stress along these preexisting faults can be defined by hydromechanical modeling, calibrated by measurements that are independent of operational parameters, as, for example, surface deformation derived from InSAR.

“...a spectrum of evidence underscores the central role of preexisting faults and their stress level before subsurface human activities.”

Instead of considering the subsurface as a uniform tank that undergoes changes controlled by well operations, a continuous data-informed and physics-based modeling approach should incorporate properties of the affected rock volume, including that of the reservoir and faults. Only then can mitigation strategies for induced seismicity, such as targeted injection or production reduction at identified high-risk sites, be optimized. ■

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STRUCTURAL BIOLOGY

Energy powerhouses of cells come into focus

High-resolution structures reveal core design features of rotary ATP synthases and ATPases

By Patricia M. Kane

In every kingdom of life, rotary adenosine triphosphate (ATP) synthases and adenosine triphosphatases (ATPases) play key roles in cellular energy generation and release processes. In mitochondria, chloroplasts, and bacteria, F-type (F_1F_0) ATP synthases synthesize ATP using energy from a proton gradient. They are also able to perform the reverse process, generating proton gradients by ATP hydrolysis. The related V-type (V_1V_0) ATPases have similar structures and serve as proton pumps. Two articles in this issue report structures of membrane-embedded ATP synthases from yeast mitochondria [Srivastava *et al.*, page 619, (1)] and spinach chloroplasts [Hahn *et al.*, page 620, (2)]. Together with other recent structures, these articles define core design principles of rotary ATP synthases and ATPases but also highlight organism-specific differences.

Rotary ATP synthases require the tightly coupled activities of two different motors: a membrane motor that uses energy from the proton gradient to drive rotation of a central rotor and a peripheral motor that uses rotation-driven conformational changes to support ATP synthesis. The peripheral motor (designated F_1 or V_1) contains the ATP binding sites. In the binding-change mechanism proposed by Boyer (3), three equivalent catalytic sites alternately bind adenosine diphosphate (ADP) and phosphate, synthesize ATP, and release the ATP produced, driven by conformational changes in the central rotor connected to the membrane motor. In 1994, the first high-resolution structure of F_1 captured the catalytic sites in three different conformations (4). More recently, structures of intact vacuolar H^+ -ATPases (V-ATPases) (5, 6) and ATP synthases (7), including the spinach chloroplast enzyme reported by Hahn *et al.*, have shown the central rotor at multiple distinct rotational positions. These structures support the universality of the binding-change mechanism and provide additional insights into mechanisms of rotational coupling.

The membrane motor (F_0 or V_0) includes a ring of proteolipid c subunits (the c-ring) bound to the central rotor (see the figure). The c-ring rotates against a membrane-bound stator complex that extends peripherally along the F_1 or V_1 domain and prevents unproductive rotation. Structures of the membrane motor were slower to emerge for a number of reasons, including the inherent dynamics of rotary motors and the loss of structural features or resolution with detergent solubilization. In the absence of high-resolution structural data, biochemical and genetic experiments provided insights into the structure and mechanism of the membrane motors. Extensive mutagenesis of F_0 and V_0 subunits in model organisms identified conserved charged and polar amino acids in the membrane-embedded a and c subunits (see the figure) that are required for function (8, 9). These residues provide a path for proton transport through the membrane at the interface of the single a subunit and the c-ring.

Recent cryo-electron microscopy structures are clarifying the membrane motor structure and its coupling mechanisms and revealing both common and organism-specific structural features. Allegretti *et al.* (10) first visualized two long transmembrane helices that are almost horizontal in the membrane, oriented in parallel with the membrane surface, in the a subunit of F_0 from the green alga *Polytomella*; this has proven to be a notably conserved feature of membrane motors (1, 2). Amino acids of the a subunit that are involved in proton transport align along one face of these horizontal helices, which make close contact with the c-ring. This contact separates aqueous pores that come from either side of the membrane. Taken together, previous data (6, 7, 10, 11) and current structures (1, 2) invoke an ATP synthesis mechanism in which each essential c-ring carboxylate of the c-ring is protonated at one side of the membrane, travels through the membrane on the outside of the c-ring until it encounters the a subunit, and is deprotonated, releasing the proton at the opposite side of the membrane (11).

The amino acid side chains at the a-c subunit interface are critical for the protonation-deprotonation cycle (see the figure). Recent

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How earthquakes are induced

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