

Figure 1 Face to face — three caricatures showing different features. The supernormal caricature of Ronald Reagan (a), produced by Susan Brennan's caricature generator, exaggerates features that are particular to Reagan's face (b), in relation to an average face (c). It is very difficult to give any biological significance to the 'Reagan-ness' of these faces, suggesting that principles of recognition are important in the evolution of signals.

were made more feminine. In contrast, and surprisingly, both men and women preferred slightly feminized male faces over the original or more masculine faces. The Japanese and Scottish subjects more or less agreed in their judgements, with one interesting variation — both groups preferred more exaggeration in faces of their own nationality than in faces from the other country.

When both male and female faces were feminized, subjects rated the person behind the face as more honest, cooperative and emotional. But the result was mixed regarding parental abilities. Whereas the feminized male was rated the better father, the average female was rated a better mother than the feminized female. More masculine faces were thought to be more dominant and older, but judgement of intelligence did not depend on masculine or feminine appearance.

On the basis of these results, Perrett *et al.*² suggest that if a female chooses a male with feminine characteristics, she may get a more honest and cooperative partner who is a better father to her children. The authors also suggest that this might have limited the degree to which male and female faces differ in humans (sexual dimorphism). But masculinity may be an advantage in social competition and dominance — this might explain why male faces do not exactly match female preferences.

Perrett and colleagues have dealt with a classical subject, dating back to Darwin's theory of sexual selection^{3–5}, that is still not satisfactorily resolved. Why do sexual signals look the way they do, and what information do they convey? According to one opinion (favoured in the paper), sexual signals convey important information about the quality of a partner⁴. All aspects of the signal serve this function. This view holds that, during evolution, signals that are reliable cues for fertility, genetic quality (yielding high-quality offspring) and parental abilities have emerged. Males and females have evolved to respond accurately to these cues in partner choice.

A different opinion is that factors related to transmission and recognition are important for the evolution of signals^{5,6}. According to this theory, biases in the sense organs or nervous system influence how we perceive and react to signals. So, sexual signals may just signal sex — the fact that we find some faces more attractive than others may be a by-product of recognition, and may not be linked to partner quality. For instance, it is well known that by altering specific aspects of a familiar stimulus, supernormal effects (stronger reactions)⁷ can usually be produced, even when the new stimulus does not provide the receiver with more information.

As an example of this second view, Fig. 1 shows an average face, a faithful portrait of the former President of the United States,

Ronald Reagan, and a caricature of him⁸. The caricature was produced by an algorithm similar to that used by Perrett and colleagues, exaggerating the differences between the average face and the face of Reagan. This caricature clearly captures and enhances some 'Reagan-ness' from the original portrait. But it is very difficult to ascribe a biological value to such a quality or to argue that we have evolved a Reagan-ness detector.

Thus, before we can distinguish between these two theories, we need to learn more. Studies of faces may provide an excellent testing ground for this. Perhaps the outcome will be a little of both — some aspects of sexual signals will give information about partner quality and others will not. But it is not enough to know what is preferred. We need to find out whether the emotions that faces evoke really do reveal qualities such as parental or social abilities, and we also need to know more about recognition. □

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Earthquakes

A deficit vanished

Steven N. Ward

The southern California earthquake deficit — “Now you see it, now you don't”, according to an article in the *Bulletin of the Seismological Society of America*¹ by Stein and Hanks. Not done with smoke and mirrors, the vanishing act enlisted a careful revision of our understanding of twentieth-century historical seismicity, and it helped to spirit away a thorny issue that arose in 1995. This was the year that the Working Group on California Earthquake Probabilities² (WGCEP/95) published the report “Seismic Hazards in Southern California: Probable Earthquakes 1994–2024”.

The WGCEP/95 document was remarkable because it struck a new path into earthquake hazard analysis. Previously, geologists and seismologists had independently staked out their own areas of earthquake rate estimation, the heart of hazard calculation. Geologists reckoned the recurrence interval and magnitude of earthquakes by locating

active faults, mapping their length and total offset, and resolving their age. Seismologists concentrated on historical catalogues. Earthquake patterns of the past, they presumed, reflect where and how often earthquakes should strike in the future, and how large they will be. Early geological and seismological studies tended to be piecemeal with few cross-checks. Publication of WGCEP/95 brought order to the field by combining diverse information into a quantitative and consistent multidisciplinary assessment. Space geodesy catalysed the leap forward by providing accurate measures of the pattern and pace of tectonic strain that eventually manifests itself as earthquakes.

Of all the advances in WGCEP/95, one finding seemed to take on a life of its own — the preferred seismicity model predicted twice the number of magnitude 6 to 7 earthquakes than had actually been observed since 1850 (red area, Fig. 1, overleaf). The shortfall

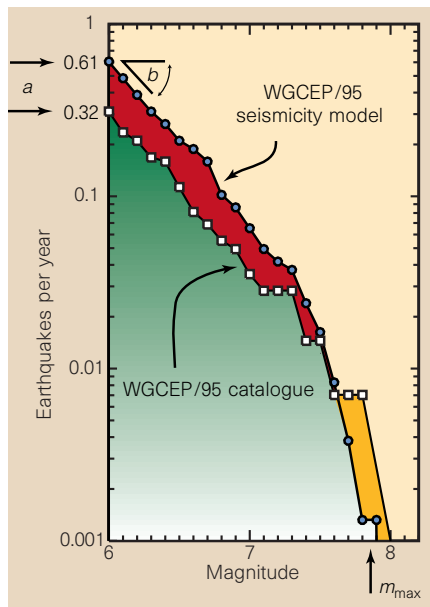


Figure 1 Annual rates of earthquakes greater than magnitude m , for southern California. The lower curve follows the observed rates of earthquakes since 1850 as catalogued by WGCEP/95. The upper curve follows the predictions from the preferred WGCEP/95 seismicity model. The red no-man's-land between the curves is southern California's earthquake deficit, now closed by Stein and Hanks¹, and Field *et al.*^{3,4}. Seismic moment M_T has units of Nm yr^{-1} .

put experts in a pickle. If the earthquake deficit was genuine, then they had to tell California that it faces a far rougher ride than it had experienced in the recent past. If the deficit was an artefact, then one or both of the curves in Fig. 1 was wrong, and those experts had to discover why if they expected to maintain credibility. To address the issue, Stein and Hanks¹ revisited the WGCEP/95 earthquake catalogue. In parallel, Field, Jackson and Dolan^{3,4} dissected the WGCEP/95 seismicity model.

Earthquake rate curves for any region are characterized by four parameters: the a -value, the b -value, the maximum magnitude m_{max} and the total earthquake moment rate M_T . The a -value relates to $n_{>}(m_{\text{min}})$, the annual number of earthquakes greater than a specified minimum magnitude ($m_{\text{min}} = 6$ for WGCEP/95). The b -value equals the negative slope of $\log[n_{>}(m)]$ versus magnitude at m_{min} . Magnitude, m_{max} , indicates the largest possible earthquake expected to strike the region. Moment rate, M_T , is proportional to the sum of the slip in every earthquake multiplied by the area faulted. In the long run, the moment rate observed from earthquakes should mirror the product of the region's tectonic strain rate times its area.

Although it would appear to be an objective matter to determine a , b , m_{max} and M_T for each curve in Fig. 1, many factors confound the process. Complicating the observational

side is the fact that the lowest-magnitude earthquakes fix a and b , whereas m_{max} and M_T depend almost entirely on the highest-magnitude ones. Sampling errors cause difficulties at both ends of the magnitude range. Values a and b suffer from incomplete accounting of small earthquakes decades ago when the density of seismic stations was low. Values m_{max} and M_T hinge upon catching the rarest earthquakes. These might recur at intervals longer than California's written history. Multidisciplinary assessments such as WGCEP/95 have an advantage over earthquake catalogues alone in that they employ geodetic strain rates and geological fault data to constrain M_T . Even so, the data inputs and internal modelling decisions that eventually shaped the predicted seismicity curve in WGCEP/95 are subject to considerable uncertainty.

Stein and Hanks¹ conclude that the factor of two mismatch between the rate of observed earthquakes and the rate predicted by the WGCEP/95 seismicity model is not real. The blame splits equally between undercounts of historical earthquakes and overstatements springing from assumptions in the WGCEP/95 model. That is, the lower curve in Fig. 1 should be raised part way, and the upper curve dropped. Stein and Hanks's review of post-1903 earthquakes gives $a = 0.49 \text{ yr}^{-1}$ and $b = 1.0$ compared to $a = 0.32 \text{ yr}^{-1}$ and $b = 0.8$ from WGCEP/95's post-1850 catalogue. They argue that many magnitude 6 to 7 earthquakes were not reported before 1903, which is why they chose the later date as a starting point.

Field *et al.*^{3,4} further identified and removed several elements that inflated M_T in the seismicity model used in WGCEP/95. These included a mistranslation of magnitude into moment and the assumption of

non-Poissonian earthquake recurrence. The most recent seismicity models that draw upon the new analyses^{3,4} show no difference between predicted and observed earthquake rates, or between the total moment expended by earthquakes and that inferred from geodesy and geology.

A deficit vanished? One might dismiss this 'news' as much ado about nothing, or conclude that earthquake hazard assessments have yet to evolve beyond magic. In my view, however, these developments demonstrate the new and critical self-evaluation mechanisms available in the current class of multidisciplinary hazard models. In particular, scientists can now recognize where a statistically significant inconsistency exists, quantitatively assess the effects of the various parameters on the inconsistency, and decide whether it is real or artificial. They can then act in response or revise the model, exactly as in the exercises carried out by Stein and Hanks, and Field *et al.*

In truth, of course, unsettled aspects of earthquake recurrence abound even in California, host to the world's most complete earthquake laboratory. Earthquakes will always be difficult to predict because of their elusive and hidden nature. Against these odds, we can make progress only by arming ourselves with the widest range of geophysical weapons. □

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Translation

Cinderella factors have a ball

Richard J. Jackson

When ribosomes synthesize proteins by translating messenger RNA, they must start the decoding at the correct point on the mRNA. In eukaryotes this is achieved by a scanning mechanism: the small (40S) ribosomal subunit binds to the mRNA near the 5' cap, and then scans in a 5'–3' direction until it encounters the first AUG triplet, which normally serves as the site for initiation of translation¹. This process requires at least nine distinct initiation-factor proteins, composed of a total of no fewer than 25 polypeptide chains.

It is easy to imagine interfering with this complicated machinery by omitting certain factors in the hope of catching the 40S subunit in the actual act of scanning. Imagination is one thing, experiment quite another,

however — hence the appeal of the paper on page 854 of this issue by Pestova *et al.*². They provide the first connections between individual eukaryotic initiation factors (eIFs), notably eIF1 and 1A, and the scanning process.

The factors directly involved in initiation-site selection have hitherto been considered to be eIF2, 3, 4A, 4B and the eIF4F complex. The first step in the process is the formation of a pre-initiation complex: the 40S ribosomal subunit binds eIF3 and a complex of eIF2 associated with the initiator methionyl-transfer RNA (Met-tRNA_i) and GTP (see ref. 3 for further details). This pre-initiation complex then interacts with the mRNA close to the 5' end, probably through the eIF4F complex, which binds to eIF3