

mation processing^{7,8}. Grandmother cells are the theoretical limit of sparseness, where the representation of an object is reduced to a single neuron.

Quiroga and colleagues³ report what seems to be the closest approach yet to that limit. They recorded neural activity from structures in the human medial temporal lobe that are associated with late-stage visual processing and long-term memory. The structures concerned were the entorhinal cortex, the parahippocampal gyrus, the amygdala and the hippocampus, and the recordings were made in the course of clinical procedures to treat epilepsy.

The first example cell responded significantly to seven different images of Jennifer Aniston but not to 80 other stimuli, including pictures of Julia Roberts and even pictures of Jennifer Aniston with Brad Pitt. The second example cell preferred Halle Berry in the same way. Altogether, 44 units (out of 137 with significant visual responses) were selective in this way for a single object out of those tested.

The striking aspect of these results is the consistency of responses across different images of the same person or object. This relates to another major issue in visual coding, 'invariance' (Fig. 1). One of the most difficult aspects of vision is that any given object must be recognizable from the front or side, in light or shadow, and so on. Somehow, given those very different retinal images, the brain consistently invokes the same set of memory associations that give the object meaning. According to 'view-invariant' theories, this is achieved in the visual cortex by some kind of neural calculation that transforms the visual structure in different images into a common format⁹⁻¹¹. According to 'view-dependent' theories, it is achieved by learning temporal associations between different views and storing those associations in the memory¹²⁻¹⁴.

Quiroga and colleagues' results³ set a new benchmark for both sparseness and invariance, at least from a visual perspective. Most of the invariant structural characteristics in images of Jennifer Aniston (such as relative positions of eyes, nose and mouth) would be present in images of Julia Roberts as well. Thus, any distributed visual coding scheme would predict substantial overlap in the neural groups representing Aniston and Roberts; cells responding to one and not the other would be rare. The clean, visually invariant selectivity of the neurons described by Quiroga *et al.* implies a sparseness bordering on grandmotherliness.

However, as the authors discuss, these results may be best understood in a somewhat non-visual context. The brain structures that they studied stand at the far end of the object-representation pathway or beyond, and their responses may be more memory-related than strictly visual. In fact, several example cells responded not only to pictures but also to the printed name of a particular person or object.

Clearly, this is a kind of invariance based on learned associations, not geometric transformation of visual structure, and these cells encode memory-based concepts rather than visual appearance.

How do you measure sparseness in conceptual space? It's a difficult proposition, requiring knowledge of how the subject associates different concepts in memory. The authors did their best (within the constraints of limited recording time) to test images that might be conceptually related. In one tantalizing example, a neuron responded to both Jennifer Aniston and Lisa Kudrow, her co-star on the television show *Friends*. What seems to be a sparse representation in visual space may be a distributed representation in sitcom space! In another example, a neuron responded to two unrelated stimuli commonly used by Quiroga *et al.* — pictures of Jennifer Aniston with Brad Pitt and pictures of the Sydney Opera House. This could reflect a new memory association produced by the close temporal proximity of these stimuli during the recording sessions, consistent with similar phenomena observed in monkey temporal cortex¹⁵.

Thus, Quiroga and colleagues' findings may say less about visual representation as such than they do about memory representation and how it relates to visual inputs. Quiroga *et al.* have shown that, at or near the end of the transformation from visual information about

object structure to memory-related conceptual information about object identity, the neural representation seems extremely sparse and invariant in the visual domain. As the authors note, these are predictable characteristics of an abstract, memory-based representation. But I doubt that anyone would have predicted such striking confirmation at the level of individual neurons. ■

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EARTH SCIENCE

New Madrid in motion

Martitia P. Tuttle

A new network of geodetic field stations has greatly improved monitoring of relative motion across a seismic zone in the central United States. It seems that rapid deformation is occurring across this fault system.

The New Madrid seismic zone lies 50–200 km from Memphis, Tennessee, and was the site of devastating earthquakes in 1811 and 1812. These earthquakes included three mainshocks and many aftershocks, with the largest earthquake having an estimated^{1,2} magnitude of 7.4–8.1. Historically, New Madrid has been the most seismically active region in central and eastern North America — what hazard might it pose today?

This question has been the subject of vigorous debate in the Earth science and earthquake engineering communities^{3,4}. The report by Smalley *et al.* (page 1088 of this issue)⁵ will enlighten that debate. From high-precision Global Positioning System (GPS) measurements, made with a newly installed network of field stations, they conclude that the New Madrid seismic zone is rapidly deforming at rates of the same order of magnitude as those at the boundaries of tectonic plates. This result

contradicts earlier estimates of low rates of deformation or strain accumulation⁶, but is consistent with geological evidence for the occurrence of repeated 1811–1812-type (New Madrid) events in the past 2,000 years^{7,8}.

During the past 12 years, geologists found a record of New Madrid events in the form of earthquake-related features, known as sand blows (Fig. 1, overleaf). The sand blows formed as a result of liquefaction, a process by which water-saturated sandy sediment below the surface is liquefied and vented on the ground in response to strong earthquake shaking. Detailed study of hundreds of sand blows, some of which are associated with Native American archaeological sites, led to the interpretation that they formed during three, possibly four, New Madrid events of magnitude 7.6 or greater in the past 2,000 years⁸.

In the 1990s, geophysicists undertook GPS measurements using a network of field



50 YEARS AGO

"Personal Factors in Accident Proneness." Dr. J. A. Smiley... has made full use of his position as medical adviser to an aircraft-manufacturing company to study the accident histories of 6,450 men, and to examine in detail 87 men classified as accident prone... His thesis may briefly be stated — accident-prone individuals are usually emotionally disturbed, with associated hypothalamic misfunction which, it is tentatively suggested, produces minor imbalance of adrenalin and acetylcholine with concomitant behaviour disturbance... [they] also show 'anxiety' sweating in interview, albumin in the urine specimens collected during medical examination, a seven-fold increase in peptic ulcer incidence and a more than four-fold increase in incidence of other medical symptoms... The problem remains, however, whether these men may adequately be described as accident prone... the main conclusion to be drawn is that proneness to report minor injury can be added to the list of other known clinical signs of emotional disturbance.

From *Nature* 25 June 1955.

100 YEARS AGO

Prof. E. Wiedemann, of Erlangen, sends us a short statement of observations described in his work on electric discharges... He agrees with Mr. Jervis-Smith as to the action of ozone, and advises persons who work for a long while with influence machines not to have these machines situated in the working room. "Ozone belongs to the poisonous gases, and is the more dangerous, since the injurious effects are not manifest at the time; on the contrary, breathing the gas produces at first a feeling of exhilaration, but afterwards it has a depressing effect on the nervous system... During my observations I have suffered somewhat severely from nervous disturbance (hyperesthesia of the feet) due to breathing ozone. These lasted for one or two years. Moreover, I always experience discomfort after performing experiments in my lectures on Tesla discharges."

From *Nature* 22 June 1905.

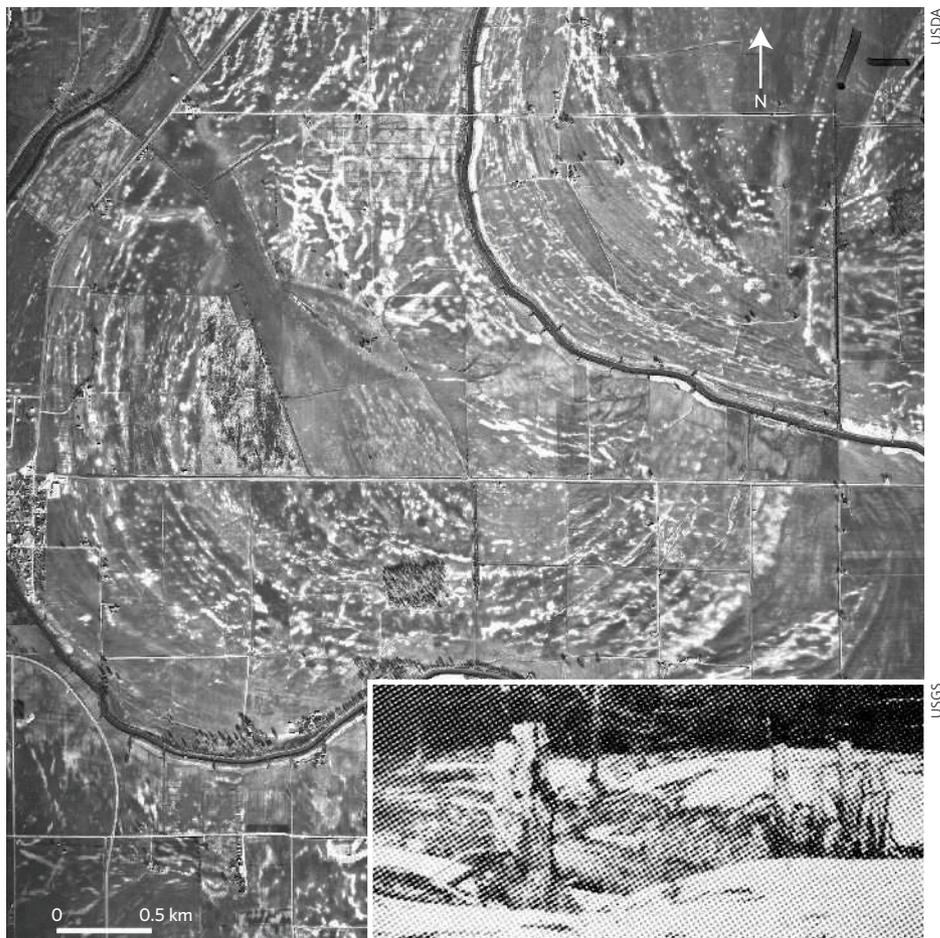


Figure 1 | Earthquake evidence. This aerial photograph, taken in 1964, shows light-coloured sand blows near the Little River in northeastern Arkansas. The inset is a ground view, taken about 100 years ago, of trees killed by the sand deposits. Some of the sand blows were produced by the New Madrid earthquakes of 1811–12; others were formed in prehistoric times. Smalley and colleagues' analyses⁵ are consistent with the finding of fairly frequently repeated New Madrid events surmised from this geological record.

stations spanning the New Madrid region to ascertain the rate at which the seismic zone is deforming in response to tectonic forces⁶. Measurements were collected for several days in 1991, 1993 and 1997, the upshot being estimated relative motion across the seismic zone of 1.4 mm yr^{-1} with uncertainties of $\pm 3 \text{ mm yr}^{-1}$. These motions were interpreted to be indistinguishable from zero, and therefore indicative of low rates of strain accumulation. Given that earthquake frequency is related to the build-up and release of strain energy, it was concluded that the New Madrid seismic zone produces either magnitude 8 earthquakes every 5,000–10,000 years or magnitude 7 earthquakes every 1,000 years⁶. This finding differed from that of the geological studies.

In the late 1990s, a network of permanent GPS stations was installed in the New Madrid region. The new network included many improvements; for example, stations were located close to and on both sides of major New Madrid faults, and strong H-beams were used that are less susceptible to non-tectonic movements than the 1-inch-diameter steel rods used in the previous network⁵. Because

the new stations are permanent and collect data continuously, the repeated setting up of field stations, which introduced measurement errors in the previous studies, could be avoided.

Smalley *et al.*⁵ have analysed four years of continuous measurements from the new network. They calculate relative motions across the seismic zone that are similar ($1\text{--}2.7 \text{ mm yr}^{-1}$) to those measured during the 1990s but with much smaller uncertainties — at most 25% of those of the previous studies. Smalley *et al.* point out that in the earlier GPS data the tectonic signal was lost in the noise, and interpret their results to indicate high rates of strain in the New Madrid seismic zone.

They also find relative motions across the seismic zone that are consistent with expected fault movements as inferred from present-day seismicity⁹ and recent fault studies⁷. For example, relative motion indicates that bedrock slips over itself along a major northwest-oriented fault, known as the Reelfoot thrust fault, that is inclined towards the southwest (see Fig. 2 on page 1089). The new findings are persuasive because they help to explain the geological observations of frequent New

Madrid earthquakes, and they make sense in terms of the active faulting in the region.

One of the most interesting results is that motions in the surrounding region are low compared with motion in the seismic zone itself. This unusual behaviour differs from that at plate boundaries, raising questions about the driving forces and earthquake processes within plates. Post-seismic afterslip — a process by which fault displacements at depths of several kilometres are expressed at the surface for a period of time following an earthquake¹⁰ — seems a reasonable explanation for the regional pattern of motions. However, there is currently insufficient information about the physical properties of the Earth in the New Madrid region to test this and competing models.

Smalley and colleagues' results are consistent with the findings of geological studies that the seismic zone produced earthquakes about every 500 years of magnitude 7.6 or greater. As such, they provide scientific justification for the adoption of stricter earthquake provisions in the building codes for Memphis and other cities in the central

United States⁴. Looking ahead, installation of additional field stations close to known faults would help to define their extent and further quantify their strain rates. One of the most daunting challenges will be to develop and test models that can explain how such large and frequent earthquakes are produced in the New Madrid region, and to see if the models also apply to other intraplate regions. ■

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was parthenogenetic, a sample of larvae was reared to adulthood in the laboratory — more than 1,900 females were produced over nine generations, but no males.

Ischnura hastata is common in North and South America, yet it occurs in these regions as a classically sexual species with both males and females. The concept of 'geographic parthenogenesis'⁵ proposes that the parthenogenetic forms of a species are more likely to occur in certain areas — such as higher latitudes and altitudes, and on islands — because of the different selection pressures that organisms face under these conditions^{6,7}. One possibility, therefore, is that certain damselfly species can include both sexual and parthenogenetic forms, and that on arriving on a remote island it is the parthenogenetic form that is favoured, at least initially, owing to the difficulty of finding mates.

One might wonder why standard sexual reproduction does not kick in once the population builds up in size, but perhaps local conditions continue to favour parthenogenesis. Indeed, *I. hastata* frequents temporary or recently established habitats⁴, and Cordero Rivera *et al.* note that there is anecdotal evidence of local extinctions of pond populations. Furthermore, chance may play a role in the establishment and maintenance of parthenogenesis: *I. hastata* is also found on the Galapagos Islands, but the population contains both males and females⁸.

In at least some odonates, there may be a degree of predisposition to parthenogenesis; for example, there is evidence that unfertilized eggs of the dragonfly *Stylurus ocellatus* can be artificially induced to develop⁹. Moreover, certain parasites that are inherited only in the female line can manipulate their insect host into producing predominantly (or only) female offspring¹⁰. Cordero Rivera and colleagues are testing whether any microbial agents are responsible for driving the absence of males in *I. hastata*, but they have ruled out one potential bacterial parasite, *Wolbachia*, which infects a range of other insect groups¹⁰. If parthenogenesis in *I. hastata* is parasite mediated, then the microbial agent might have had a beneficial effect on its host in the initial phases of colonization, allowing individuals to reproduce without mates.

There have also been intriguing accounts of other damselfly species on remote archipelagos. In particular, on the islands of Fiji, it seems that females of the damselfly *Nesobasis rufostigma* actively defend territories over aquatic habitats, whereas the males, which are infrequently encountered, reside some distance from the stream¹¹. This phenomenon has been dubbed 'sex-role reversal'¹¹ and, if confirmed, would be the first example in an odonate. If males are in short supply, then this unusual mating system might be explained by female competition for access to males¹². Furthermore, males of two rarer Fijian damselflies (*N. flavostigma* and *N. caeruleascens*) have

EVOLUTIONARY BIOLOGY

Island of the clones

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The discovery of an all-female population of damselflies in the Azores archipelago provides a novelty for entomologists. It also highlights the unique selection pressures faced by species that colonize islands.

Tucked away in the journal *Odonatologica* comes a paper by Cordero Rivera and colleagues¹ that will surprise many entomologists, and will exercise biologists studying evolution on islands and the mechanisms of sex determination. Cordero Rivera *et al.* have discovered that a species of damselfly on the Azores reproduces parthenogenetically (Fig. 1). This form of reproduction, in which females produce eggs that develop without fertilization by males², has been recorded in

almost all insect groups. But until now it was not known to occur in any natural populations of damselflies or dragonflies (the Odonata)³.

The Azores archipelago lies 1,500 km from the coast of Europe. Inspired by a report⁴ that only females of the damselfly *Ischnura hastata* had ever been found there, Cordero Rivera and his team visited 15 localities on six of the islands. Although more than 330 adult specimens of *I. hastata* were examined, none of them was male. To test whether the species



Figure 1 | Reproduction without fertilization in a damselfly. A female *Ischnura hastata* lays eggs in a pond on the island of Pico, Azores. (Courtesy of A. Cordero Rivera, Univ. Vigo.)