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100 YEARS AGO

At the recent meeting of the British Association at Southport I heard numerous complaints (repetitions of those I have heard at not a few previous meetings) by the general public, members of the Association, on the too technical character of the papers read before it. These complaints referred to all the sections except, perhaps, those of anthropology, geography, and educational science. One overheard too often to be pleasant such remarks as "I am interested in zoology, but what is the good of coming to listen to such a paper as this? I have no idea what the speaker is talking about" the paper, in one specific instance, was cytological, and of great value undoubtedly; and, "I have not gained much by becoming a member of the Association; the papers are all over my head." These complaints are being made by well educated men and women interested in science, but not versed in its technicalities... The general public have really some cause for complaint that their subscription has been obtained from them on a misunderstanding. From Nature 29 October 1903.

50 YEARS AGO

The death of Dr. E. P. Hubble from a heart attack, on September 28 at the age of sixtythree, has robbed the world of astronomy of its leading authority on nebulæ... On his return home in 1919 after the First World War. Hubble was appointed to the staff of the Mount Wilson Observatory. He soon established his position as a leading worker in the field of the nebulæ. He showed that diffuse nebulæ owe their illumination to stimulation by radiation from hot stars. He then turned to the classification of the spiral nebulæ and showed conclusively that they are stellar systems lying outside our galaxy. He established a scale of distances from a study of the brightest stars and Cepheid variables in the nebulæ. Working with Humason and the 100-in. telescope, he established the velocity-distance law from the red shifts of lines in the spectra; this increased the reliable distances to which astronomers could plumb the depths of space up to 250 million light-years. He studied the law of the red shifts in all its bearings, aiming always at cutting down the number of conflicting interpretations, and he kept always an open mind on the kinetic or other explanations of the red shifts. From Nature 31 October 1953.

Palaeontology **Smart-winged pterosaurs**

David M. Unwin

Why did ancient flying reptiles have so much processing-power in the back of their brain? To provide highly responsive flight control, is an answer to emerge from an innovative analysis of pterosaur skulls.

rains, not surprisingly, are rarely fossilized, leaving a large gap in our knowledge of the anatomy of most extinct organisms. Fortunately, in some vertebrates - mammals, birds, dinosaurs and pterosaurs — the brain fits so tightly into the braincase that its external features are faithfully reflected by the contours of the inner surface of the bones that enclose it. Unfortunately, opportunities to recover these data from fossil material are infrequent and often involve destructive techniques, thereby excluding many valuable specimens from consideration.

High-resolution X-ray computed tomography, which has proved extremely helpful elsewhere in palaeontology¹, offers the possibility of looking inside braincases and generating a digital cast without damaging the fossil. Witmer and colleagues² have successfully applied this new technique to two kinds of pterosaur (see page 950 of this issue). These are a poorly understood group of flying reptiles that flourished during the Mesozoic (between 251 million and 65 million years ago) and which remain the subject of controversy³. The new work clarifies several aspects of pterosaur neural anatomy, and prompts some startling new ideas regarding their locomotion and behaviour.

Witmer et al. looked at rare, uncrushed skulls of two specimens. One was of Rhamphorhynchus, a long-tailed, crow-sized creature from the Upper Jurassic (163-144 million years ago). The other was of Anhanguera, a large, short-tailed form dating to the Lower Cretaceous (144-97.5 million years ago). In trade jargon, Rhamphorhynchus and Anhanguera are respectively 'basal' and 'derived' - loosely put, 'primitive' and 'advanced'.

The new findings confirm earlier studies4,5

showing that pterosaurs had a remarkably bird-like brain - for example, it had reduced olfactory lobes and large, laterally displaced optic lobes. This suggests that, like modern birds, pterosaurs were usually more interested in what they could see than what they could smell. The pterosaur brain seems to have been relatively small when scaled against body mass, however, with the brains of both Rhamphorhynchus and Anhanguera plotting below the limits for extant birds. Witmer et al. propose, convincingly, that this is primarily related to differing ancestries: birds inherited their grey matter from relatively big-brained theropod dinosaurs⁶, whereas pterosaurs inherited theirs from relatively small-brained archosaurs7.

The most striking results concern brain structures called floccular lobes and semicircular canals. Floccular lobes extend outwards and backwards from the rear part of the brain and are exceptionally large in pterosaurs, while semi-circular canals encircle the floccular lobes and are involved in balance. In living vertebrates the orientation of the semi-circular canals, in particular the lateral canal, relates directly to the 'alert' position usually adopted by the head during locomotion and other activities. Exploiting this association, Witmer et al. show that, whereas the head posture of Rhamphorhynchus and probably all basal pterosaurs was normally horizontal, in Anhanguera and most, if not all, other derived forms, the head was directed sharply downwards at about 30°.

This is an elegant piece of work. But explaining the difference



Figure 1 Ground truth? Pterosaur head orientations inferred by Witmer et al.², and their interpretation in terms of posture when on the ground. a, The horizontal alignment of the lateral semi-circular canal, indicated by the red line, is consistent with a crouching posture and forwarddirected head in basal pterosaurs, represented by Rhamphorhynchus. b, In derived forms such as Anhanguera, the reorientation of the canal can be interpreted in terms of an upright position and a downward-pointing head. (Pterosaurs redrawn from ref. 10 and not to scale.)

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in head orientation is not easy. Maybe, suggest Witmer et al., it relates to the large cranial crests borne by many derived pterosaurs, including Anhanguera, which could have affected skull aerodynamics during flight and required some repositioning of the head. But this is inconsistent with the recent discovery of large cranial crests in several basal pterosaurs8,9, and their occasional absence in Anhanguera for instance. Alternatively, could head depression be related to feeding? Anhanguera and other derived pterosaurs have been interpreted as aerial fish-catchers¹⁰, a feeding style that would have benefited from a downwarddirected skull - especially as it may have permitted some stereoscopy, enabling accurate judgement of distance to a moving target. Again, however, there are inconsistencies. Many derived pterosaurs, such as the flamingo-like, filter-feeding form Pterodaustro, were not airborne fishers. But several basal forms were, as a specimen of Rhamphorhynchus with a fish in its belly eloquently testifies. Yet they still fished successfully with their level heads.

A more persuasive answer to this problem lies on the ground (Fig. 1). Like their reptilian ancestors, basal pterosaurs with their relatively short arms were condemned to walk with the body and head in a nearhorizontal position, aligned with the lateral semi-circular canal. By contrast, functional studies¹¹ suggest that derived forms used their relatively long arms to prop themselves upright. But because they still needed to see in front of them as they walked, this required some restructuring of the skull and its posture, one consequence of which would have been reorientation of the semicircular canals.

Attractive as they are, these ideas do not address the extraordinarily large size of the floccular lobes in pterosaurs. Witmer *et al.* suggest that this region of the brain may have been responsible for coordination of the head, eye and neck, permitting gazestabilization during flight. Such an ability would have been useful for aerial hunters that relied primarily on sight. But not all pterosaurs had such a lifestyle, so this is not an entirely satisfactory explanation.

Far more convincing, in my view, is Witmer and colleagues' proposal that the floccular lobes were responsible for processing large volumes of sensory data generated by the wing membranes. This is a plausible idea, because in other vertebrates the floccular lobes receive sensory inputs from skin and muscles. New, extraordinarily well-preserved pterosaur material from Germany¹² and China¹³ shows that the wing membranes were highly complex, containing structural fibres, blood vessels and a fine network of muscles. These features would have given the wings the ability to collect and transmit sensory information about local conditions within the membranes, enabling pterosaurs to build up a detailed map of the forces experienced by the wings from moment to moment. Processing via the floccular lobes could have allowed them to respond very rapidly, through localized contraction or relaxation of muscle fibres within the membrane and coordination with fore- and hind-limb movement. Equipped with their 'smart' wings, pterosaurs would have had excellent flight control. Despite their antiquity, they could even have outperformed modern birds and bats.

David M. Unwin is in the Museum für Naturkunde, Humboldt Universität zu Berlin, Invalidenstrasse 43, Berlin 10115, Germany.

e-mail: david.unwin@rz.hu-berlin.de

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Balancing the unbalanced

Frank Moss and John G. Milton

Elderly but healthy people are often seriously injured in falls. Exploiting the phenomenon of stochastic resonance, biological physicists have designed a shoe with a vibrating insole that helps maintain balance.

o stay upright, the human body uses exquisitely complicated and delicate feedback control, operating through

the sensory and central nervous systems¹. It does so in ways similar to a performer balancing a pole on a finger², by applying minute forces and torques through muscles in the feet, ankles and knees. But these muscles must receive signals that convey information on how much force to apply through which muscles. This information is initially supplied to the central nervous system by neurons located in various joints and the soles of the feet. With ageing, the sensory thresholds of these neurons increase. The information they transmit is therefore degraded, impairing balance.

As they report in the Lancet³, J. J. Collins and his colleagues have successfully tested an idea about how information from the periphery of the sensory system might be enhanced. They find that the application of a random vibratory stimulation to the soles of the feet can reduce 'postural sway', and improve balance in both young and elderly human subjects. Inexpensive, easily constructed insoles, made of viscoelastic silicone gel, generated the stimuli. Three mechanical vibrators, about the size of three stacked coins, were embedded in each insole, one in the heel and two in the forefoot regions. They were driven by random voltage generators, and the resulting vibrations propagated throughout the gel.

Collins *et al.* measured postural sway by monitoring the position of reflective markers attached to each subject's shoulder using motion-analysis cameras. They applied the vibratory stimuli at random times, unknown to the subjects, and at strengths that were slightly below each subject's threshold of perception. Analysis of tracings of the marker motion quantified the threshold at which sensory feedback mechanisms kicked in to stabilize sway, enabling the authors to statistically characterize the subjects' balance control⁴. All subjects showed clear improvement with the introduction of vibratory random fluctuations ('noise'), with the elderly group showing the largest benefit. Other studies indicate that patients whose balance is impaired by stroke or by nerve damage associated with diabetes might also benefit⁵. The insoles have not yet been tested on subjects in motion, however, nor have they actually been shown to reduce falls, for example during walking or climbing stairs.

How does the beneficial effect arise? The information content of subsensory stimuli is known to be increased by the addition of noise through stochastic resonance^{6,7}. This phenomenon is rooted in the physics of systems with thresholds, such as sensory neurons. Such systems transmit information by means of markers, or action potentials, which are generated when a threshold is crossed. Noise added to a subthreshold stimulus increases the threshold-crossing rate, thus improving the quality of the transmitted information, and the optimal noise intensity yields the maximum improvement. Much has been written on the subject (for instance, for a review focused on perception, see