

and thus to the reduction in availability of suitable habitat. If this is a major threat to the saiga, it too should also be tackled urgently. The Mongolian subspecies is apparently not affected by poaching, but is urgently in need of protection because of its very small size (about 336; ref. 1). Concentrating solely on the problem of poaching sidelines this population.

If poaching is not yet affecting population sizes, one reason may be the recent reduction in legal hunting, and particularly in the proportion of males in the legal hunt. Thus, a key issue not being addressed is the acquisition of large revenues from saiga poaching by commercial traders, revenues which are being denied to the government cooperatives and local people who bear the costs of saiga preservation. As horns did not form a large proportion of the cooperatives' revenues before 1990, this lost opportunity goes unacknowledged. If saigas are to continue to form a valuable and respected resource for the residents of their range areas, the revenues should be accruing to the correct parties.

Clearly, poaching must be brought under control rapidly both to secure the future of the population and to allow legal harvests to continue. However, we would like to present the story of the saiga antelope as a positive one. It is rare to find a species that reached near-extinction but recovered in 30 years, and which was then harvested for 40 years in an apparently sustainable way. The products of that harvest were both sold to local people as cheap meat and went to support the general economy. The population was well researched and regularly censused. Only in the last five years has the financial situation for the management authority become problematic and poaching a serious problem. This rare example of a successful, sustainable management system should be supported by the international community before it is lost, and managers should be enabled to use the new markets for horn effectively, to secure the future of the saiga antelope and its users.

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Touching the phantom limb

SIR — Despite a vast clinical literature on phantom limbs (for example, refs 1, 2), there have been no experimental studies on the effect of vision on phantom sensations. We used a mirror to resurrect the phantom visually in order to explore intersensory effects³.

Nine arm amputees were studied (see table). A tall mirror was placed vertically on the table, perpendicular to the patient's chest, so that he could see the mirror reflection of his normal hand 'superimposed' on the phantom. In the first seven patients, when the normal hand was moved so that the phantom was visually perceived to move in the mirror, it was also 'felt' to move; that is, a vivid kinaesthetic sensation emerged. (These sensations could not be evoked with the eyes closed.) In patient D.S., kinaesthetic sensations were evoked even though he had not experienced movements in the phantom for the preceding 10 years. Repeated use of the mirror over a 3-week period (15 min per day) resulted in a permanent 'telescoping' of the hand in this patient.

In six of these patients, a similar revival of movements in the phantom occurred if the experimenter's hand was substituted for the patient's normal hand. No such effects were seen in four normal 'control' subjects given identical instructions.

Five patients (R.L., P.N., R.T., B.D. and J.P.) experienced painful involuntary 'clenching spasms' of the phantom hand ("As though the nails were digging in the phantom," as J.P. told us). Remarkably, in four of them, the spasms, which normally lasted for an hour or more, could be relieved immediately on looking into the mirror and opening 'both' hands simultaneously. (R.T. compared 8 eyes-closed/eyes-open trials; P.N., 8 trials; R.L. 6 trials and J.P. 12). No eyes-closed trials were effective in relieving spasms.

When motor commands are sent from the premotor and motor cortex to clench the hand, they are normally damped by error feedback from proprioception. In a phantom, such damping is not possible, so the motor output is amplified further and this outflow itself may be experienced as a painful spasm. Visual feedback from the mirror may act by interrupting this loop.

The elimination of spasms was unequivocal in all four patients. Interestingly, the associated pain also disappeared. Given the notorious susceptibility of pain to 'placebo', however, double-blind experiments would be needed to determine whether the effect on pain is a specific consequence of the visual feedback.

In two patients (J.P. and L.C.), touching the normal hand evoked precisely localized

CLINICAL DETAILS OF PATIENTS TESTED

| Patient | Age | Pathology | Location | Time of testing |
|---------|-----|---------------------------------------|--|-----------------------------------|
| J.P. | 31 | Self inflicted amputation | To right forearm 5 cm below elbow | 5 months after amputation |
| R.L. | 56 | Melanoma infiltrating brachial plexus | Right upper limb disarticulation at shoulder 1 year after onset of melanoma | 2 months after amputation |
| P.N. | 48 | Arm crushed in car accident | Left arm 8 cm below elbow | 7 months after amputation |
| R.T. | 55 | Sarcoma infiltrating ulnar nerve | Left arm 6 cm above elbow | 7 months after amputation |
| P.N.N. | 40 | Airplane propeller cut off arm | Right arm above elbow | 8 years 3 months after amputation |
| D.B. | 23 | Car accident, crush injury | Left arm, disarticulation of shoulder | 3 years after amputation |
| D.S. | 28 | Brachial plexus avulsion | Left above-elbow amputation 1 year after avulsion | 9 years after amputation |
| B.D. | 29 | Brachial plexus avulsion | Right above-elbow amputation 2 years after avulsion | 3 months after amputation |
| L.C. | 23 | Crush injury following train accident | Right forearm below elbow | 19 days after amputation |

All patients underwent a thorough neurological evaluation by one of us (V.S.R.) to rule out central nervous system pathology and to ensure that their 'mental status' was normal. None of the patients (except L.C.) could produce voluntary movements in the phantom. When D.S., J.P. and D.B. were touched on the lower-face region, ipsilateral to the amputation, sensations were referred to the phantom fingers, as occurred in some of the patients we had previously studied^{4,5}. D.S. also had magnetoencephalographic evidence of 'remapping' in the cortex^{5,6}. B.D. did not show any inter-manual referral of sensations whether or not he used the mirror box. Also, he could not generate any movements in the phantom, whether or not he used the box, and there was no relief from pain. ("It's frustrating, doctor. I can see it move; I want it to move; but it doesn't feel like it's moving!") Thus, the procedure may not work on all patients and the reasons for the variability remain to be explored.

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touch sensations in exact mirror-symmetrical locations in the phantom. In two additional patients (R.L. and D.B.), such effects occurred only if the patient simultaneously 'saw' the phantom being touched — a curious form of 'synaesthesia' (14 out of 14 trials). Vibration was also referred intermanually in all four patients, but there was no referral of pain, heat or cold. For example, if patients J.P. or L.C. dipped their intact hand in a jar of cold water with ice cubes, they responded that they felt the 'cubes' in the phantom, but not the cold. These effects are not due to suggestion or confabulation for three reasons. First, touch and vibration were referred but not temperature or pain, and this was consistent across patients. Second, the patients experienced a latency of 2–4 s before the sensation was felt in the phantom. Third, the patients often expressed considerable surprise when they noticed these effects.

Even in normal individuals, the two hands may be linked in the brain as a result of frequent co-activation. Hence, sensory input from the left thumb might project not only to the right hemisphere but — by unidentified commissural pathways — to mirror-symmetrical points in the other hemisphere. This latent input may ordinarily be too weak to express itself, but when the right hand is amputated this input may become either disinhibited or progressively strengthened, so that touching the left hand evokes sensations in the right hand as well. The reason pain and temperature are not referred may be that there are no commissural pathways concerned with these modalities. In R.L. and D.B., however, the reactivation may not reach threshold amounts unless visual 'confirmation' is also provided (cells with bimodal receptive fields⁷ may be involved).

Our technique lends itself readily to brain-imaging studies. There must be considerable latent plasticity in the adult human brain. Precisely organized new pathways spanning the hemispheres can emerge in three weeks or less. Also, there must be great interaction between vision and touch, and so the strictly modular, hierarchical model of the brain currently in vogue must be replaced with a dynamic, interactive model in which 're-entrant' signalling⁸ plays an important role.

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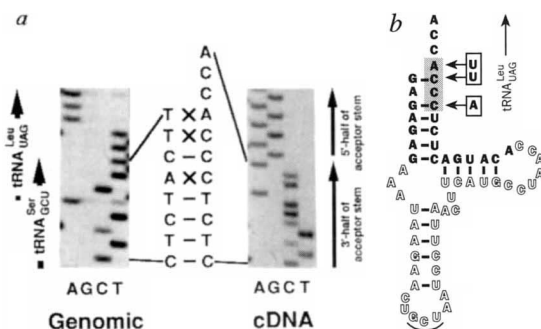
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tRNA editing in metazoans

SIR — RNA editing, the modification of a transcript such that it differs from that inferred from its genomic sequence, is a common phenomenon in organelles of plants and unicellular organisms¹. In metazoan mitochondria, polyadenylation is used to create termination codons² and may be involved in the editing of several

acceptor stem had been replaced by cytidine residues (see figure). Curiously, one mismatch remained unchanged. In addition, the discriminator base had changed from the genomic uridine residue to an adenine residue. Because the complete sequence of the mitochondrial genome of the platypus is known⁶ and import of cyto-



a, cDNA and gene sequences of the platypus mitochondrial seryl-tRNA anticodon GCU (tRNA^{Ser}_{GCU}). Only relevant parts of the autoradiographs of sequence ladders are shown. Differences between the genomic and cDNA sequences are indicated by crosses, identities by dashes. b, Inferred secondary structure of platypus mitochondrial tRNA^{Ser}_{GCU}. The region used for primers in cDNA synthesis and polymerase chain reaction (PCR) are indicated by outlined characters. The region that in the gene overlaps with the downstream tRNA for leucine is indicated by the shaded background and the genomic versions of the edited nucleotide positions are boxed. tRNA circularization, cDNA synthesis, PCR and sequencing were carried out as in ref. 3. RNA of platypus and the clone carrying the platypus tRNA^{Ser}_{GCU} gene were gifts from A. Janke. The primer used for cDNA synthesis was 5'-GGATTAGCAGTCTTATT-3' (platypus-S-FW). For amplification, this primer and 5'-TTAACTTCATGCCTAAC-3' (platypus-S-RV) were used.

transfer RNAs in land snails³. In addition, another RNA-editing mechanism changes an anticodon of a tRNA in marsupial mammals^{4,5}. Here we show that the tRNA of a monotreme mammal is edited at three positions and that RNA editing is likely to be common in metazoan mitochondria.

The genomic sequence for the mitochondrial seryl-tRNA anticodon GCU of the platypus (*Ornithorhynchus anatinus*)⁶, a monotreme mammal, has two mismatches and one G-U base pair in its predicted aminoacylacceptor stem. In contrast, other features of the inferred tRNA structure are common to other seryl-tRNAs (data not shown). To investigate whether these unusual features are corrected by an RNA-editing mechanism affecting the 5' or 3' halves of the acceptor stem, RNA was circularized³ by T4 RNA ligase before synthesis of complementary DNA. The acceptor stem was then amplified, cloned and the nucleotide sequence of more than 20 clones determined.

It was found that one mismatched adenosine residue and the uridine residue of the G-U base pair in the 3' part of the

acceptor stem had been replaced by cytidine residues (see figure). Curiously, one mismatch remained unchanged. In addition, the discriminator base had changed from the genomic uridine residue to an adenine residue. Because the complete sequence of the mitochondrial genome of the platypus is known⁶ and import of cyto-

plasmic tRNAs into mitochondria is not believed to occur in vertebrates⁷, the tRNA gene is unlikely to represent a pseudogene; more probably, an RNA-editing mechanism changes the primary sequence of the tRNA post-transcriptionally. RNA editing has recently been found to affect aminoacylacceptor stems of mitochondrial tRNAs in a protozoan (*Acanthamoeba castellanii*)⁸ and a land snail (*Euhadra herklotsi*)³. In the latter, the 13 changes observed in three tRNA species are similar to the three changes found in the platypus in that they involve events in the 3' parts of the aminoacylacceptor stems. A further similarity between the platypus and land snail is that the genes of the tRNAs affected overlap with downstream genes encoded on the same strand. Such overlaps also exist in the mitochondrial

genomes of various metazoans, for example, human, mouse and chiton^{9–11}. Thus, the finding of tRNA editing in a land snail as well as the platypus makes it likely that an RNA-editing activity is involved in the processing of the transcripts in many, if not all, metazoan mitochondria.

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