with the action could be gain-regulated during the dichoptic stimulation, and consequently subject to homeostatic enhancement after normal binocular synchronous vision is re-established. This hypothesis is consistent with previous evidence that suppression from consciousness of monocular signals, without visual deprivation, can also promote a homeostatic shift of ocular dominance[9,10]. More generally, the idea of a top-down signal gating homeostatic plasticity provides a novel framework for understanding the effects of short-term deprivation. We suggest that homeostatic plasticity could be driven by mismatch between contingent sensory signals and sensory signals anticipated by voluntary action.

Clearly, the de-synchronization of contingent and expected visual information produces large errors during voluntary actions, but also monocular contrast deprivation is associated with an increase of visuo-motor error, as the patched eye fails to transmit the visual changes produced by the participant's own movements. Besides reinterpreting the impact of physical exercise and environmental enrichment in modulating primary visual cortical plasticity[1], this model also highlights the importance of predictive and/or multisensory error signals in shaping visual processing based on one's own actions.

In conclusion, our results show that ocular dominance plasticity is not only related to the balance of monocular V1 representations but also gated by internal motor and/or cognitive information, suggesting that homeostatic plasticity is at the service of sensory-motor coordination.

SUPPLEMENTAL INFORMATION

Supplemental information includes two figures and experimental procedures, and can be found with this article online at https://doi.org/10.1016/j.cub.2023.08.062.

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AUTHOR CONTRIBUTIONS

G.S.: Methodology and Resources; C.S.: Investigation; P.B.: Formal Analysis and Resources; P.B., M.C.M.: Writing – first draft; P.B., C.S., M.C.M.: Conceptualization; All authors: Writing – Review & Editing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse and equitable conduct of research.

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Genomic insights into the mystery of mouse mummies on the summits of Atacama volcanoes

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Our understanding of the limits of animal life is continually revised by scientific exploration of extreme environments. Here we report the discovery of mummified cadavers of leaf-eared mice, *Phyllotis vaccarum*, from the summits of three different Andean volcanoes at elevations 6,029–6,233 m above sea level in the Puna de Atacama in Chile and Argentina. Such extreme elevations were previously assumed to be completely uninhabitable by mammals. In combination with a live-captured specimen of the same species from the nearby summit of Volcán Llullaillaco (6,739 m)[1], the summit mummies represent the highest altitude physical records of mammals in the world. We also report a chromosome-level genome assembly for *P. vaccarum* that, in combination with a whole-genome re-sequencing analysis and radiocarbon dating analysis, provides insights into the provenance and antiquity of the summit mice. Radiocarbon data indicate that the most ancient of the mummies are, at most, a few centuries old. Genomic polymorphism data revealed a high degree of continuity between the summit mice and conspecifics from lower elevations in the surrounding Altiplano. Genomic data also revealed equal numbers of males and females among the summit mice and evidence of close kinship between some individuals from the same summits. These findings bolster evidence for resident populations of *Phyllotis* at elevations >6,000 m and challenge assumptions about the environmental limits of vertebrate life and the physiological tolerances of small mammals.

During the course of high-altitude surveys of mammals in the Puna de Atacama, we discovered a total of 13 mouse mummies on the summits of Volcán Salín (6,029 m; Argentina and Chile), Volcán Púlar (6,233 m, Chile), and Volcán Copiapó (6,052 m, Chile) (Figures 1A and S1). On the summits of Salín and Púlar, we excavated mummified cadavers of multiple individual mice from the crevices of volcanic rock (Figure S1B,E,F).

Radiocarbon dating revealed that the Salín and Copiapó specimens are at most a few decades old, as lower bounds of the 95.4% high-probability-density range were uniformly >1955 AD. The Volcán Púlar samples are at most ~350 years old, as the lower bounds of the 95.4% high-probability-density range were 1670–1675 AD and upper bounds were >1950 AD (Table S1).

To test whether the summit mice are representative of a genetically distinct subpopulation with a colonization history distinct from that of conspecifics from the surrounding region, we first sequenced and assembled a chromosome-level *de novo* reference genome of *P. vaccarum*. We assembled PacBio HiFi long-read sequences (26.7x coverage) followed by chromosome-scale scaffolding using Illumina sequencing of long-range proximity ligation of endogenous chromatin (Omni-C technology). We used these data to generate a 2.66 GB assembly that was highly contiguous (scaffold N50 = 147.8 Mb; N90 = 59.3 Mb) with near complete coverage of conserved eukaryotic orthologs (251 of 255 complete BUSCO copies, 98.4%). Most of the genome was assembled into 19 large scaffolds, consistent with a complete chromosome-scale assembly matching the described karyotype for the species (2N = 38)[2]. We then generated low-coverage whole-genome sequences of 44 mice (1.3–13.2x coverage, median 2.6x), including the mummies from Volcán Salín (*n* = 8), Volcán Púlar (*n* = 4), and Volcán Copiapó (*n* = 1), the single live-trapped mouse from the summit of Volcán Llullaillaco, and 30 additional live-trapped specimens from lower elevation sites (3,100–5,070 m) in the region (Figure 1A).

Our sample of mice from the summits included an equal number of males and females: the live-captured Llullaillaco mouse was male, and genomic analysis revealed that the set of summit mummies included 6 males and 7 females. The Salín sample also included two pairs of close relatives (coefficients of kinship, $\Theta = 0.427$ and 0.418), representing full siblings or parent–offspring pairs, whereas remaining individuals were not closely related ($\Theta < 0.01$). Since dispersal in small rodents is typically sex-biased and generally occurs over short distances[3], the equal representation of males and females in our sample of summit mice and evidence for close kinship within groups from the same summit is consistent with the idea that the summit mice represent members of resident populations and were not simply transient sojourners. In conjunction with video records, identification of active burrows, and other observations[1,4,5], summit records of both live and dead mice bolster evidence for long-term resident populations of *Phyllotis* at elevations >6,000 m.

Average genome-wide pairwise nucleotide diversity for the total sample of mice was typical for natural populations of rodents (π = 0.42%)[6]. After filtering our dataset to 42 mice, excluding two closely related individuals, we confirmed that the summit mice exhibited close affinities to the *Phyllotis vaccarum* reference genome and other live-trapped specimens of *P. vaccarum* from lower elevations on the flanks of the same volcanoes and in the surrounding Altiplano (Figure 1B,C). Results of a model-based clustering analysis revealed very low population structure in the total sample, as proportional assignments of ancestry to genetically defined clusters were similar for mice from all localities (Figure 1B). A principal component analysis of genomic variation also revealed low levels of population structure across the surveyed region, as PC1 and PC2 explained only 6.94% and 2.36% of total variation, respectively, and the patterning of variation did not distinguish the set of summit mice from mice collected at less extreme elevations in the surrounding region (Figure 1C).

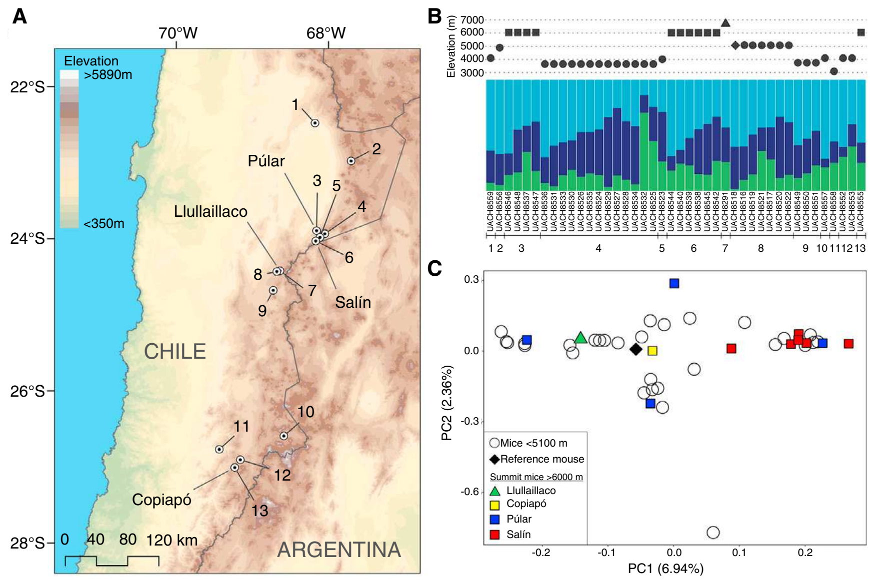

Figure 1. Genomic variation in *Phyllotis vaccarum* from the summits and surrounding regions of four >6,000 m volcanoes: Púlar, Salín, Llullaillaco, and Copiapó.
(A) Sampling localities for mice from >6,000 m summits and conspecifics from lower elevations in the surrounding Altiplano. (B) Structure analysis reveals low levels of population structure across the surveyed region, as indicated by similar estimates of admixture proportions in 42 unrelated specimens of *Phyllotis vaccarum* from spatially disparate sites that span a range of elevations (3,100–6,739 m). Samples are grouped by locality and numbered according to panel A. The elevation at which each specimen was collected is displayed above the estimated admixture proportions; squares denote summit mummies, the triangle denotes the live-caught mouse from the summit of Llullaillaco, the diamond denotes the mouse that served as the source of the reference genome, and circles denote live-caught mice from the surrounding Altiplano. (C) Principal component analysis of genomic variation in the same set of samples shown in panel B.

The first reports of mice at elevations > 6,000 m came not from biologists but from archaeologists, as mouse mummies have occasionally been discovered in association with Incan ceremonial structures and burial sites at or near the summits of several high Andean volcanoes[7,8]. It has even been hypothesized that the animals were used as part of sacrificial rituals[8]. The mouse mummies considered here were not found in close association with Incan ceremonial structures and radiocarbon dating confirm that they were all < 500 years old, so they could not have been contemporaneous with the Incas. Although we can rule out transport by Incas to explain the existence of mouse mummies on the summits of Atacama volcanoes, it remains a mystery as to why the animals ascended to such extreme elevations of their own accord.

SUPPLEMENTAL INFORMATION

Supplemental information includes one figure, one table, and experimental procedures, and can be found with this article online at https://doi.org/10.1016/j.cub.2023.08.081.

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AUTHOR CONTRIBUTIONS

J.F.S., S.L., M.Q.-C., G.D., and J.M.G. designed the research; J.F.S., M.Q.-C., N.M.B., and G.D. performed the field work; S.L. and T.B.W. performed the laboratory work; S.L., J.C.O., G.D., and J.M.G. analyzed data; J.F.S., S.L., M.Q.-C., N.M.B., G.D., and J.M.G. prepared figures and wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Illusory optical defocus generated by shaded surface texture

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The human visual system is tasked with the problem of extracting information about the world from images that contain a conflated mixture of environmental sources and optical artifacts generated by the focal properties of our eyes. In most contexts, our brains manage to distinguish these sources, but this is not always the case. Recent work showed that shading gradients generated by smooth three-dimensional (3D) surfaces can elicit strong illusory percepts of optical defocus[1,2] — the perception of illusory blur is only eliminated when the surface appears attached to self-occluding contours[3], surface discontinuities[1], or sharp specular reflections[1,2], which all generate sharp ('high spatial frequency') image structure. This suggests that it should also be possible to eliminate the illusory blur elicited by shaded surfaces by altering the surface geometry to include small-scale surface relief, which would also generate high-frequency image structure. We report the surprising result here that this manipulation fails to eliminate the perception of blur; the fine texture fails to perceptually 'bind' to the low-frequency image structure when there is a sufficient gap between the spatial scales of the fine and coarse surface structure. These findings suggest that discontinuous 'gaps' in the spatial scale of textures are a segmentation cue the visual system uses to extract multiple causes of image structure.

The main effect can be experienced in Figure 1A, which was created by adding fine surface relief to a smooth bumpy plane rendered as a matte (Lambertian) surface. It is clear from informal inspection that the shading generated by the coarser scales elicits a sense of blur even though the fine