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Normal somatotopy in SI of a tyrosinase-negative albino cat

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Because of known abnormalities in both the visual and auditory pathways of tyrosinase-negative albino cats, we mapped the primary somatosensory cortex (SI) in one such cat electrophysiologically. We detected absolutely no sign of abnormality in terms of somatotopy, and conclude that if anomalies do exist in the albino somatosensory system, they are either very subtle or lie outside SI.

Albinism is a relatively rare genetic defect characterized by the absence of melanin, an ubiquitous biological pigment. Associated with this rather specific metabolic deficiency are certain sensory disturbances. For example, relative to pigmented conspecifics, albinos have visual spectral sensitivity shifted towards the red¹¹, reduced visual acuity²⁴, and oculomotor disturbances^{4,5,19}. The most significant anatomical abnormality within the visual system of albinos is that almost all retinofugal fibers which would normally project ipsilaterally decussate at the optic chiasm to innervate the contralateral lateral geniculate nucleus^{7,10,17,18,23,26}. Abnormalities have also been observed in the albinistic auditory system^{1,8,9,14,20,21,25,32}, raising the possibility that other sensory systems might also show some abnormalities. We report here on the somatotopic map in the first somatosensory area (SI) of a tyrosinase-negative albino cat.

Our mapping procedures were identical to those employed in other mapping experiments in the somatosensory cortex of cats in this laboratory^{13,15}. Briefly, the cat was anesthetized with a mixture of ketamine hydrochloride and xylazine and placed in a stereotaxic frame. A craniotomy and durotomy were performed over SI and surrounding cortex, and an acrylic dam was constructed around the craniotomy to contain a pool of silicon. A photograph was made of the exposed cortex so that an enlarged print could be used to site electrode penetrations with respect to the surface vasculature. We used the published map of Felleman et al.¹³ to guide our electrode

penetrations, and to evaluate the relative normality of the resulting map. We conclude, based on 152 multiunit recording sites, that the somatotopic map in SI of this tyrosinase-negative albino cat is normal*.

Fig. 1 presents the summary somatotopic map from this cat. The somatotopy was normal both globally and in its detail. As in normally pigmented cats (cf. Ref. 13), the representations of the forepaw, head and face were located mainly in the coronal sulcus; the forepaw on the medial wall (i.e. the lateral bank of the anterior sigmoid gyrus) and the head and face on the lateral wall (i.e. the medial bank of the coronal gyrus). The arm and forearm were represented on the crown and caudal bank of the anterior sigmoid gyrus, extending down the rostral wall of the lateral ansate sulcus. The trunk and thigh were represented more medially on the anterior sigmoid gyrus and onto the rostral wall of the medial ansate sulcus. Thus, the representations of the major body parts in this albino cat's cortex are in precisely the same locations as they are in normally pigmented cats (cf. Fig. 1, Ref. 13).

The numbered receptive field sequences from the trunk and forepaw regions of the map illustrate the general finding that local topographic details are also the same for this albino and normally pigmented cats. These representative sequences show continuities characteristic of somatic maps in general (e.g. see Ref. 22), and of the progressions which would be predicted from the SI maps of pigmented cats¹³. Thus, in the representation of the trunk, receptive fields are located on progressively more

* We had no reason to expect that this cat was anything other than a true tyrosinase-negative albino. We obtained the cats from R.S. and H.E. Heffner, who had developed a colony with cats obtained directly from D.J. Creel. Moreover, an intraocular injection of horseradish peroxidase conjugated with wheat germ agglutinin revealed a pattern of retinogeniculate label identical to that reported by others for these cats¹⁰.

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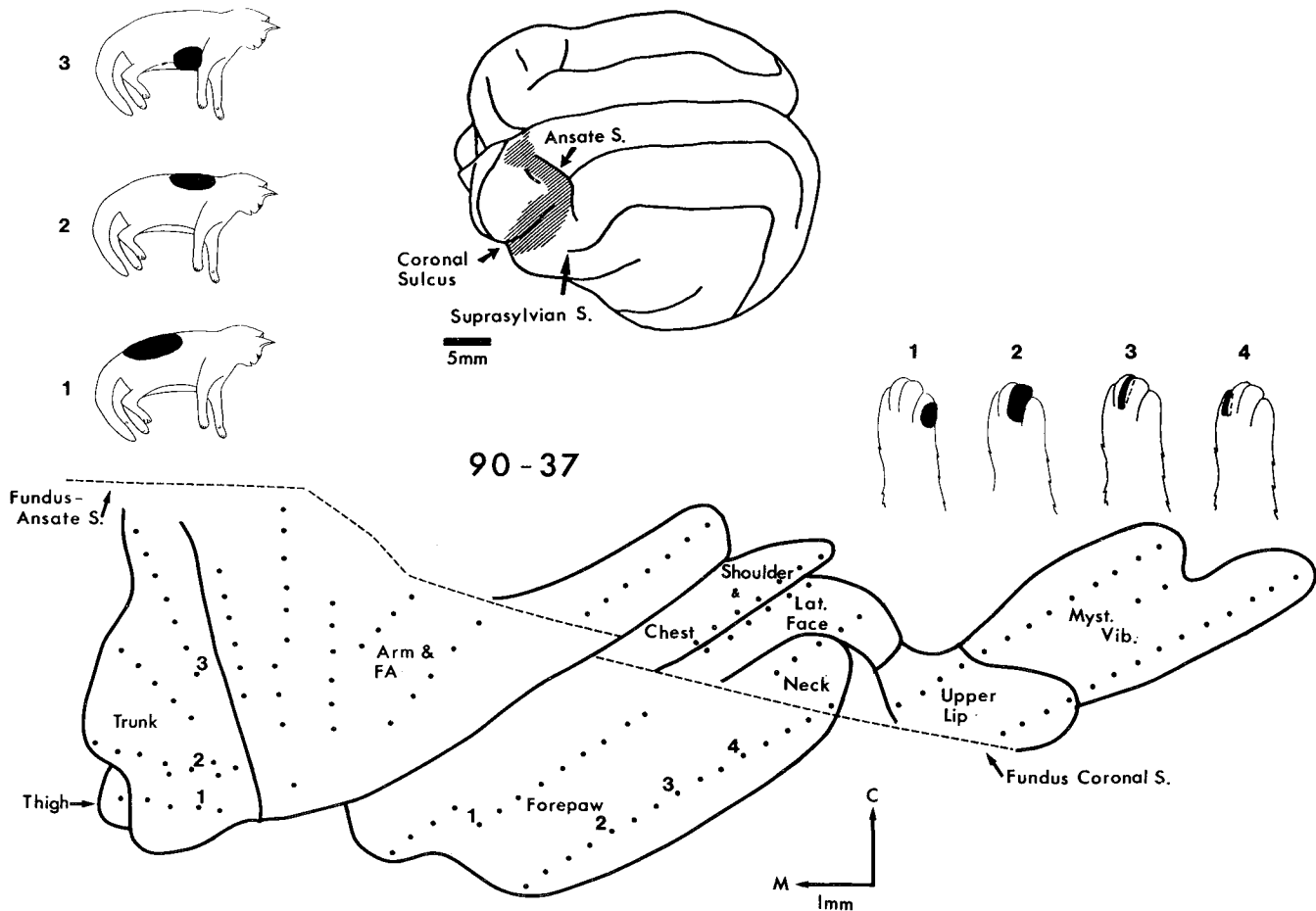


Fig. 1. Somatosensory mapping data from the tyrosinase-negative albino cat (90-37). Top center: dorsolateral view of cat brain with the location of primary somatosensory cortex (SI) indicated with crosshatching. Bottom: summary of the mapping data. Recording sites with receptive fields on common body parts are enclosed. The dashed lines represent the fundi of the ansate and coronal sulci which have been opened to display the recording sites on a flattened view. Heavy, solid lines separate parts of the map where neurons had receptive fields on the identified part of the body. Receptive fields for the numbered recording sites in the representation of the trunk are illustrated in the top left part of the figure. Receptive field locations shifted from dorsal to ventral at progressively more caudal recording sites. Receptive fields for the numbered recording sites in the representation of the forepaw are illustrated in the middle right part of the figure. Successively more radial digits are represented at progressively more lateral recording sites (i.e. at progressively greater depths within the coronal sulcus). Abbreviations: FA, forearm; Lat. Face, Lateral face; Myst. Vib., Mystacial vibrissae; C, caudal; M, medial.

ventral parts of the torso as recording sites progress caudally (cf. Fig. 3, Ref. 13). Further, in normally pigmented cats, the forepaw digits are represented from ulnar-to-radial in a medial-to-lateral array (cf. Fig. 2, Ref. 13). The forepaw receptive field sequence illustrated in Fig. 1 presents an identical organization. The ventrum of the forepaw, the forelimb, and the face and head were also all represented with precisely the same internal order in this albino cat as in normally pigmented cats. We should also note that all 152 multi-unit recording sites had receptive fields which were completely contiguous and located solely on the contralateral body surface. A thorough examination revealed no activity evoked by stimulation of the homotypic ipsilateral skin surface, and no receptive fields crossed the body midline. Thus, our data indicate that the topography of SI in the albino cat

is identical to that found in normally pigmented cats.

The primary visual anatomical abnormality associated with hypopigmentation involves a misrouting of retino-geniculate fibers at the optic chiasm such that the ipsilateral projection is greatly reduced (e.g. Ref. 10). The correlation between albinism and retinofugal projection anomalies certainly suggests a causal link, and the elegant experiments of Silver and Sapiro²⁷ and Webster et al.³⁰ provide data implicating melanin, which is normally present in the retina, in the process of retino-fugal axonal guidance. Melanin is also normally present in the inner ear³¹, but whereas melanin is absent from the inner ear of albino cats⁶, the defects found in the albino auditory system appear to require a more central mechanism³². In the somatosensory system, melanin is obviously normally present in the vicinity of the peripheral

receptors, but the present data demonstrate that the presence or absence of pigment in the skin plays no obvious role in forming the somatotopic organization in cat SI. In retrospect, this is not surprising as albino rats are widely used in studies of the somatosensory system, and apparently do not differ from their pigmented conspecifics, though we are aware of no direct comparisons. Thus, the possible role of melanin in axonal guidance during retinofugal development may well represent a unique role for the pigment in that particular system. Finally, it has been suggested that the abnormalities in the auditory system might be secondary to the visual anomalies¹. That is, the development of the

auditory projections might be altered such that the auditory map which emerges in the superior colliculus remains in register with the visual map^{12,16}. If a comparable adjustment occurs in the somatosensory map in the superior colliculus^{16,28}, one would not necessarily expect changes in topography in SI³. Rather, changes might be present in SIV, para-SIV, and the rostral aspect of the suprasylvian sulcus, known cortical regions with tectal projections^{2,29}.

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- 1 Baker, G.E. and Guillery, R.W., Evidence for the delayed expression of a brainstem abnormality in albino ferrets, *Exp. Brain Res.*, 74 (1989) 658–662.
- 2 Clemo, H.R. and Stein, B.E., Topographic organization of somatosensory corticocortical influences in cat, *J. Neurophysiol.*, 51 (1984) 843–858.
- 3 Clemo, H.R. and Stein, B.E., Effects of cooling somatosensory cortex on response properties of tactile cells in the superior colliculus, *J. Neurophysiol.*, 55 (1986) 1352–1368.
- 4 Collewijn, H., Apkarian, P. and Spekreijse, H., The oculomotor behavior of human albinos, *Brain*, 108 (1985) 1–28.
- 5 Collewijn, H., Winterson, B.J. and Dubois, M.F.W., Optokinetic eye movements in albino rabbits: inversion in anterior visual field, *Science*, 199 (1978) 1351–1353.
- 6 Conlee, J.W., Parks, T.N., Schwartz, I.R. and Creel, D.J., Comparative anatomy of melanin pigment in the stria vascularis. Evidence for a distinction between melanocytes and intermediate cells in the cat, *Acta. Otolaryngol.*, 107 (1989) 48–58.
- 7 Creel, D., Visual system anomaly associated with albinism in the cat, *Nature*, 231 (1971) 465–466.
- 8 Creel, D., Conlee, J.W. and Parks, T.N., Auditory brainstem anomalies in albino cats. I. Evoked potential studies, *Brain Research*, 260 (1983) 1–9.
- 9 Creel, D., Garber, S.R., King, R.A. and Witkop, Jr., C.J., Auditory brainstem anomalies in human albinos, *Science*, 209 (1980) 1253–1255.
- 10 Creel, D., Hendrickson, A.E. and Leventhal, A.G., Retinal projections in tyrosinase-negative albino cats, *J. Neurosci.*, 2 (1982) 907–911.
- 11 Dodt, E., Copenhaver, R.M. and Gunkel, R.D., Electroretiniographic measurement of the spectral sensitivity in albinos, caucasians, and negroes, *Arch. Ophthalmol.*, 62 (1959) 795–803.
- 12 Dräger, U.C. and Hubel, D.H., Responses to visual stimulation and relationship between visual, auditory and somatosensory inputs in mouse superior colliculus, *J. Neurophysiol.*, 38 (1975) 690–713.
- 13 Felleman, D.J., Wall, J.T., Cusick, C.G. and Kaas, J.H., The representation of the body surface in S-I of cats, *J. Neurosci.*, 3 (1983) 1648–1669.
- 14 Garber, S.R., Turner, C.W., Creel, D. and Witkop Jr., C.J., Auditory system abnormalities in human albinos, *Ear Hearing*, 3 (1982) 207–211.
- 15 Garraghty, P.E., Pons, T.P., Huerta, M.F. and Kaas, J.H., Somatotopic organization of the third somatosensory area (SIII) in cats, *Somatosens. Res.*, 4 (1987) 333–357.
- 16 Gordon, B.J., Receptive fields in deep layers of cat superior colliculus, *J. Neurophysiol.*, 36 (1973) 157–178.
- 17 Guillery, R.W., An abnormal retinogeniculate projection in the albino ferret (*Mustela furo*), *Brain Research*, 33 (1971) 482–485.
- 18 Guillery, R.W., Okoro, A.N. and Witkop, Jr., C.J., Abnormal visual pathways in the brain of a human albino, *Brain Research*, 96 (1975) 373–377.
- 19 Hahnenberger, R.W., Differences in optokinetic nystagmus between albino and pigmented rabbits, *Exp. Eye Res.*, 25 (1977) 9–17.
- 20 Heffner, R.S. and Heffner, H.E., Auditory function in albino cats, *Assoc. Res. Otolaryngol.*, 10 (1987) 217.
- 21 Henry, K.R. and Haythorn, M.M., Albinism and auditory function in the laboratory mouse. I. Effects of single-gene substitutions on auditory physiology, audiogenic seizures, and developmental processes, *Behav. Genet.*, 5 (1975) 137–149.
- 22 Kaas, J.H., What, if anything, is SI? Organization of first somatosensory area of cortex, *Physiol. Rev.*, 63 (1983) 206–231.
- 23 Leventhal, A.G. and Creel, D., Retinal projections and functional architecture of cortical areas 17 and 18 in the tyrosinase-negative albino cat, *J. Neurosci.*, 5 (1985) 795–807.
- 24 Loshin, D.S. and Browning, R.A., Contrast sensitivity in albino patients, *Am. J. Optom. Physiol. Optics*, 60 (1983) 158–166.
- 25 Maxson, S.C., Strain differences in lateralization of acoustic priming for susceptibility to audiogenic seizures, *Exp. Neurol.*, 63 (1979) 436–443.
- 26 Sanderson, K.J., Guillery, R.W. and Shackelford, R.M., Congenitally abnormal visual pathways in mink (*Mustela vison*) with reduced retinal pigment, *J. Comp. Neurol.*, 154 (1974) 225–248.
- 27 Silver, J. and Sapiro, J., Axonal guidance during development of the optic nerve: the role of pigmented epithelia and other extrinsic factors, *J. Comp. Neurol.*, 202 (1981) 521–538.
- 28 Stein, B.E., Magalhaes-Castro, B. and Kruger, L., Relationship between visual and tactile representations in cat superior colliculus, *J. Neurophysiol.*, 39 (1976) 401–419.
- 29 Stein, B.E., Spencer, R.F. and Edwards, S.B., Corticotectal and corticthalamic efferent projections of SIV somatosensory cortex in cat, *J. Neurophysiol.*, 50 (1983) 896–909.
- 30 Webster, M.J., Shatz, C.J., Kliot, M. and Silver, J., Abnormal pigmentation and unusual morphogenesis of the optic stalk may be correlated with retinal axon misguidance in embryonic Siamese cats, *J. Comp. Neurol.*, 269 (1988) 592–611.
- 31 Wolff, D., Melanin in the inner ear, *Arch. Otolaryngol.*, 14 (1931) 195–211.
- 32 Yin, T.C.T., Carney, L.H. and Joris, P.X., Interaural time sensitivity in the inferior colliculus of the albino cat, *J. Comp. Neurol.*, 295 (1990) 438–448.