Multiple maps and activity-dependent representational plasticity in the anterior Wulst of the adult barn owl (*Tyto alba*)

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Abstract

In the present study we addressed the issue of somatosensory representation and plasticity in a nonmammalian species, the barn owl. Multiunit mapping techniques were used to examine the representation of the specialized receptor surface of the claw in the anterior Wulst. We found dual somatotopic mirror image representations of the skin surface of the contralateral claw. In addition, we examined both representations 2 weeks after denervation of the distal skin surface of a single digit. In both representations, the denervated digital representation became responsive to stimulation of the adjacent, mutually functional, digit. The mutability and multiple representations indicates that the Wulst provides the owl with sensory processing capabilities analogous to those in mammals.

Introduction

The structure of the telencephalic roof in amniote vertebrates varies, from an elaborated laminar cerebral cortex in mammals, to a nuclear or laminated structure in birds and reptiles. Despite these structural differences, the underlying connectivity of the sensory systems remain similar (Butler & Hodos, 1996; Medina & Reiner, 2000). Although there is considerable knowledge of the connectivity of the telencephalon of nonmammalian amniotes, few studies have addressed the issue of physiological representations and none the potential mutability of representations in adult animals.

Until recently, it was thought that multiple maps of sensory surfaces in more complexly organized mammalian cortices evolved from an ancestor who possessed only a single map of each sensory system (Kaas, 1982). Early mapping studies of pigeon (Delius & Bennetto, 1972) and dunlin (Pettigrew & Frost, 1985) telencephalon have revealed only a single somatotopic representation. Similarly, reports of the visual Wulst of the barn owl (Pettigrew & Konishi, 1976), chicken (Wilson, 1980) and pigeon (Parker & Delius, 1972), and the visual cortex of the turtle (Ulinski, 1990), describe a single retinotopic map. However, studies of monotremes (Krubitzer *et al.*, 1995), marsupials (e.g. Elston & Manger, 1999) and small-brained mammals (e.g. Krubitzer *et al.*, 1997) have shown that all mammals possess multiple representational maps (Kaas, 1995a). Furthermore, a mapping study of the dorsal ventricular ridge of the iguana described multiple representational maps of visual space (Manger *et al.*, 2002). Clearly, there is uncertainty as to whether there may be multiple representations in the telencephalon of nonmammalian amniotes (Medina & Reiner, 2000).

In addition, contrary to earlier reports suggesting that adult mammalian cortical circuitry and functional representations were immutable, more recent studies have shown large-scale, rapid and long-term, remodelling of both circuitry and representations (Merzenich *et al.*, 1983a, 1983b; Calford & Tweedale, 1988; Kaas *et al.*, 1990; Pons *et al.*, 1991; Gilbert & Wiesel, 1992). This plasticity of the mammalian cerebral cortex is thought to underlie the process by which mammals learn from sensory experiences, acquire new skills, compensate for peripheral damage and recover from central nervous system damage, and it appears to be an inherent feature of adult mammalian cerebral cortex (Kaas, 1995b). To date, activity-dependent representational plasticity of this sort has not been examined in the representational maps of the telencephalon of nonmammalian species. In the present study we addressed both the issues of multiple representational maps and activity-dependent representational plasticity in the telencephalon of birds. Examination of the normal representation of the digits in the anterior Wulst and mutability of the representation following denervation of a single digit yielded data which suggests that dual somatic representational maps and representational plasticity are functional properties of the anterior Wulst of the barn owl. These findings are discussed in relation to concepts regarding the physiological similarities of the telencephalic roof across amniote species (Medina & Reiner, 2000) and to the underlying processes of sensory-based learning of amniote species.

Materials and methods

Six adult barn owls (*Tyto alba*) were used in this study. The experimental procedures were approved by the Animal Ethics Committee at the University of Queensland, Australia, and conform to the Australian Guidelines for the Care and Use of Animals in Scientific Experiments. Two animals were used for the acquisition of

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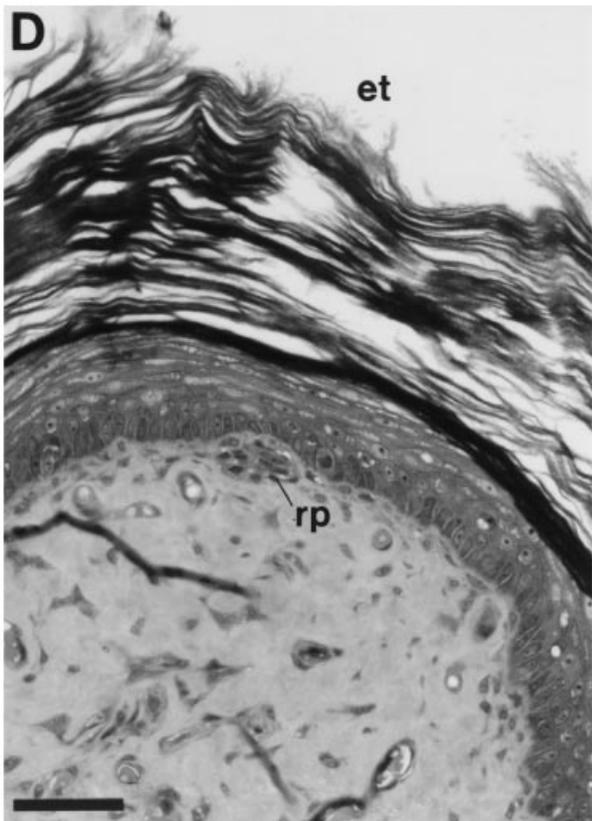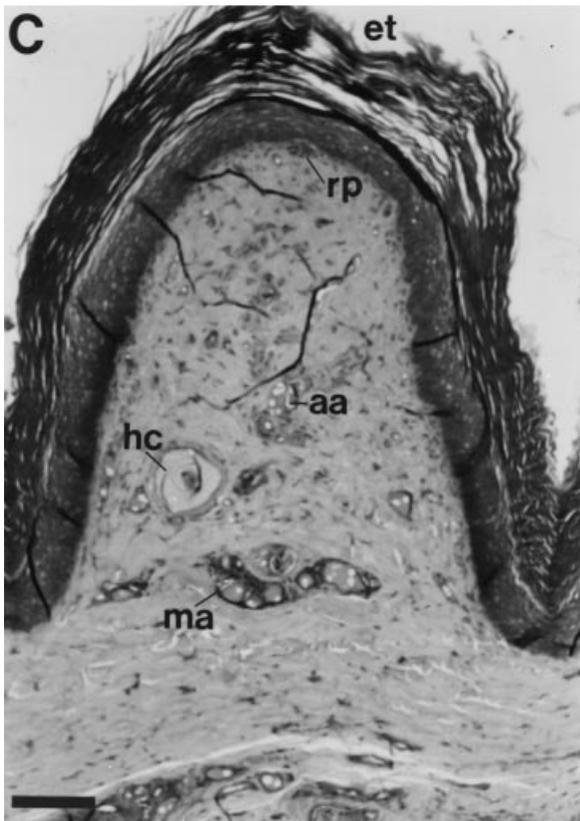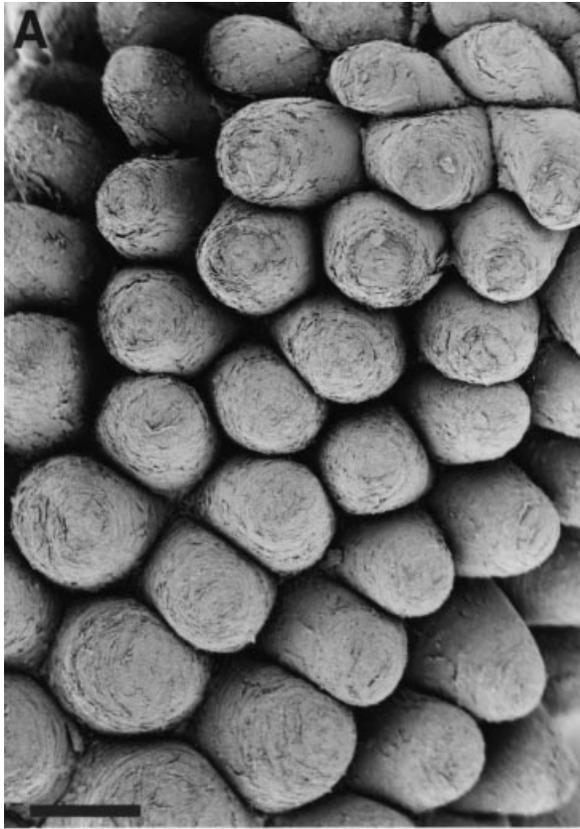
control data. A further four animals underwent denervation of the distal two phalanges of the third digit (D3), two weeks prior to the mapping session.

Digital denervation

Animals were anaesthetized with ketamine hydrochloride (40 mg/kg, i.m.). A small incision (< 5 mm) was made in the skin on each side of the proximal phalanx of D3 and the large digital nerves exposed. A 1-mm portion of the nerve was excised. The incision was closed with surgical glue.

Electrophysiological mapping

Animals were anaesthetized with an intramuscular injection of ketamine hydrochloride (40 mg/kg). Maintenance doses of anaesthetic (half the initial dose) were given as necessary to maintain a surgical level of anaesthesia. Anaesthetic level was determined from eye-blink and pinch reflexes and respiratory rate. The scalp was cut and separated from the skull. Three surgical screws were inserted in the back of the skull and a bar modified for attachment to a stereotaxic frame was fixed to the screws with dental acrylic. The bone overlying the anterior Wulst was removed and the dura cut and retracted. A photograph of the surface of the Wulst was taken and enlarged to allow matching of recording sites to the pattern of blood vessels. Tungsten-in-glass microelectrodes (1 MΩ resistance), with an exposed recording tip of around 10 μm, were introduced into the Wulst, perpendicular to the surface. The depth of the electrode tip was controlled by a hydraulic microdrive. The neural responses were amplified and filtered using an AM Systems Model 1800 Microelectrode AC amplifier (AM Systems, Everett, WA, USA) and a 50-Hz eliminator (Humbug, Quest Scientific, Vancouver, Canada). The skin was stimulated with either a small paint brush or a fine pointed wooden probe, providing stimuli such as light strokes, small indentations of the skin and light taps.

Tissue preparation and cytoarchitecture

Following the recording sessions the animals were given an overdose of pentobarbitone and perfused intracardially with a rinse of 0.9% saline, followed by 4% paraformaldehyde in 0.1 M phosphate buffer. The brain was removed and postfixed overnight in a solution of 4% paraformaldehyde and 10% sucrose in 0.1 M phosphate buffer at 4 °C. The telencephalon was then sectioned at 40 μm in the sagittal plane using a freezing microtome. Alternate serial sections were stained with cresyl violet and reacted for myelin (Schmeud, 1990). Electrode tracks and recording sites were matched to architecture and physiological maps reconstructed into a 2-D plane as though examining the surface of the anterior Wulst.

Following perfusion as described above, portions of the digital skin from three animals were removed and postfixed overnight in 4% paraformaldehyde in 0.1 M phosphate buffer. These blocks of skin tissue were used for scanning electron microscopy of the skin surface and histological examination of the internal structure of the tubercle. An Electro-scan (location?) Environmental Scanning Electron Microscope was used in this study, as the specimen had to undergo no more than a final rinse in distilled water prior to viewing. Avoiding dehydration in this way meant that there was minimal distortion and damage to the superficial keratinocytes.

Specimens of skin for histological examination were processed for embedding in glycol methacrylate (Historesin, Jung, location?). The skin specimens were dehydrated through a graded series of ethanol to 95% (overnight in 95% alcohol) and then transferred to a 1 : 1 solution of 95% alcohol/infiltrating solution (hydroxyethylmethacrylate plus 0.5 g benzol peroxide per 50 mL) for 3 days. These specimens were then placed in the infiltrating solution overnight, orientated and placed in embedding medium (infiltrating solution plus hardener, dimethyl sulfoxide) and the medium allowed to polymerize at room temperature. These blocks were attached to chucks with dental acrylic and 3-μm sections were cut on an LKB 2218 Historange microtome with disposable steel knives. The sections were flattened on tap water, slightly above room temperature, and picked up on glass slides. The sections were then dried in a 37°C oven until ready for staining. The slides were heated to 60°C for 20 min and then the stain was applied over the sections (1 g toluidine blue plus 1 g sodium tetraborate in 1000 mL distilled water). The stain was allowed to act for 5 min and then the slides were rinsed in running tap water until the staining was only evident in the section and not the resin. The stain was then differentiated with 70% alcohol for ≈ 10 s. The sections were dehydrated in 100% ethanol, cleared in xylene and coverslipped with Depex.

Results

The claw as a sensory apparatus

The claw of the owl consists of four digits, two that are directed posteriorly [digits 1 and 2 (D1, D2), although digit 1 (medial) can be extended through a large range of movements], and two digits that are directed anteriorly – D3 and D4 (medial), when the owl is perched or grasping prey. The plantar epidermal surface has an unusual appearance not dissimilar in appearance to the digit skin of the raccoon (Rice & Rasmusson, 2000). Microscopic examination revealed that the plantar skin is composed of a series of 'tubercles', which appear as steep-sided domes that cover the entire plantar surface, including the sole (Fig. 1A and B). Each tubercle has a diameter between 400 and 600 μm, the density being ≈4/mm^2 over the entire plantar surface. A conspicuous circular thinning of the most superficial layer of the epidermis, the stratum corneum, was noted at the apex of each tubercle (≈ 150 μm diameter), similar to that described for the Eimer's organ of the star-nosed mole (Catania, 1995).

Histological examination of the tubercle revealed that it receives a dense innervation, presumably from the digital nerves (Fig. 1C and D). At the base of each tubercle, in the dermis, a single, moderate-sized Herbst corpuscle (the avian equivalent of the mammalian Pacinian corpuscle) was located (diameter ≈ 100 μm). Several large myelinated nerve fibres were seen to pass around the Herbst corpuscle

FIG. 1. Structure of the specialized tactile receptor, the tubercle, of the owl plantar skin. (A)SEM of the tubercles on the plantar surface of one phalanx, demonstrating the distribution, density and dome-like structure. (B)Higher magnification SEM of a single tubercle, showing the disc-shaped thinning of the epidermis at the tip of the tubercle. This thinning may be related to natural wear of the skin surface, but may also be related to sensory structures within the dermis. (C)Photomicrograph of a section through an entire tubercle. In the dermis below the tubercle large fasciculi of nerve fibres can be seen. At the base of the tubercle a smaller bundle of myelinated axons (ma) is seen in close proximity to the singular Herbst corpuscle (hc). Ascending myelinated axons (aa) are seen dorsal to the Herbst corpuscle and innervate a cluster of Merkel-like cells forming a rete peg (rp) that lie in apposition to the stratum germinativum, immediately below the epidermal thinning (et) at the tip of the tubercle. (D)Photomicrograph of a section through the skin of a tubercle, just below the epidermal thinning (et), showing the cluster of Merkel-like cells forming a rete peg (rp) located at the tip of the tubercle. This configuration of sensory cells is very similar to that described for the raccoon digital skin (Rice & Rasmusson, 2000). Scale bar, 500 μm (A and D), 100 μm (B and C).
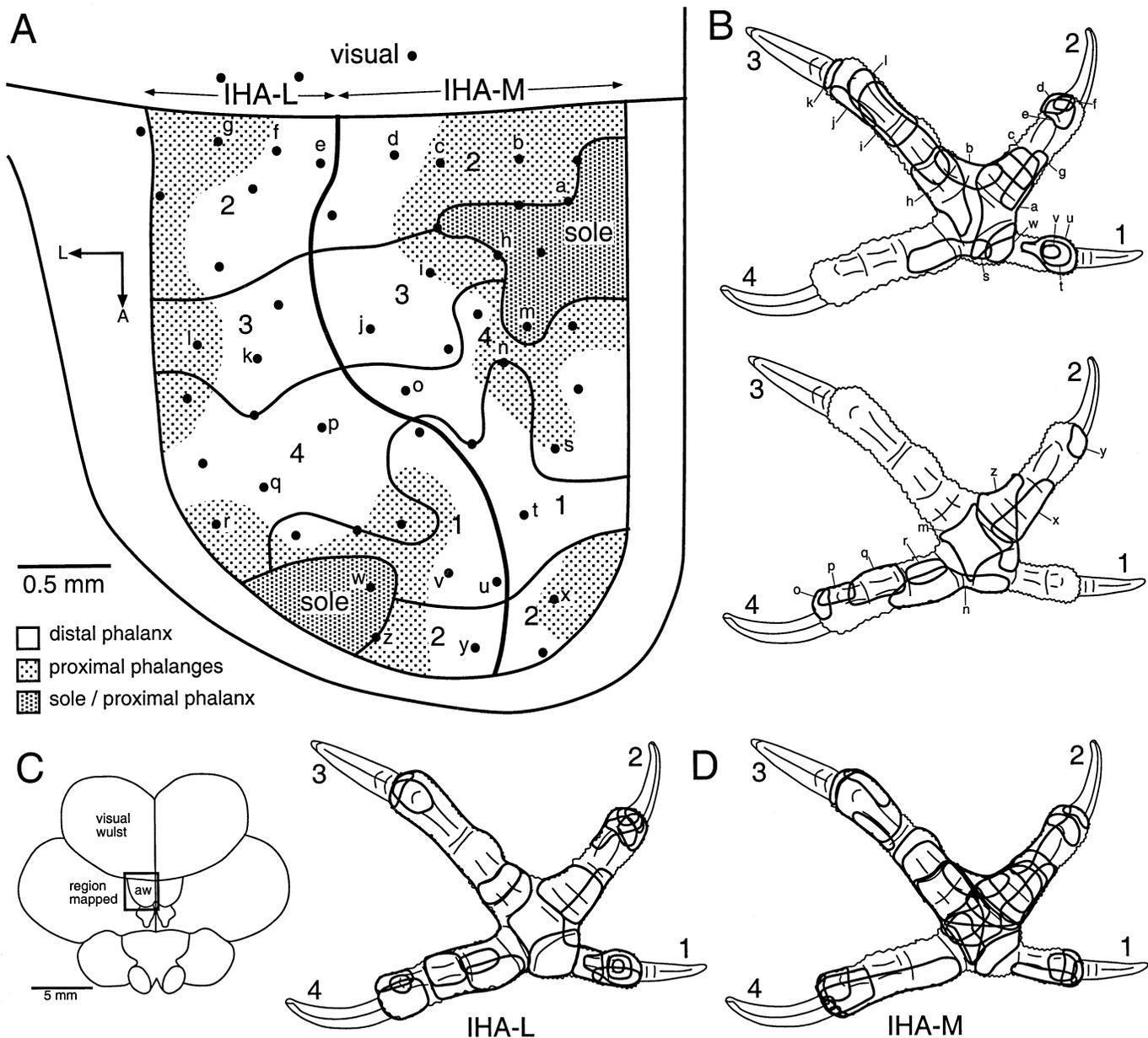
FIG. 2. Reconstruction of the representation of the digits within the anterior Wulst of the barn owl. (A) Reconstruction and subdivision of the representation of the digits and sole within two areas, IHA-M and IHA-L. Both of these areas present a mirror image of the other. (B) Examples of receptive field progression recorded in a medio-lateral progression across the Wulst. The letters in B correspond to the small letters in A. (C) Rostral view of the owl brain showing the location of the AW in relation to the other structures of the brain, and the region of the brain enlarged in A. (D) Compilation of all the receptive fields recorded in IHA-M and IHA-L, showing that each area contains a full representation of the plantar surface of the skin.

on passage to the epidermis and terminate in one or more 60–100-µm clumps of Merkel-like cells. These Merkel-like endings (or rete pegs; Rice & Rasmusson, 2000), were located in apposition to the stratum germinativum, directly below the aforementioned thinning in the stratum corneum (Fig. 1B and D). The external form and internal structure of the tubercle suggests it is analogous to other specialized tactile receptor complexes (Gottschaldt, 1985; Catania, 1995; Manger & Pettigrew, 1996; Rice & Rasmusson, 2000).

Dual representation of the claw in the anterior Wulst

Within the anterior Wulst (AW), vigorous neuronal responses were recorded to light stimulation of the surface of the contralateral claw skin. No ipsilateral or bilateral responses were found. All neuronal

responses were restricted to a prominent band 700–1100 µm below the pial surface, corresponding to the architectonic lamina of the AW termed the hyperstriatum accessorium, pars intercalatus (IHA) (Wild & Williams, 2000). In the barn owl, this lamina is parallel to the pial surface. Thus, by introducing the microelectrode perpendicular to the surface we were able to obtain a map of this lamina in a manner similar to the cortical maps generated for mammals (e.g. Manger *et al.*, 1997).

Within IHA we found evidence for two representations of the plantar surface of the contralateral claw. Dual representations of the skin surface, and reversals in receptive field progressions, were used to define the borders of the two fields. Each field occupied approximately half the IHA, a field in the medial half (IHA-M) and
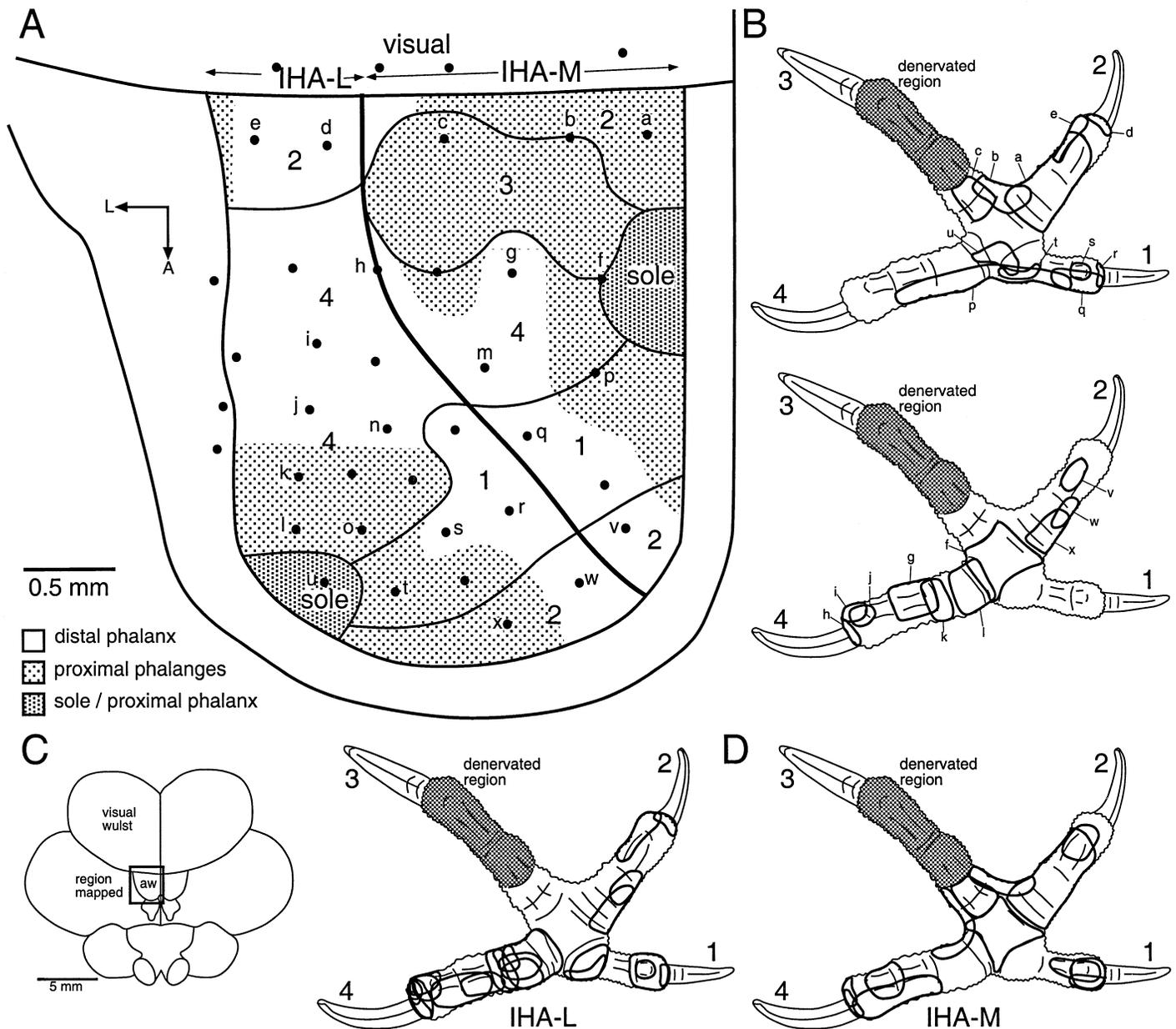
FIG. 3. Reconstruction of the somatic map generated 2 weeks following denervation of the distal portion of the third digit. Conventions as in Fig. 1. The region of IHA deprived of input has in large part been subsumed by the representation of D4. This is particularly apparent in IHA-L. The remaining representation of the proximal portion of D3 has also expanded in IHA-M. It is of interest to note that neither the D1 nor D2 representations have enlarged. In the owl, D3 and D4 point anteriorly and D1 and D2 point posteriorly; thus the representational plasticity found here is selective for the more behaviourally relevant representation of D4.

a field in the lateral half (IHA-L) (Fig. 2). Each field presented a mirror image of the other. In both fields, the progression of digit representation from the posterior portion of the field to the anterior portion was identical. The portion of D2 adjacent to D3 was represented most posteriorly then, as recording sites progressed anteriorly, the representations of D3, D4 and D1 were found. At the most anterior portion of each field, the remainder of the representation of D2, that part adjacent to D1, was found. In IHA-M, the representation of the sole was found at the medial-most part of the field, revealed as a small semicircle abutting the representations of the proximal portions of each digit. In IHA-L the representation of the sole was located at the lateral-most portion of the field, in a similar manner to that of its equivalent representation in IHA-M. In both

fields, the representations of the digits appeared to radiate out from the representation of the sole, with the representation of the proximal phalanges adjacent to the representation of the sole and the representation of the distal phalanx furthest away. At the border between IHA-M and IHA-L the representation of the most distal part of each digit was located. Thus, as recording sites progressed from medial to lateral in the IHA, the first receptive fields encountered in IHA-M were found on, or close to, the sole. As recording sites progressed laterally in IHA-M, the receptive fields were found further distally on the digits. As recording sites progressed into IHA-L, the receptive fields were located away from the distal portion of the digits and, as recording sites progressed to the lateral part of IHA-L, receptive fields were found on the proximal phalanges or the sole
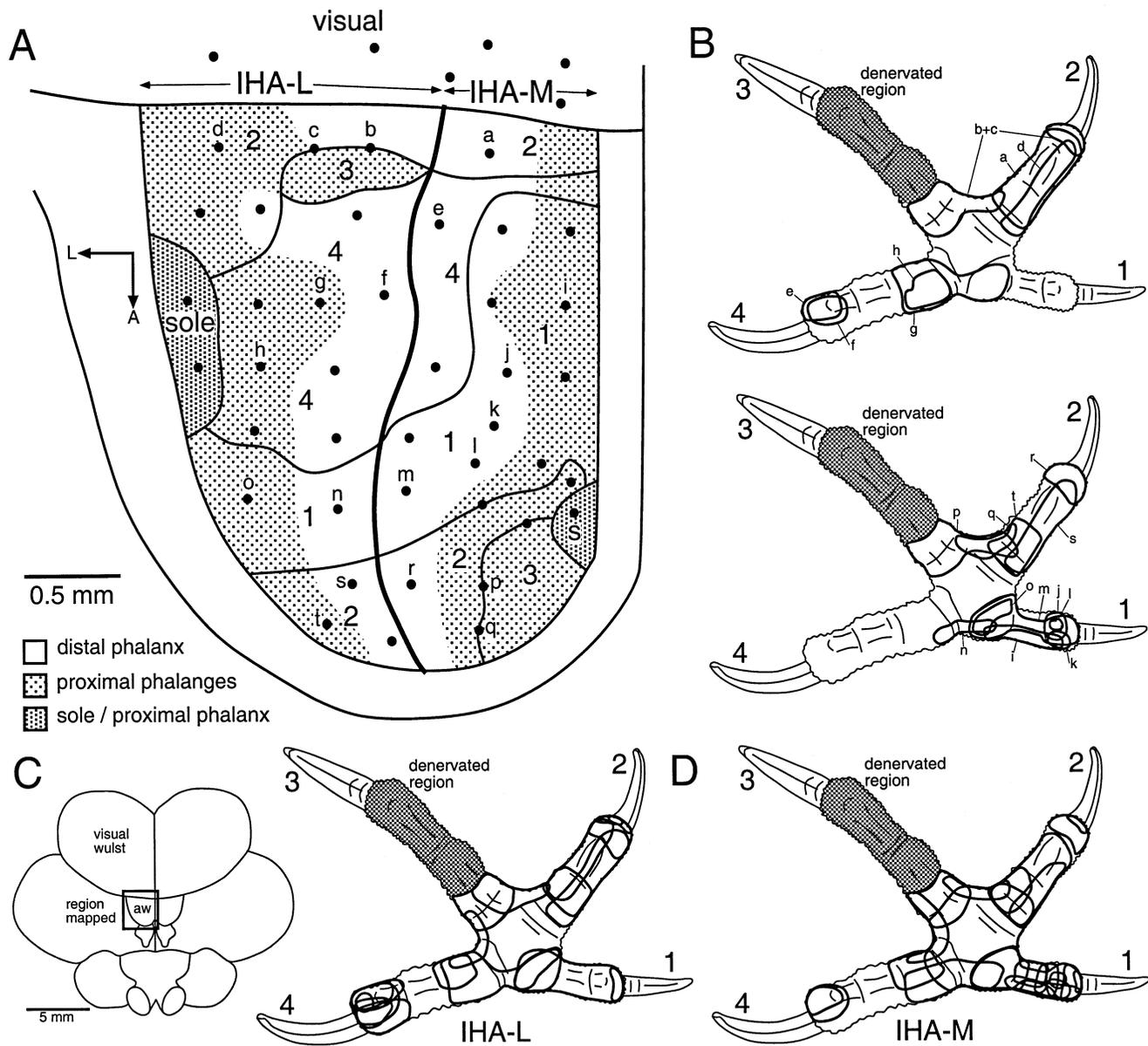
FIG. 4. Second example of the somatic map generated two weeks following denervation of the distal portion of the third digit. Conventions as in Fig. 1. The region of IHA deprived of input is taken over mostly by the representation of D4, although a slight increase in the size of the D1 representation may be seen in this case. Two small regions remained responsive to the still-innervated region of D3; however, in IHA-M, this region appears to be located ectopically. As in the other cases, no region of the IHA was found to be unresponsive, and the representational plasticity that has occurred appears to be of behavioural relevance.

(Fig. 2). Two features are noteworthy; first, the representation of D2 is split into two parts, at the posterior and anterior of each field. This split representation may indicate that this digit is innervated by two distinct peripheral nerves, and exposes a unique solution to the mapping of an appendage that is somewhat circular in nature (the claw) onto a quasi-rectangular surface. Second, the most distal portions of the digits are mapped onto the border between fields, possibly taking advantage of shorter connectivity for sensory processing.

Not every receptive field recorded was located on the plantar surface of the claw. Some fields were localized on the dorsal surface of the claw and on the leg. These were found close to the representation of the sole, lateral in IHA-L and medial in IHA-M. Further lateral or medial, receptive fields were occasionally found

within the intraoral region. While not systematically explored in the present study, it is possible that full representations of the body are to be found in each field. However, due to the enormous magnification of the plantar surface of the claw, the remainder of the body representation would necessarily be very small and may have been concealed from recording by large blood vessels surrounding the borders of the AW.

Plasticity of the representational map following digit denervation

In the four cases that underwent denervation of the distal two phalanges of D3 prior to mapping we found marked reorganization of the somatotopic maps in both representations defined in the control animals. In no case did we find unresponsive regions in either of the

areas of the IHA. Instead, the region of the IHA deprived of sensory input by the denervation became responsive to tactile stimulation of the distal two phalanges of D4 or the innervated proximal phalanx of D3 (Figs 3 and 4). The largest portion of the reorganized region was given over to the representation of the distal phalanx of D4 (Figs 3 and 4). Within the reorganized region the representation of D3/4 resembled the normal medial-to-lateral sequence of proximal to distal to proximal. No apparent increase in the size of the posterior representation of D2 was seen, and neither were there any significant changes in the representation of D1 or the anterior D2 representation.

The maps generated from these plasticity studies add further weight to the observation of two somatic fields as, in each case, a dual representation of the sole and proximal phalanges were clearly determined. These were separated by the representations of the distal phalanges. Furthermore, reversals in receptive field progressions were seen as recording sites progressed from medial to lateral across the AW (Figs 3 and 4).

Discussion

In the present study we have confirmed an earlier finding of a precise topographic representation of the claw in the AW of the owl (Karten *et al*., 1978). Moreover, we extended this observation and obtained three results of significance: (i) the skin of the claw of the owl is a specialized sensory array; (ii) there are two representational maps of the claw in the AW; and (iii) there is activity-dependent representational plasticity following digit denervation. One difference between the present study and the previous (Karten *et al*., 1978) was the size of the receptive fields. Karten *et al*. (1978) found receptive fields often limited to a single tubercle; however, the smallest receptive fields determined in the present study encompassed ≈ 10 tubercles, these being located at the distal portions of the digits, while those in more proximal locations involved a far larger number of tubercles (this increase in receptive field size in proximal locations is very similar to what is seen in mammalian cortex). This difference in the magnitude of the receptive fields may be due to differing techniques used [single-unit recording by Karten *et al*. (1978) vs. multiunit recordings in the present study], or it may be a species-specific difference [*Speotyto cunicularis*, the burrowing owl, was used by Karten *et al*. (1978) whereas *Tyto alba*, the barn owl, was used in the present study]. A single-unit study of the barn owl, with a more exacting stimulation paradigm, would resolve this difference; however, this was not the aim of the present study. The receptive fields mapped in the present study had robust and sharply defined borders and the responses of the multiunit clusters to stimulation were reliable and consistent.

The owl's claw as a model for sensory perception in non-mammalian amniotes

The plantar skin of the claw of the owl is covered with an elaborated tactile sensory receptor, the tubercle. The dome shape and internal receptor complex of the tubercle (Merkel cell-like rete pegs and Herbst/Paciniform corpuscles) indicate a tactile receptor array of similar complexity and function to that found in the digital skin of the raccoon (Rice & Rasmusson, 2000). This is not the first elaborated tactile receptor complex found in an avian species, that being the bill-tip organ (Gottschaldt, 1985); however, this is the first nontrigeminal tactile receptor complex reported for birds. Thus, the claw of the owl is not only a useful appendage for perching and grasping prey but appears to be an elaborate sensory surface. Given the potential sensory acuity of the owl claw skin and its sophisticated representation in the AW (dual maps and representational plasticity), the owl

claw provides a useful model for studying neural mechanisms of sensory processing and perception in a nonmammalian amniote.

Multiple representational maps indicate sophisticated perceptual abilities

The second major finding of the present study was that there are two somatotopic maps of the claw skin in the IHA of the AW. This is the first report of multiple representations of a somatic surface in the telencephalic roof (i.e. the homologue of mammalian cerebral cortex) of a nonmammalian amniote. The IHA receives projections from the lemniscal pathway of the somatosensory system (Butler & Hodos, 1996; Medina & Reiner, 2000). Thus, on the basis of hodological and other studies, the IHA has been considered a field homology of the somatosensory cortex of mammals. However, the lamina of the AW are not homologous to the layers of cerebral cortex, as the trans-layer columnar organization is not apparent (Medina & Reiner, 2000). Instead, the IHA forms what can be considered an elongated and flattened nucleus, or pseudo-layer (Medina & Reiner, 2000). Despite the fact that we found two representations of the claw in the IHA, due to the differences of internal cellular and somatotopic organization these representations cannot be considered as direct avian homologues of any of the somatosensory areas (e.g. primary and secondary somatosensory areas) found in mammalian cerebral cortex.

Our finding indicates that multiple representations of sensory surfaces in the roof of the telencephalon are not only a potentiality of mammalian cerebral cortex but that all telencephalic roof sensory structures might possess the ability to represent a sensorial surface in multiple topographically organized maps. The present findings indicate that, at least, the telencephalic roof of the common ancestor of birds and mammals had the potential to, and quite possibly did, possess multiple topographic representations. This finding, combined with several recent findings of multiple topographic sensory representations in the cerebral cortex of a variety of mammals (Krubitzer *et al*., 1995, 1997; Elston & Manger, 1999; Huffman *et al*., 1999; Catania *et al*., 2000), and the dorsal ventricular ridge of the iguana (Manger *et al*., 2002), indicates that the earliest mammals probably had multiple sensory representations in their cerebral cortex (Kaas, 1995a).

It has been postulated that increased numbers of cortical areas, or representations of sensory surfaces, is a basis for increased behavioural complexity in mammals (Kaas, 1982). The singular representational maps previously reported for the avian telencephalon did not provide neurophysiological support for the observable complexity of avian behaviour (Delius & Bennetto, 1972; Parker & Delius, 1972; Pettigrew & Konishi, 1976; Wilson, 1980; Pettigrew & Frost, 1985). The present study demonstrates that, at least with the somatosensory system of the owl, the complexity of processing of tactile information may provide a perceptual basis equal to that of some mammals (Catania *et al*., 2000). Further studies of other avian species with specialized tactile receptors may reveal multiple representational maps that may be found to be homologous across avian species in a manner similar to that described for mammals (Krubitzer, 1995).

Representational plasticity is not a strictly mammalian feature

The finding of activity-dependent representational plasticity within the sensory representations of the claw in the AW of the owl indicates that, as in mammals, the mature nervous system is mutable rather than static. Plasticity of representational maps in the cerebral cortex of mammals is thought to underlie the ability of mammals to learn and modify behaviour as a result of sensory experience (Kaas, 1995b). Thus, the adaptive advantages attributed to representational

plasticity in adult mammalian sensory systems must also now be considered for birds.

In addition to being modifiable, the sensory representations in the AW follow a specific pattern in reorganization rather than being random. In the present experiments we denervated one of the anterior-pointing digits (D3). The inactivated region of IHA became responsive to the representation of the other anterior-pointing digit (D4), despite the adjacent representation of the posterior-pointing D2. This is of interest as it indicates that representational plasticity can be selective and is not determined solely by divergence of ascending projections. While it is possible that a certain degree of specificity in the ascending pathways may result in the type of selective plasticity observed, studies in mammals have not yet exhibited this selectivity (Merzenich *et al.*, 1984). The mechanisms that may underlie this difference are unknown but may be due to a nonselective divergence of ascending pathways in mammals (Rausell *et al.*, 1998). The present results then raise the question as to whether similar mechanisms underlie representational plasticity in birds as those reported for mammals (Jones, 1990; Kaas, 1991; Calford *et al.*, 1998; Gilbert, 1998).

Acknowledgements

Abbreviations

AW, anterior Wulst; D1, first digit of the claw (directed posteriorly); D2, second digit of the claw (directed posteriorly); D3, third digit of the claw (directed anteriorly); D4, fourth digit of the claw (directed anteriorly); IHA, hyperstriatum accessorium, pars intercalatus; IHA-L, lateral claw representation of the hyperstriatum accessorium, pars intercalatus; IHA-M, medial claw representation of the hyperstriatum accessorium, pars intercalatus.

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