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THE MORPHOLOGY, DISTRIBUTION AND BEHAVIORAL SIGNIFICANCE OF MECHANORECEPTORS IN THE GLABROUS PAW SKIN OF SQUIRRELS

By

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Neuroscience Program and Department of Zoology

1978

ABSTRACT

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The relationship between sensory specializations and behavioral specializations in two ecologically distinct species of squirrels was examined. On the basis of the behavior and natural history of these species, it was predicted that the relative density of receptors in the glabrous forepaw skin of tree squirrels (Sciurus niger) would be higher than that in ground squirrels (Spermophilus tridecemlineatus). In addition to testing this prediction, several other aspects of the distribution of receptors were quantitatively examined in silver stained material. As predicted, the relative density of receptors in the glabrous forepaw skin of tree squirrels was significantly higher than that in ground squirrels. Receptors were randomly dispersed and different types of receptors (corpuscular vs. non-corpuscular) were intermingled in the palmar skin of both species. The proportions of the different receptor types did not differ among species.

Another series of experiments examined the role that sensory input plays in the control of food handling behavior in the two

species of squirrels. First, using different size food items, it was shown that food handling (rate of manipulation) was subject to sensory control in both species. Second, comparison of sham operated groups with groups receiving median nerve lesions indicated that tactile input from the volar surface of the forepaw contributes to the sensory control in the two squirrels. Third, changes in behavior over the time taken to eat large food items indicated continuous sensory feedback rather than only an initial evaluation of the food item. Fourth, as predicted from the results of the anatomical studies described above, tree squirrels depended upon tactile input from the volar surface of the forepaw to a greater extent than ground squirrels in the handling of food.

The first series of experiments shows that the relative densities of receptors in the glabrous paw skin of ecologically distinct species of squirrels can be predicted from information about their behavior and natural history. The second series of experiments indicates that differences in the extent to which the behavior of those species is influenced by somatic sensory input can be predicted from information about differences in the organization of their somatic sensory systems. Together, these studies indicate that a species sensory specializations and behavioral specializations are closely related and that both reflect its ecology and natural history.

This dissertation is dedicated to

Nathan and Ruth Flaum Brenowitz

ACKNOWLEDGMENTS

I would like to thank my advisor Dr. John A. King for his guidance throughout this study. I would also like to acknowledge Drs. Martin Balaban and John I. Johnson for their continued interest in my research and well being; it was above and beyond the call of duty. I would also like to thank Drs. Rudy A. Bernard and Glenn I. Hatton who served on my committee. Pat Cromwell, an undergraduate student in the Department of Zoology, helped me by doing histology. This research was supported, in part, by funds from the Neuroscience Program. My personal support was provided by teaching assistantships from the Department of Zoology.

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INTRODUCTION

Interspecific variability in central somatic sensory projections reflects variability in behavioral and ecological specializations (Welker and Campos 1963, Pubols and Pubols 1972, Welker 1973, 1976, Johnson et al. 1974, Johnson 1978). It is also thought to reflect the differential distribution of receptors peripherally (Woolsey and Fairman 1946, Mountcastle and Henneman 1952, Welker and Seidenstein 1959, Pubols and Pubols 1971, Welker 1973, 1976). This study was designed to test the hypothesis that the distribution of cutaneous receptors differs among two behaviorally and ecologically distinct species of squirrels (Sciuridae): one a tree squirrel, the other a ground squirrel.

Tree squirrels (Sciurus niger) occur in open forest and forest edge habitats and use their forepaws in a broad range of skilled motor patterns that require tactile discrimination. This behavioral repertoire includes climbing and balancing on small diameter branches and procuring and processing food items that require extensive manipulation (Svihla 1931, Allen 1943, Moore 1957, Reichard 1976). The ground squirrels studied were thirteen-lined ground squirrels (Spermophilus tridecemlineatus) which occur in prairie and other open habitats and use the digits and palms of their forepaws in excavating extensive underground burrow systems (Evans 1951, Rongstad 1965, Desha 1966, Hildebrand 1974, Wistrand 1974). Their diet consists largely of seeds and other items that do not require extensive

manipulation (Whitaker 1972). These behavioral comparisons were used to predict that the relative density of receptors in the glabrous forepaw skin (defined here as forepaw receptor density/hindpaw receptor density ratio) of tree squirrels would be greater than that of ground squirrels.

In addition to testing this specific neuroethological hypothesis, quantitative techniques were used to examine spatial relationships within receptor arrays. Array properties examined include: proportional representation of receptor classes, patterns of dispersion (random, clumped, uniform) and degree of segregation between receptor classes. Receptor arrays in the glabrous palm skin of tree squirrels and ground squirrels were compared. Descriptions of the specific receptors found in the glabrous paw skin of these two species are presented.

Preliminary results from the above study indicated that the relative density of receptors in glabrous forepaw skin was greater in tree squirrels than in ground squirrels. It was predicted that eliminating somatic sensory (tactile) input from the volar surface of the forepaw by bilaterally lesioning the median nerve would affect the behavior of tree squirrels more than that of ground squirrels. Testing this prediction was the main purpose of this study.

In addition to testing the above prediction, more general questions about the role of sensory input in controlling food handling in squirrels were examined. First, varying food size, shown to affect food handling in chipmunks (Lockner 1970), was used to examine whether food handling is subject to control by sensory input, in general. It was predicted that large food items would be manipulated

more per unit time than small ones. Second, the lesion described above was used to determine whether somatic sensory input contributes to the sensory control of food handling. Third, data obtaind in answering the first two questions were re-analyzed to determine whether sensory input acts via an initial evaluation of the food item or continued feedback from it. It was hypothesized that if feedback occurs, foodhandling should change as a food item is eaten and gets smaller.

LITERATURE REVIEW

Introduction

The primary function of this literature review is to provide background for the experiments presented in this dissertation. The first of three sections concerns the relationship between an animal's behavior and the organization of its somatic sensory system, especially its cerebral neocortex. The second section consists largely of a detailed discussion of the morphology, physiology and phylogenetic distribution of cutaneous mechanoreceptors. The concept of a receptor array also is considered. The third section contains a general introduction to the sensory control of behavior and a detailed discussion of the role of tactile input in controlling behavior. I have approched this literature with an interest in the interface between behavior and sensory neurobiology. A secondary function of this review is to criticize methods of looking at this particular "brain-behavior" relationship.

Relationships Between Central Somatic Sensory Projections and Behavior

Our ability to examine the proposed relationship between an animal's behavior and the relative development of its central somatic sensory pathways (Ariëns Kappers, et al. 1936; pp. 261-262) increased greatly when Woolsey's group began a long series of cortical mapping studies in several species of mammals (Woolsey et al. 1942, Haynes and Woolsey 1944, Woolsey and Wang 1945, Woolsey and Fairman 1946, Chang et al. 1947, Woolsey and Le Messurier 1948, Woolsey et al. 1952, Pinto Hamuy et al.

1956, Woolsey 1958). These early mapping studies frequently revealed disparities between the relative surface areas of different regions of an animal's body and the amount of cortical surface receiving input from them. For instance, in the primary somatic sensory area (SmI) of rats (Woolsey and Le Messurier 1948), rabbits (Woolsey and Wang 1945), pigs, sheep (Woolsey and Fairman 1946), and dogs (Pinto Hamuy et al. 1956) parts of the head, face and intra-oral regions are represented to a much greater extent (the representations are disproportionately large) than would be expected based on their surface area relative to that of other regions of the body. Welker and Seidenstein (1959) hypothesized that such disproportionalities in cortical representations are related to a species' behavior. On this basis, they predicted that in the raccoon's (Procyon lotor) cortical map the forepaw, which is used extensively to manipulate food items and explore other objects, would be highly represented. Their results indicate that the forepaw representation constitutes fully 68% of SmI (Welker and Seidenstein 1959, Welker and Campos 1963), supporting their original hypothesis.

Present evidence indicates that in mammals the relative sizes of afferent projections from different regions of the body surface onto the cortical surface correlate with behavioral specializations rather than with the relative surface areas of those regions. However, this correlation is straightforward only when behavioral specializations and disproportionalities in representations are pronounced (Welker and Campos 1963). One of the clearest examples is the enlargement of facial, peri-oral and intra-oral representations in browsing and grazing species which have hoofed limbs (Woolsey and

Fairman 1946, Johnson et al. 1974, Welker et al. 1976). In sheep, Johnson et al. (1974) found these representations to be so enlarged that they were unable to find any body or limb representations in SmI. Enlarged representations of the furry buccal pads in capyberas (Hydrochoerus hydrochaeris) and guinea pigs (Zeigler 1964, Campos and Welker 1976), peri-oral and intra-oral tissue in rabbits (Woolsey and Wang 1945, Woolsey 1958) and the bill of the platypus (Ornithorhynchus anatinus) (Bohringer and Rowe 1977) are also considered to be related to foraging behavior. In rats and Three-toed sloths (Bradypus tridactylus) vibrissae and forelimbs, respectively, are used in more general exploratory behavior and have disproportionately large cortical representations (Vincent 1912, 1913, Welker 1964, Welker 1971, Saraiva and Magalhães-Castro 1975).

Welker (1976) suggested that the proportions in a species' cortical map are determined by a variety of selective pressures associated with specific behavioral-ecological parameters. For species with striking disproportionalities in their maps, it can be assumed that either these selective pressures are additive or that one is dominant. In other species in which selective pressures conflict and none is clearly dominant one might expect to find a map in which disproportionalities are less striking. Different species of monkeys (Woolsey et al. 1942, Pubols and Pubols 1971, 1972), cats (Haynes and Woolsey 1944, Woolsey 1958, Rubel 1971), beavers (Castor canadensis) (Carlson and Welker 1976), two species in the genus Didelphis (Lende 1963, Pubols et al. 1976, Magalhães-Castro and Saraiva 1971), gray squirrels (Siurus carolinensis) (Nelson and Sur 1977, Sur et al. 1978), porcupines (Erethizon dorsatum) (Lende

and Woolsey 1956) and slow lorises (Nycticebus coucang) (Krishnamurti et al. 1976) all fall in this category. In these cases it is more difficult to correlate cortical organization with behavior. The nature of the mapping and behavioral data also contribute to this difficulty and will be considered next.

Presentation of Mapping Data

Mapping data are presented in four different formats, three are graphic and one is numerical. The animalcule-like figure positioned on one cortical hemisphere is the best known graphical technique (Woolsey 1958, Johnson et al. 1974, Krishnamurti et al. 1976). It provides a concise summary of the relative sizes of representations of the different regions of the body surface. A second approach is to plot the representations as an areal map of the cortex (Welker and Campos 1963, Pubols and Pubols 1971, 1972, Sur et al. 1978). What these maps lack in esthetics they gain back with improved accuracy. The last graphic format is the use of figurines to depict response properties for each recording site (Woolsey 1958, Johnson et al. 1974, Pubols et al. 1976). Use of figurines in lieu of other formats (Lende 1964, Rubel 1971) makes it difficult to visualize sizes of representations. The fourth format is the numerical statement of the amounts of cortical surface to which different regions of the body surface project. Frequently tables containing a detailed breakdown of the actual or relative sizes of cortical projections from different body regions are presented (Welker and Campos 1963, Pubols and Pubols 1971, Sur et al. 1978).

A detailed table containing relative or actual sizes of

cortical representations is the single most useful data format for individuals interested in correlating behavior and cortical organization. Its great advantage is that it lends itself to the designing of quantitative behavioral experiments to test predictions that one might make from mapping studies. In addition some graphic presentation of data is helpful in trying to visualize both sizes and locations of various body surface representations.

As indicated earlier, disparities between sizes of cortical representations and the relative surface areas of those regions of the body form the basis for correlations of behavior and somatotopic maps (Welker 1973, Johnson 1978). Surprisingly, Pubols and Pubols (1971, 1972) appear to have published the only study in which surface areas for both cortical representations and the corresponding regions of the body surface were measured. Whereas cortical areas receiving input from glabrous hand skin and tail pad of spider monkeys (Ateles sp.) were similar, cortical area/skin area ratios were very different (0.39 for hand and 0.20 for tail pad). Thus, the hand skin is more highly represented than tail skin, despite the fact that this was not at all evident from examining the cortical map alone. These findings formed the basis for an interesting behavior experiment discussed in the next section of this review. In summary, our understanding of the relationship between behavior and a species' cortical organization would benefit from a more quantitative approach to the study of cortical representation and more rigorous analysis of the relationship between central and peripheral portions of the system.

Relating Cortical Representations to Behavior

Relating a species' behavior to its cortical map has been approached in a number of ways. Welker and Seidenstein (1959) used information about the raccoon's extraordinary use of its forepaws to develop a testable prediction about the structure of its cortical map. Unfortunately, the powerful approach of testing progressively refined a priori predictions based on prior experimental work has been fairly limited in this area (Herron 1978). In other studies behavioral documentation is presented to support a proposed correlation, however these correlations remain largely post-hoc (Welker and Campos 1963, C. Welker 1971, Saraiva and Magalhães-Castro 1975, Welker and Carlson 1976). Occasionally, proposed correlations rest on post-hoc reasoning and lack behavioral documentation (Lende and Woolsey 1956, Johnson et al. 1974, Welker et al. 1976). There are also studies demonstrating the importance of somatic sensory input in controlling several types of behavior (see discussion of this literature in section three, below), but they are not addressed to different roles for input from differentially represented regions of the body.

Studies designed specifically to relate a species behavior to the differential representation of the body surface in its cortex are rare. L. Pubols' preliminary experiments comparing the spider monkey's ability to perform tactile discriminations with its tail vs. its hand are an exception (Pubols 1966, Pubols and Pubols 1972). She demonstrated that whereas monkeys could perform roughness discriminations with both parts of the body, learning ability and performance with the forepaw was superior. Recall that in spider monkeys

the forepaw representation is almost twice that of the tail pad (Pubols and Pubols 1971). The importance of these experiments is that they show that even when cortical maps do not show striking disproportionalities one can design critical experiments to test the relationship between an animal's behavior and the organization of its cortical representations.

The comparative approach, which has proven extremely useful in examining cortical maps of different species (Welker and Campos 1963, Welker 1976, Johnson 1978), has been underexploited in looking at their behavior. Two closely related yet behaviorally and ecological distinct species that use a given part of their body in different ways (e.g. the use of the forepaw by burrow digging vs. tree climbing squirrels) could be compared in controlled behavioral tests. The results from the tests could then be used to develop testable predictions about the representation of the forepaw in the cortices of the two species. One might also begin with the mapping study and make predictions about behavior. Work on species in which a disproportionate cortical representation appears to correlate with more than a single behavior (e.g. foraging and general habitat exploration in rats) is needed as well. One might block somatic sensory input from the body part in question and compare the effects of this deficit on the behaviors in question.

In summary, there is little doubt that disproportionalities in cortical representations reflect a species behavioral repertoire, however, in most cases the correlations between the two are relatively general. Critical experiments, relating the differential representation of the body surface (within and between animals) to

specific behaviors are needed. Also, a shift towards the use of more quantitative procedures to collect and present data would be useful. The remainder of this section will serve as a bridge between the present discussion and a review of the cutaneous mechanoreceptor literature. It will help to explain the significance of examining cutaneous mechanoreceptors per se, rather than central projections from them.

The Relationship Between Central Projections and Peripheral Receptor Density

A cortical map is a description of the end point of an orderly projection of afferent input from peripheral receptor tissue (Celesia 1963, Werner and Whitsel 1968). Both this orderliness and the relative sizes of projections from different regions of the body surface can be found at other levels in the medial lemniscal pathway. For several species it is known that the relative sizes of projections onto cells in the ventrobasal complex of the thalamus match the relative sizes of cortical projections (Rose and Mountcastle 1952, Emmers 1965, Welker and Johnson 1965, Pubols and Pubols 1966, Pubols 1968, Cabral and Johnson 1971). Studies on the organization of the dorsal column nuclei show that the relative sizes of central projections are established by this level as well (Chang and Ruch 1947, Nord 1967, Johnson et al. 1968, Woudenberg 1970, Hamilton and Johnson 1973).

Generally, recording sites in the regions of enlarged representations have smaller peripheral receptive fields than sites elsewhere (Nord 1967, Woudenberg 1970, Rubel 1971, Pubols and Pubols 1971, 1972, Johnson et al. 1974, Campos and Welker 1976, Krishnamurti et al. 1976). This differential distribution of receptive field

sizes is considered to reflect the differential distribution of receptors peripherally (Welker 1973). The central representation of the body surface is considered more directly related to peripheral receptor density than to body surface proportions (Mountcastle and Darian-Smith 1968). A logical extension of this argument is that the distribution of receptors in the skin of an animal is correlated with its behavioral specializations. As mentioned at the outset, Ariëns Kappers et al. (1936; pp. 261-262) had suggested these relationships by 1936. Since then they have played a central role in explanations of the relationship between peripheral and central portions of the somatic sensory system (Woolsey and Fairman 1946, Mountcastle and Henneman 1952, Mountcastle and Darian-Smith 1968, Welker and Seidenstein 1959, Welker 1973, 1976, Pubols and Pubols 1971, 1972, Rubel 1971, Johnson 1978) and in understanding relationships between the organization of that system and behavioral specializations (Welker 1973, 1976, Johnson 1978). There are, however, few experimental data to support (or negate) the proposed relationships.

The most frequently cited study is that of Zollman and Winkelmann (1962). Staining for acetylcholinesterase activity in the glabrous digital skin of raccoons, they found more positive staining loci (which they assumed were receptors) in samples from the forepaw digits than in samples from corresponding hindpaw locations. These results match what is known about the relative sizes of central representations of these regions (Welker and Seidenstein 1959, Welker and Johnson 1965, Johnson et al. 1968). The authors were not able to morphologically identify these structures from their preparations nor was the study a rigorous quantitative analysis of the

distribution of acetylcholinesterase activity. If their positively staining loci were simple corpuscles, as Munger and Pubols (1972 suggest, then Zollman and Winkelmann were looking at one subpopulation of receptors. In a more quantitative study, Lee and Woolsey (1975) found that the number of neurons in the cortical barrels of mice is highly correlated with the number of fibers innervating the vibrissa follicle providing input to a given barrel. They did not look at morphologically identified receptors per se. Although there is some suggestive evidence, the actual relationship between peripheral receptor density and the relative sizes of central projections remains more a hypothesis than a firmly established fact. By deduction, the relationship between behavioral specializations and the differential distribution of receptors also remains a largely untested hypothesis.

Cutaneous Mechanoreceptors

The nature of cutaneous innervation and sensation are topics of long standing interest evidenced, in part, by frequent discussion and review of that literature (Adrian 1928, Weddell et al. 1955, Winkelmann 1960a, b, Melzack and Wall 1962, Weddell and Miller 1962, Sinclair 1967, Catton 1970, Munger 1971, Andres and v. Düring 1973, Winkelmann and Breathnach 1973, Halata 1975, Bohringer 1977, Horch et al. 1977, Montagna 1977, Munger 1977, Smith 1977). The primary objective of this section is to provide morphological and physiological descriptions of mechanoreceptors found in squirrel glabrous skin. The innervation of hairy skin will be considered only indirectly, in the context of understanding receptors found in glabrous skin. Munger (1971), Andres and v. Düring (1973), Halata (1975) and Cauna (1976)

have recently discussed that literature in more detail. This section will close with a consideration of the receptor array concept.

My use of the term mechanoreceptor does not preclude a receptor's response to other forms of stimulation, only that a receptor primarily responds to mechanical forces. This usage is based on a synthetic theory of cutaneous sensation (Melzack and Wall 1962) rather than on Von Frey's theory (each sensation is subserved by a different receptor type) (as discussed in Melzack and Wall 1962) or the pattern theory (patterns of input rather than receptor morphology are responsible for sensation) advanced by Weddell (1955) and Sinclair (1955). As Munger (1965, 1971) and Halata (1975) point out, the identification, naming and classification of cutaneous receptors have been problematic for quite some time. Frequently names have implied unsubstantiated functional properties, variants of a single receptor type are given their own names (which often correspond to the investigator's) and successive reviews change classification schemes back and forth. Halata (1975) recently provided a reasonable classification of receptors based on ultrastructural characteristics. For instance, he is able to take Botezat's (1912) 38 classes of glabrous skin receptors and with very little information loss integrate them into three types.

In the discussion that follows I will adopt Halata's (1975) general principles of classification and will avoid unjustified functional names. To be consistent with my experimental work I will divide receptors into two classes based on light microscopic characteristics: non-corpuscular endings and corpuscular endings. This scheme is also similar to Cauna's (1966). The first category,

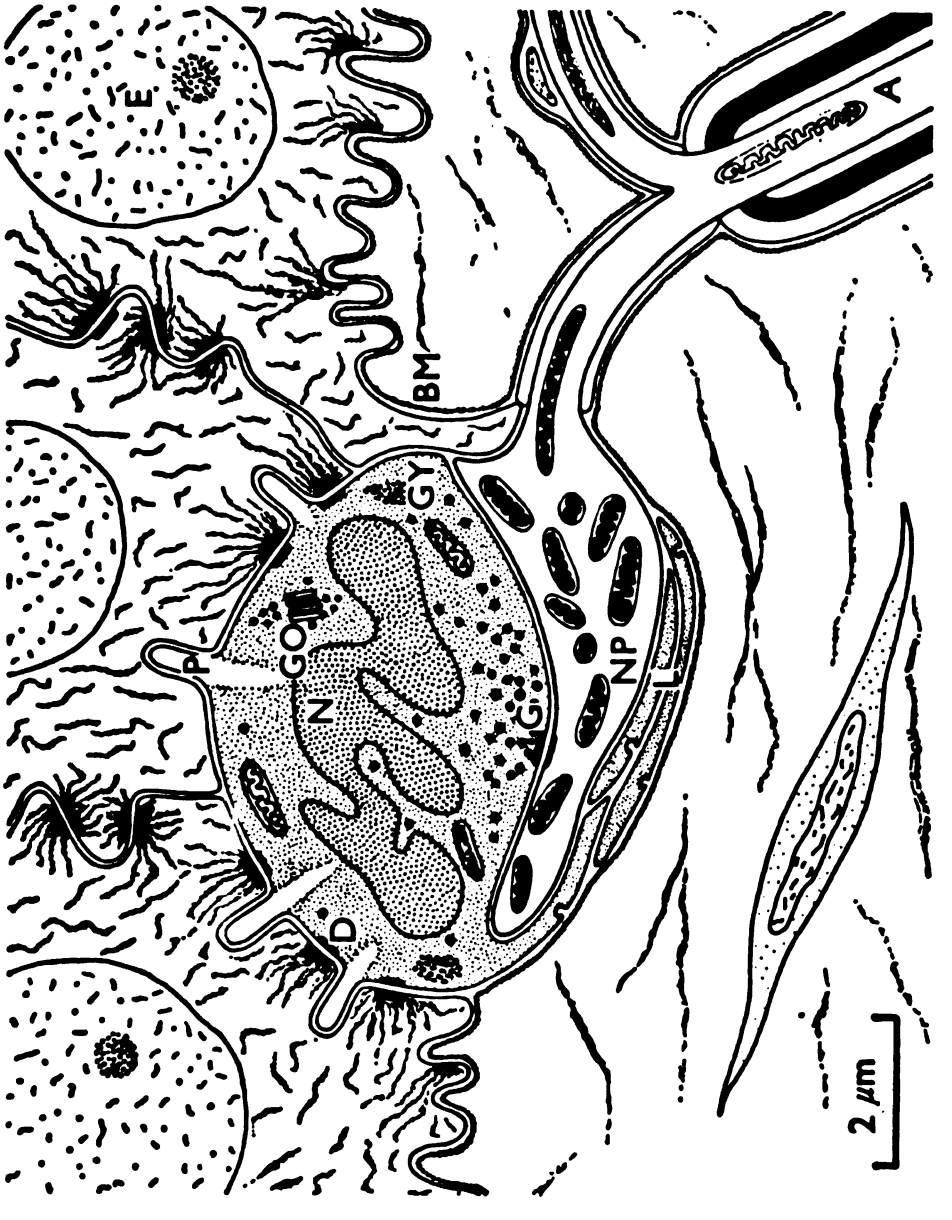
including Merkel cell- neurite complexes and free endings (Halata's dermal simple bulboid endings and epidermal free endings) will be discussed first. Corpuscular endings (Halata's dendritic bulboid endings, simple encapsulated corpuscles with inner cores and Pacinian corpuscles) will be discussed last.

Merkel Cell- Neurite Complexes

Originally, Merkel (as discussed in Munger 1965) found specialized, large vesicular cells with large pale nuclei in the bases of rete pegs (extensions of the epidermis down into the dermis) in the glabrous snout skin of moles (Talpa spp.). He reasoned that these cells acted as transducers of mechanical stimuli to the disc-like terminal expansions of neurites that he found adjacent to many of them and named them Tastzellen (touch cells). Similar endings were found in both hairy skin (Brown and Iggo 1963, Cauna 1954, Mann 1965, Smith 1967) and glabrous skin (Cauna 1954, Miller et al. 1958, Miller and Kasahara 1959a). A consistent feature of Merkel cells in material embedded in paraffin is a vacuolated cytoplasm (Munger 1965). In 1965 Munger (1965) described the ultrastructure of these cells and their associated neurites and, removing functional implications, named the unit the Merkel cell- neurite complex. The following description, based largely on his study of the snout skin of opossums (Didelphis marsupialis virginiana) fits virtually all of the Merkel cell- neurite complexes found to date (see Munger 1971, Winkelmann and Breathnach 1973, Halata 1975 and Smith 1977 for reviews) (see Figure 1 for a schematic diagram of a Merkel cell).

Large (5-10um) fibers course up through the dermis, branch in

Figure 1. A diagram of a Merkel cell- neurite complex. Granular vesicles (G) are the same as dense-cored granules. (From Iggo and Muir 1969)



Text-fig. 2. A diagram showing the structure of a tactile cell and its associated nerve plate. A, myelinated axon; BM, basement membrane; D, desmosome; E, epithelial cell nucleus; G, granular vesicles in the tactile cell near a junction with the nerve plate, NP; GO, Golgi apparatus; GY, glycogen; L, lamellae underlying the nerve plate; N, multilobulated nucleus; P, cytoplasmic process from the tactile cell.

Figure 1.

the superficial dermis and then lose their myelin sheaths shortly before reaching the epidermis. These unmyelinated fibers then reach the dermal- epidermal (D-E) junction where the basement membranes of their Schwann cells and epidermal cells interdigitate and become contiguous with each other. The neurite is then enveloped in a unique fashion by processes of epidermal cells (Munger 1965, Halata 1975). The neurite expands into a plate or disc-like terminal and contains microtubules, neurofilaments, mitochondria and lipid material (Munger 1965), as well as lysosome-like inclusions and sometimes small vesicles (Munger et al. 1971, English 1977b).

The Merkel cell itself lies in the basal layer of the epidermis, is less electron-opaque than surrounding cells and has a highly lobulated nucleus. A prominent Golgi apparatus is present in the cytoplasm on the side of the nucleus away from the neurite. The cell's most striking characteristic is the collection of osmiophillic, dense-cored granules (measuring roughly 1000$\mathring{A}$ in diameter) adjacent to the nerve terminal. The dark core is surrounded by a membrane-limited pale halo (Mustakillio and Kiistala 1967). Munger (1965) described them as secretory granules and McGavran (1964) likened them to granules in adrenergic cells in the adrenal medulla. Other characteristics of Merkel cells include desmosomal attachments to adjacent cells, finger-like cytoplasmic extensions and tonofilaments (Munger 1965, Hashimoto 1972a, English 1977b). Some authors report synapse-like structures between Merkel cells and adjacent neurites (Andres 1966, Halata 1970, 1972a, 1975, Chen et al. 1973) but others fail to find any (Munger 1965, Munger et al. 1971, Smith 1970).

Several aspects of Merkel cell biology have attracted considerable

attention. The granules have been examined as possible sites for neurotransmitter storage, however, there is no consensus concerning their chemical composition (Winkelmann and Breathnach 1973, Halata 1975). Pharmacological agents known to affect standard neurotransmitter activity usually fail to alter activity in Merkel cell-neurite complex afferents when applied to groups of Merkel cells (Smith and Creech 1967). The suggestion that the granules indicate a trophic relationship between the Merkel cell and neurite (Smith and Creech 1967, Kasprzak et al. 1970) is presently being examined (Cooper et al. 1975, 1977, Diamond 1976). The role of the neurite in the development and maintenance of Merkel cells is also under investigation (Brown and Iggo 1963, Smith 1966, 1967, English 1974, 1977a, b, Tweedle 1978, Brenowitz 1978). The embryological origin of Merkel cells (do they migrate into the skin or differentiate in situ) is a matter of debate with no conclusion established yet (Breathnach and Robins 1970, Breathnach 1971a, Lyne and Hollis 1971, Hashimoto 1972a, b, Winkelmann and Breathnach 1973, English 1977a, b, Tweedle 1978, Brenowitz 1978).

Merkel cell-neurite complexes occur in several configurations in both glabrous and hairy skin. In glabrous skin they are found singly or in clusters (up to 36/cluster) at the bases of rete pegs and ridges or in the epidermis above dermal papillae (Cauna 1954, Miller and Kasahara 1959a, Halata 1970, 1975, Munger et al. 1971, Munger and Pubols 1972, Hashimoto 1972a, Chouchkov 1974, Loo and Kanagasuntheram 1972, 1973). They are also associated with specialized receptor structures such as Eimer's organ in the mole (Halata 1972a) and the similar rod organ in platypus (Bohringer 1977).

Clusters of up to 50 Merkel cell-neurite complexes occupy small (200-400um in diameter) domed shaped elevations known as Haarscheiben, touch domes, touch spots or Iggo corpuscles in the hairy skin of mammals (Brown and Iggo 1963, Mann 1965, Iggo and Muir 1969, English 1974, 1977a, b). These receptor complexes also are located within the root sheath of tylotrich or sinus hair follicles (Mann and Straile 1965, Andres 1966, Patrizi and Munger 1966, Gottschaldt et al. 1972).

The Merkel cell-neurite complex is phylogenetically the most widely distributed cutaneous receptor, yet in most species they are strikingly similar. Teleost fish have cells that fulfill ultra-structural criteria for Merkel cells (Lane and Whitear 1977). Urodele (Cooper and Diamond 1977, Cooper et al. 1975, 1976, 1977, Diamond 1976, Tweedle 1978) and Anuran amphibians (Nafstad and Baker 1973), as well as reptiles (Order: Squamata) (v. Düring 1973) have them. Nafstad (1971) found cells that resemble Merkel cells in the hard palate of birds. And, in addition to Monotremes (Quilliam and Armstrong 1963b, Bohringer 1977) and Marsupials (Munger 1965, Brenowitz 1978) the following placental mammals have Merkel cell-neurite complexes: Insectivores (Quilliam and Armstrong 1963b, Halata 1972a, 1975), Primates (Breathnach and Robins 1970, Breathnach 1971a, b, 1977, Loo and Kanagasuntheram 1972, 1973, Chouchkov 1974, Halata 1975), Lagomorphs (Smith 1967), Rodents (Patrizi and Munger 1966, Smith 1966, 1967, Chen et al. 1973), Carnivores (Brown and Iggo 1963, Iggo and Muir 1969, Gottschaldt et al. 1972, Munger et al. 1971, Munger and Pubols 1972, Stephens et al. 1973) and Artiodactyls (Mann 1965, Lyne and Hollis 1971, Nafstad 1971).

Intraepidermal fibers, probably associated with Merkel cells, are found in elephants (Order: Proboscoidea) (Montagna et al. 1975).

The physiological properties of the Merkel cell-neurite complex were first established as a result of studies of the Haarschieben in cats and primates. Iggo and Muir (1969) demonstrated that these receptors are the morphological correlate of the Type I slowly adapting (SA) mechanoreceptor unit (Chambers and Iggo 1968). Its characteristics include spot-like receptive fields, irregular firing rate (ISI varies greatly) and the lack of a resting discharge. After an initial decrease in firing rate following the dynamic phase of stimulation (while a mechanical stimulus is actively displacing the skin) these units continued firing for over 30 minutes (Iggo and Muir 1969). A decrease in temperature also evokes a discharge from Merkel cell afferents (Iggo and Muir 1969). These results agree with those of Tapper (1964, 1965), Lindblom and Tapper (1966) and Smith (1967). Additional studies in glabrous skin (Jänig 1971, Munger et al. 1971, Munger and Pubols 1972) clearly establish the Merkel cell-neurite complex as the Type I SA mechanoreceptor in mammals. Recently, however, studies in amphibians indicate that their Merkel cell-neurite complexes may be rapidly adapting (RA) (Cooper et al. 1976, Parducz et al. 1977), although these results are not yet confirmed in other laboratories. In terms of behavioral correlates, Tapper (1970) has shown that minute displacement of one Haarscheibe is sufficient to elicit a behavioral response (conditioned avoidance) in cats.

Free Endings

By definition free endings lack the non-neural elaborations (Merkel cells or corpuscles) present in other receptor types. They were originally described in many light microscopic studies (Miller and Kasahara 1959a, b, Winkelmann 1960a, Palmer and Weddell 1964, Giacometti and Machida 1965, Cauna 1966), however, the precise definition of a free terminal is difficult (Munger 1975, Halata 1975). Failure to locate non-neural elaborations can be because one is not looking at a fiber's terminal or because they really do not exist.

In the epidermis free endings seen in light microscopy are almost always associated with Merkel cells (Munger 1965, Breathnach 1977). In the glabrous snout skin of opossums fibers in the epidermis appear to be continuations of neurites innervating Merkel cells (Munger 1965). In other studies free endings were always found relatively close to Merkel cells (Chouchkov 1974), suggesting that they were probably part of Merkel cell-neurite complexes situated in nearby sections. Despite these reservations, ultrastructural studies of Eimer's organs in the glabrous snout skin of moles (Halata, 1972a, 1975), the platypus' rod organ (Bohringer 1977) and human hairy skin (Cauna 1973, 1977) indicate that in some instances epidermal free endings may exist. In view of the light microscopic nature of the experimental part of this dissertation, all fibers found within the epidermis will be called intraepidermal endings and no attempt will be made to subdivide this category into free endings and Merkel cell-neurite complexes.

Dermal free endings (Halata's simple bulboid endings) are found

in the corium (superficial dermis) of several mammals (Munger and Pubols 1972, Hensel et al. 1974, Halata 1975). In such endings a large (5-7um) myelinated fiber courses up into a dermal papilla (an extension of the dermis up into the epidermal region) and ramifies into a number of terminal branches. These branches can form a tangled skein of fibers (Munger and Pubols 1972) and their terminals are frequently unmyelinated (Munger and Pubols 1972, Hensel et al. 1974). Sometimes a Schwann sheath is absent and the terminals contact the surrounding connective tissue (Munger and Pubols 1972). Halata (1975) considers the presence of clusters of mitochondria in parts of the unmyelinated branches evidence that they are terminals. In raccoons these endings are intimately associated with vascular channels (Munger and Pubols 1972).

Because much of the information about free endings is based on light microscopy and is therefore subject to the criticisms detailed above, a discussion of the phylogenetic distribution of these endings seems unwarranted and will not be undertaken. Physiologically, free endings are poorly understood. In Horch et al. (1977) free endings are suggested as the possible morphological correlates of different types of mechanoreceptor units. On the basis of fiber diameter and position Munger and Pubols (1972) consider dermal free endings part of the somatic afferent system. They were unable to associate these endings with a specific set of physiological parameters. There is at least one study that indicates that free endings may be thermoreceptors (Hensel et al. 1974). Because of their probable role in the somatic afferent system and their potential mechanoreceptor function dermal free endings will be treated as non-corpuscular receptors along with

intraepidermal fibers.

Corpuscular Endings

Corpuscular mechanoreceptors consist of one or more terminal neurites associated with a complex of epithelial cells and extracellular connective tissue, yielding a bulb-like appearance at the end of the neurite(s). Light microscopic studies have concentrated on the variability of such endings (Miller et al. 1958, Miller and Kasahara 1959a, b, Winkelmann 1960a, Poláček 1961, Kadanoff and Spassova 1962, Palmer and Weddell 1964, Malinovský 1966a, b, c). Different classical names such as Krause end-buld, genital end-bulb, Meissner corpuscle, Golgi-Mazzoni corpuscle, and mammalian end organ are given to relatively similar endings. More recently, ultrastructural studies have made it possible to identify similarities between many of these receptor types (Munger 1971, Andres and v. Düring 1973). Halata (1975) has proposed that there are essentially two types of corpuscular endings: dendritic bulboid endings and encapsulated corpuscles with inner cores. While his scheme underplays actual differences it provides a useful framework for this discussion. I will describe the main characteristics of the different types of corpuscles using information about the specific variations found in squirrels to fill in details.

Dendritic bulboid endings are found in the papillary dermis and consist of one or more terminal fibers which, in close association with lamellar cells, form complex structures (Halata 1975). In the glabrous skin of mammals the Meissner corpuscle is the most widespread ending in this category (see Halata 1975 for a review of the early

literature). Large myelinated fibers originating in the corial plexus course up into dermal papillae and enter the Meissner corpuscle proper (see Figure 2). These fibers frequently ramify into terminal branches which follow a tortuous course, winding around within the corpuscle (Cauna 1954, 1956, Cauna and Ross 1960, Miller and Kasahara 1959a, b, Winkelmann 1960a, Idé 1976, 1977). In light microscopic material it was not clear whether an outer capsule was present (Miller and Kasahara, 1959a, b, Weddell and Miller 1962).

The following description of the ultrastructure of Meissner corpuscles is based largely on Cauna and Ross' (1960) original description. After entering the base or side of the corpuscle, a fiber(s) loses its myelin and Schwann cell sheaths and enters into a close, often appositional relationship with laminar (lamellar) cell processes. Synaptic structures sometimes occur (thickenings and vesicles) (Cauna and Ross 1960, Hashimoto 1973). The bulk of the corpuscle in humans and other species is composed of flattened stacks of lamellar cells which stretch across the corpuscle parallel to the skin surface and have their nuclei at the edges of the corpuscle (Cauna and Ross 1960, Munger 1971, Andres and v. Düring 1973, Halata 1975, Idé 1976). Based on ultrastructural and developmental data, lamellar cells are considered modified Schwann cells (Cauna and Ross 1960, Saxod 1970, 1973, Hashimoto 1973, Idé 1976, 1977).

The fiber (or its terminal branches) meanders between lamellar cell processes (extracellularly). The nerve endings are described as non-ramified, ramified with discoid expansions or ramified with varicosities (Cauna and Ross 1960, Halata 1975, Idé 1976) and are filled with mitochondria (Cauna and Ross 1960, Idé 1976). Fibers

Figure 2. A diagram of a Meissner corpuscle. (from Andres and v. Düring 1973)

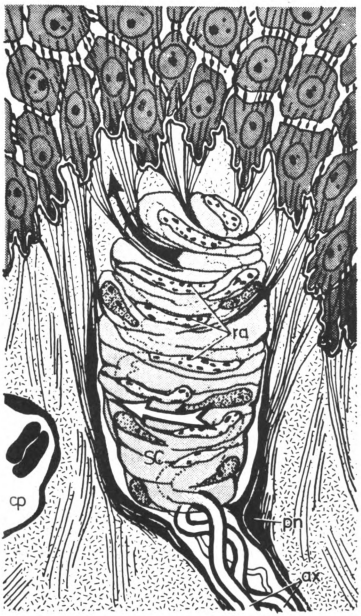


Fig. 10. Schematic representation of a Meissner corpuscle showing the tonofibrilis of the epithelial cells in continuity with collagen fibres of the corium, some of which enter the upper part of the corpuscle. Others are continuous with the endoneural sheath at the basal half of the corpuscle. The tonofibril-collagen system may act directly on the receptor axon (black arrow). The white arrow indicates a possible consecutive movement of the lower part of the corpuscle which could eliminate the mechanical stimulus. Such a mechanism could explain the rapid adaptation of this receptor. Coiled receptor axon (ra); Schwann cells (sc); cup shaped perineural sheath (pn); myelinated axons (ax); capillary (cp)

Figure 2.

sometimes exit the corpuscles and terminate in the epidermis above it (Hashimoto 1973, Idé 1976). Cauna and Ross (1960) found that Meissner corpuscles in humans are surrounded by collagen fibers and fine fibrils similar to those found between lamellar cell processes. Halata (1975) confirms this finding but adds that fibrocytes may also form part of the capsule. He emphasizes that the corpuscle is not surrounded by a true perineural capsule. Tonofibrils often radiate out from part of the corpuscle to the surrounding connective tissue and epidermis (Andres and v. Düring 1973). In mice it appears that there is a cup of perineural tissue around the bottom part of the capsule (Idé 1976). Occasionally, small unmyelinated fibers are associated with these corpuscles (Idé 1976). These endings reach 100um in length by 50um in width in primates (Halata 1975) but are considerably smaller in other species (Idé 1976). Meissner corpuscles are largely confined to glabrous skin.

Encapsulated endings in the rat's penis (Patrizi and Munger 1965), genital end-bulbs (Polácek and Malinovský 1971) and Ruffini endings (Chambers and Iggo 1967, Chamber et al. 1972, Halata 1976) are other dendritic bulboid endings found in mammals. The Grandry corpuscle, an avian mechanoreceptor consisting of specialized cells similar to Merkel cells, dendritic nerve terminals and a capsular structure (Quilliam and Armstrong 1963a, b, Munger 1966, Saxod 1970, 1975, Gottschaldt 1974, Gottschaldt and Lausmann 1974, Idé and Munger 1978) is another similar corpuscle.

Encapsulated corpuscles with inner cores are the second type of corpuscular ending and can be divided into simple and Paciniform

corpuscles (Halata 1975). This sensory ending consists of a neurite, an inner core, a subcapsular space (also called capsular space) and a capsule (Halata 1975). Both simple and Pacinian corpuscles will be discussed. Simple corpuscles are extremely variable, even within an individual: the axon may or may not be branched, the number of axons varies, the inner core and the outer capsule may branch separately or together and the overall size may vary (Malinovský 1966a, b, c). The size and form of simple corpuscles are thought to be a function of where in the body they are found and how deep in the dermis they lie (Poláček 1961). The ultrastructural description presented below is based on Halata's (1972b, 1975) studies of moles, Munger and Pubols' (1972) study of raccoons and Mac Intosh's (1975) study of rats.

A large myelinated fiber from the corial plexus proceeds up into the papillary dermis and enters a corpuscular structure (see Figure 3) either in a dermal papilla or below an epidermal extension (Munger and Pubols 1972, Halata 1972b, 1975, Bohringer 1977). As the fiber enters the corpuscle it loses its myelin and then its Schwann sheath. The fiber becomes surrounded with a variable number of lamellar cells which appear to be modified Schwann cells (Halata 1972b, 1975, Saxod 1973). Successive lamellae are separated by connective tissue (Munger and Pubols 1972, Halata 1975, Mac Intosh 1975) and there are mixed opinions as to whether these lamellae are attached to each other by desmosomal structures (Munger and Pubols 1972, Halata 1975). These lamellae constitute the inner core. There are additional, concentric lamellae which are noticably less tightly packed than those of the inner core (Munger and Pubols

Figure 3. A diagram of a simple corpuscle with inner core. (1) Bead-like expansion of the axon with digitate processes. The middle portion of the axon (2) runs inside the inner core. The afferent nerve fibre (3) is myelinated. The inner core is formed of a lamellar system of Schwann cells (4). The lamellae are linked by desmosome-like structure (*). The sub-capsular space (5) contains fibrocytes and collagen fibres. The capsule (6) is a continuation of the perineurium and is lined and covered with a basal lamina (↑).

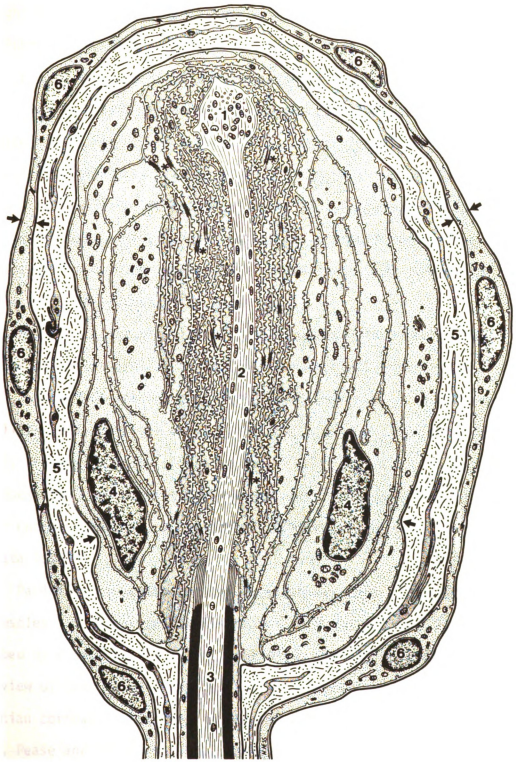


Figure 3.

1972, Mac Intosh 1975) and often a subcapsular space filled with connective tissue (Halata 1975). A capsule of cellular material thought to be of perineural origin encloses this structure (Munger and Pubols 1972, Halata 1975).

Within the inner core the nerve fiber(s) forms a terminal expansion which is filled with mitochondria and sometimes clear vesicles (Halata 1972b, Munger and Pubols 1972). Simple corpuscles in moles and raccoons generally measure 15-25um in diameter and 30-50um in length (Halata 1972b, Munger and Pubols 1972). The orientation of the longitudinal axis of simple corpuscles varies from parallel to the skin surface to perpendicular to it (Halata 1972b, Munger and Pubols 1972, Mac Intosh 1975).

Endings in the naso-labial region in cats (Malinovský 1966b, Poláček and Halata 1970), mammalian end organs (Winkelmann 1957, 1960b, Loo and Kanagasuntheram 1972, 1973), innominate corpuscles (Quilliam 1966, Quilliam et al. 1973, Loo and Kanagasuntheram 1972, 1973), Krause end-bulbs (Spassova 1973), Golgi-Mazzoni corpuscles (Polácek 1961) and mucocutaneous end organs (Winkelmann 1960a) are other endings that can be considered variants of simple corpuscles (Halata 1975).

Pacinian corpuscles are larger and more complex than simple corpuscles. They were first discovered in the mid 1700's and described by Pacini in the 1840's (see Pease and Quilliam 1957 for a review of this early literature). The structure and function of Pacinian corpuscles have been discussed frequently (Weddell et al. 1955, Pease and Quilliam 1957, Loewenstein 1966, 1971, Quilliam 1966, Munger 1971, Andres and v. Düring 1973, Halata 1975). While

they are found in the deep dermis of the skin and in subdermal tissue (Cauna 1958, Miller et al. 1958, Munger and Pubols 1972, Malinovský and Sommerová 1972, Brenowitz 1978), they have been most thoroughly studied in mesenteric tissue (Pease and Quilliam 1957, Loewenstein 1971, Ilyinsky et al. 1976). Based on light microscopy the corpuscle is divided into an inner core containing the nerve terminal, an intermediate zone and a capsule (Cauna 1958, Cauna and Mannan 1959, Miller et al. 1958a, Quilliam 1966). The description of Pacinian corpuscle ultrastructure presented below is based on Pease and Quilliam's (1957) original description of corpuscles from the cat's mesentery.

A large myelinated fiber (5-10um) enters the Pacinian corpuscle at its base, loses its myelin sheath and proceeds further into the corpuscle before losing its Schwann sheath and becoming surrounded by lamellae. The fiber terminates in an ellipsoid expansion twice the diameter of the fiber and contains numerous mitochondria. The lamellae, once again, are thought to be modified Schwann cells (Cauna 1958, Halata 1975). The inner core is composed of closely packed cytoplasmic lamellae which are bilaterally organized into two opposing groups on either side of the nerve. The nuclei of the lamellar cells are found at the outer edge of the core. Because of this arrangement of lamellae, there is a symmetrical bilateral cleft running parallel to the ellipsoid nerve terminal in which no lamellae are found. Often blebs of the neural terminal extend into these clefts (Pease and Quilliam 1957, Nishi et al. 1970). Vesicles are sometimes found in the terminal as well.

Next, there is an intermediate zone which surrounds the inner

core (Munger and Pubols 1972) and appears to be the site from which the corpuscle grows during development (Pease and Quilliam 1957). In this zone, lamellae are much less tightly packed and are concentrically arranged, with several cells contributing overlapping processes to each lamella so that no cleft is present. Inter-lamellar spaces are filled with connective tissue, including collagen fibrils (Pease and Quilliam 1957, Halata 1975). The outermost structure is the capsule, which was initially described as being composed of approximately six lamellae tightly packed together and underlying a condensation of connective tissue (Pease and Quilliam 1957). The outermost layer of the capsule is now thought to be composed of tightly packed layers of perineural cells (Halata 1975).

Halata (1975) found that in general the deeper a Pacinian corpuscle lies from the surface, the greater the number of layers in the capsule. Several studies show that Pacinian corpuscles can take on rather complex shapes in the skin and can reach sizes greater then 1mm long (Cauna and Mannan 1959, Brenowitz 1978). In addition to the large mechanoreceptor fiber, smaller, unmyelinated noradrenergic fibers have been seen entering the corpuscle in the cat's mesentery (Santini 1968). Corpuscles also contain vascular profiles, especially in the outer portion (Cauna 1958, Nishi et al. 1970). Herbst corpuscles in the skin and other tissues in birds are strikingly similar to Pacinian corpuscles but are much smaller. They have an inner lamellar core surrounding a central unmyelinated fiber, an intermediate zone and a capsule (Quilliam 1963, 1966, Quilliam and Armstrong 1963a, b, Munger 1966, Anderson and Nafstad 1968, Saxod 1970, 1973, 1975, Gottschaldt and Lausmann 1974).

Physiological properties have been correlated with morphological characteristics for a relatively small number of corpuscular endings. Generally, the physiological response properties of a primary afferent fiber are determined and the piece of skin containing its receptive field is examined histologically. By repeated sampling it is possible to identify the receptor type present in all or most pieces of skin associated with a particular set of response properties. These tehcniques are, however, subject to sampling error. Pacinian corpuscles have been studied singly *in vitro* and are an exception.

The most thoroughly studied dendritic bulboid ending is the Ruffini corpuscle which has been identified as the morphological correlate of the Type II SA mechanoreceptor in hairy skin (Chambers and Iggo 1967, Chambers et al. 1972, Biemesderfer et al. 1978). It has a resting discharge, a larger receptive field than the Type I SA receptor (Merkel cell-neurite complex) and a regular firing rate (ISI is uniform). The discharge rate during the dynamic phase of mechanical stimulation is a function of velocity and final amplitude of displacement, contrary to Horch et al.'s (1977) categorization. Ruffini corpuscles also respond to changes in temperature (a decrease in temperature increases discharge rate) (Chambers et al. 1972). The Grandry corpuscle, which I include in the dendritic bulboid category, is a rapidly adapting (RA), receptor that is sensitive to the velocity of stimulation. It is not sensitive to displacement amplitude, lacks a resting discharge and acts as a vibration detector (1 to 1 following of stimuli up to approximately 200/sec) (Gottschaldt 1974). In the absence of information about other receptors in this category it is premature to draw any general

conclusions about their physiology.

Among simple corpuscles with inner cores, the simple corpuscle of raccoons (Pubols et al. 1971, Munger and Pubols 1972) and the Krause end bulb-like ending in cats (Iggo and Ogawa 1977) have been studied. Both are associated with RA afferent units responding to the dynamic phase of mechanical stimulation with a velocity sensitive discharge rate. The simple corpuscles of raccoons do not respond to temperature changes and these data are not given for Krause end bulbs. Tuning curves for sinusoidal vibratory stimulation of both endings show that threshold amplitudes are lowest at 20-100 Hz (Munger and Pubols 1972, Iggo and Ogawa 1977).

Response properties of Pacinian corpuscles are relatively well known (see Loewenstein 1966, 1971 and Ilyinsky et al. 1976 for reviews). They are extremely rapidly adapting and follow stimulation rates of up to 1000 Hz with a 1 to 1 response. Tuning curves for Pacinian corpuscles have best frequencies of 100-300 Hz (Sato 1961, Iggo and Ogawa 1977) and they are described as vibration detectors (Sato 1961, Hunt 1961, Loewenstein 1966, Halata 1975). These tuning curves have been shown to be temperature sensitive (Sato 1961). Loewenstein (Loewenstein and Mendelson 1965, Loewenstein 1966) and Ilyinsky et al. (1976) have demonstrated that the outer capsule with its lamellar structure is responsible for the rapid adaptation rate and the "off" response seen when a stimulus is withdrawn from a corpuscle.

The ellipsoid shape of the unmyelinated terminal (Pease and Quilliam 1957) appears to be responsible for directional sensitivity in Pacinian corpuscle responses. This shape maximizes the efficiency

with which a mechanical stimulus is transduced by the terminal (Ilyinsky et al. 1976). The corpuscular structure also acts as a mechanical filter and is important in transferring mechanical displacements to the terminal (Loewenstein 1966, 1971). The unmyelinated terminal part of the nerve fiber is responsible for producing a generator potential as well as an action potential (Gray and Sato 1953, Sato and Ozeki 1966). Recently, Gottschaldt (1974) found that Herbst corpuscles which are morphologically similar to Pacinian corpuscles share many of the physiological properties with the latter. For instance, they are RA vibration detectors capable of 1 to 1 following of stimulation rates up to 500 Hz.

The phylogenetic distribution of corpuscles has been presented, in large part, in describing these endings. The discussion that follows will focus on establishing the presence of receptors in various groups and will not contain exhaustive lists of studies on a particular group (this applies to mammals especially). Lamellated receptors with inner cores occur in the skin of Anuran amphibians (Bolgarskij 1964, v. Düring and Seiler 1974) and appear similar to mammalian simple corpuscles. Reptiles (Order: Squamata) have a variety of encapsulated endings that resemble Ruffini and Pacinian corpuscles of mammals and Herbst corpuscles of birds (v. Düring 1973, Jackson 1977). As mentioned above, birds have dendritic bulboid corpuscles known as Grandry corpuscles and Herbst corpuscles which resemble Pacinian corpuscles (Quilliam and Armstrong 1963a, b, Gottschaldt 1974). They also have simple corpuscles with inner cores in their eyelid skin (Malinovský 1968).

Dendritic bulboid endings occur in the following mammals: Insectivores (in hairy skin: Halata 1975), Primates (Cauna and Ross 1960, Munger 1975, Biemesderfer et al. 1978), Rodents (Idé 1976, 1977), Carnivores (Malinovský 1966a, Chambers et al. 1972) and Artiodactyls (pig hairy skin: Halata 1975). Simple corpuscles with inner cores are more widely distributed and are found in: Monotremes (Quilliam and Armstrong 1963b, Bohringer 1977) and Marsupials (Brenowitz 1978) and in Insectivores (Giacometti and Machida 1965, Halata 1972b), Primates (Loo and Kanagasuntheram 1972, 1973), Rodents (Patrizi and Munger 1965, Mac Intosh 1975), Carnivores (Winkelmann 1960b, Palmer and Weddell 1964, Malinovský 1966a, Munger and Pubols 1972) and Artiodactyls (Malinovský 1968, Quillaim et al. 1973). Pacinian corpuscles are the most restricted corpuscles and have been identified in the skin of Marsupials (Brenowitz 1978) and in Primates (Cauna and Mannan 1959, Kanagasuntheram et al. 1971) and Carnivores (Nilsson and Skoglund 1963, Munger and Pubols 1972).

Receptor Arrays

This review of the mechanoreceptor literature has concentrated on descriptions of individual types of receptors. In this regard it is an accurate reflection of the major emphases of investigators working in this area. As Munger (1971) suggests, understanding these receptors is a prerequisite for understanding cutaneous sensation in general. However, a natural tactile stimulus such as a food item, a potential mate, or a burrow entrance, will impinge upon large numbers of receptors as it moves across a patch of skin (or the animal moves the patch of skin across it). The individual receptors that

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a stimulus excites will depend on the mechanical properties of the skin (Cauna 1958, Quilliam 1966, 1975, Halata 1975) and upon the distribution of receptors in the piece of skin being stimulated (Quilliam 1966, 1975).

Quilliam (1966, 1975) has approached the question of distribution of receptors by considering complex, highly specialized aggregations of receptors such as the Eimer's organ in the snout skin of moles which consists of free endings, Merkel cell-neurite complexes and simple corpuscles (Quilliam and Armstrong 1963b, Halata 1975). He has applied the term "array" to these orderly arrangements of receptors. Other examples of complex arrays are the rod organ or the platypus (Quilliam and Armstrong 1963b, Bohringer 1977), the bill organs of geese (Gottschaldt 1974) and sinus hairs in mammals (see Halata 1975 for a recent review). Quilliam has also applied the term to groups of receptors found in the ridged digital skin in primates (Quilliam 1975). In a larger sense, any patch of skin can be considered to have an array of receptors, although defining units in the array and the pattern of the array will be more difficult where receptors are not organized into striking, highly specialized and localized aggregations.

While the significance of specialized arrays is widely recognized (Quilliam 1966, 1975, Quilliam and Armstrong 1963b, Cauna 1958, Munger 1971, Pubols et al. 1971, Andres and v. Düring 1973, Halata 1975, Montagna 1977), little research into the nature of these more diffuse arrays exists. In addition to understanding the relationships of individual receptors to other skin structures (Cauna 1954, Quilliam 1966, 1975, Halata 1975), the only array characteristic

examined in detail is the density of receptors (number per unit area) (Miller et al. 1958, Miller and Kasahara 1959a, Fitzgerald 1961, Jänig 1971, Gottschaldt and Lausmann 1974). There is also some data concerning the relative proportions of different receptor types in a variety of locations (Malinovský 1966a, b, c, Malinovský and Zemanek 1969, Gottschaldt and Lausmann 1974). Other aspects of distribution such as dispersion patterns (random, clumped or uniformly distributed) and the degree to which different receptor types are segregated from each other are unknown.

The advantage of having several different receptor types in a piece of skin is that they can act in combination and thereby respond to broad ranges of environmental stimuli (Quilliam and Armstrong 1963a). While understanding individual receptors is important (Munger 1971), Freeman (1976) argues that understanding spatial relationships between elements in neural systems and their interactions are crucial as well. He suggests that there are properties of neural systems that are not predictable on the basis of known properties of individual elements within those systems, but are predictable when complex interactions of elements are considered. Loewenstein (1966) suggested that our emphasis on individual elements within the peripheral somatic sensory system has led to an increase in entropy in that area. While only a starting point, attempts to define properties of arrays rather than single elements within arrays seem like steps in the right direction.

The Sensory Control of Behavior

The role of sensory input in controlling behavior played a central role in the historical development of the field of animal behavior. Ethologists were particularly impressed by "instinctive" "reflex-like" Fixed Action Patterns (FAP's) which they considered immune to the effects of sensory stimuli (Lorenz 1950, Tinbergen 1951, Eibl-Eibesfelt 1970). They also concentrated on finding specific features in patterns of sensory input (such as a mother gull's beak) that elicit behavioral responses (Sign Stimuli) (Lorenz 1950, Tinbergen 1951, Tinbergen and Perdeck 1951, Hailman 1967). It is ironic that Lorenz (1950) described FAP's as reflex-like for physiologists had cited reflexes as evidence that behavior (locomotion) is controlled primarily by peripheral sense organs (Sherrington 1906, 1910, Gray 1950).

A question that developed as a result of early behavioral studies, as well as physiological work is to what extent is behavior controlled by the central nervous system and to what extent is it controlled peripherally (by sensory input)? Bullock (1961) considered behavior to be primarily centrally controlled with sensory input serving to trigger or modulate centrally generated activity. Experiments such as those by Hamburger and Balaban (1963) showed that rhythmic motor patterns occur prior to the time sensory-motor hookup occurs. Studies on vertebrates and invertebrates showed that patterns of activity could also be maintained in preparations deprived of existing sensory input (Ikeda and Wiersma 1964, Kennedy et al. 1966, Fentress 1973, Edwards 1977). On the other hand, there is considerable evidence that sensory input is important in the development and

maintenance of behavior (Konishi 1965, King 1968, Gottleib 1971, 1976, Duysens 1977). Gray (1950) questioned whether central control had any role in controlling behavior (locomotion in amphibians).

In practice, early and recent models of the organization and control of behavior involve roles for peripheral and central control mechanisms (Weiss 1950, Lorenz 1950, Tinbergen 1951, Andrew 1976, Baerends 1976, Dawkins 1976, Fentress 1976). Fentress (1976) has proposed that the much debated boundaries between central and peripheral control are dynamic rather than static. The relative contributions made by these two sources of control and, therefore, the precise location of the boundary lines depend upon a host of interacting factors including an animal's specific motivational state. One might carry his argument further and suggest that the relative contributions of the different sensory modalities to the sensory control of behavior also are variable depending on specific sets of circumstances. For instance, when a pigeon is able to see the sun it will use it to navigate with, however, when the sun becomes clouded over the pigeon is able to switch to other sensory cues in order to continue its flight (Keeton 1974).

To study the role of sensory input in controlling a behavior one can change the stimuli reaching an animal or one can alter an animal's ability to detect that input (by altering the animal) (Beach and Jaynes 1956, Welker 1964, Konishi 1965, Marler 1970, Webster and Webster 1971, Kow and Pfaff 1976). The most commonly employed experimental manipulation for studying the role of tactile (somatic sensory) input in controlling behavior is cutting that input out all together. This can be done for short periods of time with

local anesthetics or for longer periods by lesioning peripheral nerves or central structures. While the primary effects of these procedures appear to be somatic sensory (largely tactile) deficits, other sensory deficits generally are not looked for. Stimulation studies to examine motor changes are uncommon. In studies using local anesthetics independent tests for the effect of the drug (e.g., recordings) are not routinely performed. While these may be minor considerations, they suggest that more thorough definition of lesion effects would add weight to conclusions about the role of tactile input in controlling behavior. Bearing these considerations in mind, somatic sensory input has been shown to play a role in controlling sex behavior, aggression, "predatory behavior," feeding behavior and habitat exploration. Each of these will be discussed in turn.

Sexual Behavior

The first category to be discussed is sexual behavior which has been more thoroughly investigated than any other behavior. In male cats sectioning the dorsal penile nerve (Cooper and Aronson 1962) and removing lumbosacral spinal cord segments (Root and Bard 1937) eliminate sensory input from the penis. They do not interfere with normal penile erection. Lesioned animals were capable of ejaculation and showed normal sexual excitement, however, their ability to guide their penises into place for intromission was reduced. Similar results were obtained with rats when they were given local anesthetics in the penis (Carlsson and Larsson 1964, Sachs and Barfield 1970). In rats an important difference is that anesthetization interferes with normal penile erection (Carlsson and Larsson

1964). Sachs and Barfield (1970) found that while tetracaine prevented intromission it markedly increased mounting behavior. Input from the penis is necessary for modulating or orienting the motor patterns concerned with normal intromission. Lesioned animals compensate for the deficit by increasing motor output.

Tactile stimulation of the lower back, rump, flanks and perineum initiates the reflex-chain leading to lordosis in female rates (Gerall and McCrady 1970, Diakow et al. 1973, Pfaff et al. 1974). Deaf, blind, anosmic females show strong lordosis reflexes in response to either a male's mounting or manual stimulation. Extensive cutaneous denervation or local anesthetization of the areas listed above reduces lordosis reflexes under most hormonal regimes (Kow and Pfaff 1976). The length of time a female remains in lordosis is also dependent upon tactile input. Desensitization of the cervix via pelvic nerve section shortens a female's time in lordosis, indicating that stimulation to the cervix maintains the reflex (Diakow 1970). Normally, the further through a mating sequence a female rat is allowed to proceed, the longer the interval before it will seek out additional sexual contact (Bermant and Westbrook 1966). Swabbing the genital region with lidocaine significantly reduces this interval and indicates that adequate stimulation temporarily inhibits further sexual behavior.

The above results indicate that somatic sensory input (and cervical stimulation) initiates the normal mating sequence (from point of contact on). A female's failure to produce a normal lordosis reflex results in a decrease in its mate's intromission performance (Kow and Pfaff 1976) and therefore seriously compromises the entire

mating sequence. Continued sensory input also plays a role in modulating the timing of the motor patterns concerned with lordosis as well as in motivational components of sex behavior.

In light of the importance of somatic sensory input in the control of the mating sequence, it is particularly interesting to note results of studies on the effects of estrogen treatment of ovariectemized females. Estrogen replacement has been found to increase the size of the receptive field of the pudendal nerve (the entire nerve) to include regions on the hind legs which are stimulated (actually palpated) by males during mounting sequences (Komisaruk et al. 1972, Kow and Pfaff 1973a, b). Receptive field size in untreated ovariectemized females are significantly smaller and generally do not include these hind-leg sites. These results might be taken as an indication that through hormonal influence females are maximizing their chances of receiving adequate stimulation to enable them to proceed through the mating sequence successfully.

Aggression

Tactile input plays an important role in the control of inter-male aggression in rats and mice (Flory et al. 1965, Bugbee and Eichelman 1972, Thor and Ghiseli 1973a, b, 1974, Katz 1976). While studying the effects of visual impairment on inter-male aggression in rats, Flory et al. (1965) noted that removal of vibrissae decreased levels of aggression beyond that of blinding alone. This finding is important because the deficit produced by cutting vibrissae off should be strictly tactile and moreover is reversible, as the vibrissae grow back out. In fact, Bugbee and Eichelman (1972) showed that

removing vibrissae in male rats significantly reduced the number of attacks in a shock-induced aggression test, but as the vibrissae grew back out aggression increased again. Essentially one can titrate levels of aggression by adjusting vibrissae length. Bilateral local anesthetization of the vibrissal regions produces deficits similar to those of vibrissae removal (Thor and Ghiselli 1973a, b).

Reduction in aggression has also been demonstrated in tests where male rats receiving local anesthetization of the vibrissal pad and male mice receiving local anesthetization plus vibrissae removal were allowed to interact with male conspecifics without artificial induction of aggression (shock or drug) (Thor and Ghiselli 1973a, Katz 1976). In mice these procedures reduced the number of aggressive encounters and increased the latency to aggression. They did not alter more general social contact (Katz 1976). In summary, the effect of altering tactile input via the vibrissae is to inhibit specific motor patterns associated with aggression. Thor and Giselli (1973a) suggest that a rat uses vibrissal input to orient towards its opponent. In this case tactile input would play a modulating role. However, evidence on attack behavior presented in the next part of this discussion as well as Katz's (1976) study indicate that vibrissal input may also serve to trigger aggressive behavior.

The role of somatic sensory input in controlling "aggression" has also been examined in experiments on hypothalamically induced predatory attack behavior in cats (MacDonnell and Flynn 1966, Flynn 1967, Flynn et al. 1971, Bandler and Flynn 1972). While these studies suffer from use of extremely biased subpopulations of animals and bear a very tenuous relationship to adaptive (naturally occurring) behavior,

they contain some information of potential use in understanding the tactile (somatic sensory) control of behavior. Sectioning sensory branches of the trigeminal nerve reduces biting attacks against rats in hypothalamically stimulated cats. There are also data to suggest that peripheral somatic sensory receptive field properties may be altered by changing the status of the CNS. Stimulation of sites on the forepaws that do not normally elicit a striking reflex, produces this reflex when hypothalamic sites are stimulated (Bandler and Flynn 1972). The role of somatic sensory input in attack behavior is considered one of triggering a reflexive motor pattern (jaw movements) rather than orienting the animal towards its prey (modulating motor patterns) (MacDonnell and Flynn 1966).

Habitat Exploration

Somatic sensory input has been implicated in the control of non-social behaviors, as well. Vincent, who studied tactile hairs (vibrissae) in rats (Vincent 1913) examined the effect of vibrissae removal on open maze running and tactile discrimination of surfaces (Vincent 1912). These behaviors should be relevant to general habitat exploration in this species. Animals without vibrissae took slightly longer to learn mazes, had a higher number of errors in their performance, moved through the maze more slowly and slipped and fell from it more frequently than animals with their vibrissae intact. Animals with their vibrissae were also able to learn tactile discriminations more rapidly and spent less time in a given trial than animals without vibrissae. In an analysis of sniffing behavior in rats, Welker (1964) found that deprivation of normal snout somatic

afferent input decreased an animal's efficiency in finding food pellets but did not reduce vibrissae movements. In these instances tactile input apparently acts in orienting and modulating motor output rather than initiating it. In both cases preventing normal input increases the time taken to perform a given task, indicating a general decrease in efficiency.

Feeding Behavior

Zeigler and co-workers have been examining the role that tactile (and proprioceptive) input plays in controlling feeding behavior in pigeons. They have looked at the organization and response properties of trigeminal structures (Zeigler and Witkovsky 1968, Silver and Witkovsky 1973, Witkovsky et al. 1973, Zeigler et al. 1975) and have analyzed the effects of trigeminal lesions on both motivational and sensorimotor components of feeding behavior (Zeigler 1973, 1974, 1975a, b, Zeigler and Karten 1974, 1975, Zeigler et al. 1975: see Zeigler 1974 and 1976 for reviews). Their findings concerning sensorimotor components of feeding behavior are of particular interest.

Normal feeding behavior in pigeons consists of three sets of motor patterns: pecking, mandibulating and swallowing (described in Zeigler 1974). Pecking is the downward movement of the head and terminates when the beak is opened and a food item is contacted. Mandibulating involves moving the food item from the front of the beak to the rear of the buccal cavity where it is then swallowed. Response properties and receptive field orientations of neurons in the nucleus basalis (a second order forebrain structure in the

trigeminal afferent pathway) indicate that tactile and proprioceptive input should be important in the mandibulating process (Witkovsky et al. 1973).

Peripheral trigeminal deafferentation does not affect general pecking responses in operant tasks (Zeigler 1975a), however, cinematographic analysis indicates that pecking accuracy with grain feed is somewhat impaired (Zeigler et al. 1975). Grasping of the food item and subsequent mandibulating are seriously impaired, resulting in an increase in the number of pecks needed to successfully consume a single grain of food (Zeigler 1974, 1975b). Swallowing appears to be unaffected if the food item can be moved into position at the back of the buccal cavity (Zeigler et al. 1975). These changes occur after an initial post-lesion period characterized by depression of both motivational and sensorimotor components of feeding behavior (Zeigler 1975b). In conclusion, lesioning trigeminal structures leads to a short term decrease in motor output followed by a longer period during which there is an actual increase in motor output. This increase is due to a decrease in the efficiency of individual movements (e.g., the number of pecks needed to successfully eat one grain increases). The role of tactile (and proprioceptive) input in feeding behavior in pigeons is one of orienting and guiding motor output rather than triggering it.

Behaviors Not Controlled by Somatic Sensory Input

Somatic sensory input apparently has little or no effect on some behaviors. Beach and Jaynes (1956) examined the effects of enucleation, trigeminal deafferentation and anosmication on maternal

retrieval of young in rats. Trigeminal deafferentation and its combination with enucleation both had only minor effects in comparison to anosmication. Fentress (1973) has shown that removal of the entire forearm of mice does not alter the execution of motor patterns used by mice in grooming their head and face. In normal animals, as the forelimb moves over the eye region, the eye is closed for protection. In forelimb amputees as the stump is moved in a fashion that would have brought a paw into position over the eye, the eye is still closed despite the absence of any physical contact with that area. Fentress uses these observations as an example of the central control of behavior (Fentress 1976).

Conclusions

In conclusion, somatic sensory (tactile) input plays an important role in the control of a variety of different behaviors, but its role is varied. In the cases of lordosis in female rats, "predatory attack" in cats, and possibly inter-male aggression in rats and mice, this input serves to initiate or trigger behavioral sequences. Ethologists would consider this a "releaser" role (Lorenz 1950, Tinbergen 1951). In these cases, failure to receive proper sensory input results in an overall decrease in motor output such as a decrease in attacking behavior, a shortening of the time spent in lordosis, or a decrease in the lordosis quotient. On the other hand, in mounting and intromission by male rats and cats and feeding behavior in pigeons somatic sensory input serves to orient or modulate ongoing behavior. Failure to receive normal input appears to increase motor output in these situations: pecks/food grain increase and intromission attempts

become more vigorous. This increase can be taken as an indication of a reduced efficiency of individual movements. In the case of rats in open mazes and in tactile discrimination tests (Vincent 1912) it is not clear what is happening with respect to actual motor output.

Summary

In summary, this literature review has concentrated on three basic areas and their inter-relationship. The first section established a relationship between an animal's behavior and the organization of its somatic sensory system, and set up the hypothesis that receptor distribution should be predictable based on a species' behavior. The second section provided detailed descriptions of those receptors and considered the importance of receptor arrays to behavior. The third section examined the varied role that somatic sensory (tactile) input plays in controlling behavior.

CHAPTER I

NEUROANATOMICAL EXPERIMENTS

Purpose

The primary purpose of this study was to test the prediction that the relative density of receptors in the glabrous forepaw skin of tree squirrels would be greater than that of ground squirrels. Additionally, this study used quantitative techniques to examine spatial relationships within receptor arrays.

Methods and Materials

Subjects

Subjects were 13 tree squirrels and 12 ground squirrels captured in the vicinity of East Lansing, Michigan. Seven individuals per species were included in the quantitative analyses described below.

Histological Procedures

Squirrels were anesthetized with sodium pentobarbital and perfused intracardially with 0.9% saline solution followed by 10% formalin or 10% neutral buffered formalin, in 0.9% saline. Neutral buffered formalin left skin less brittle than unbuffered formalin and was used on all animals included in quantitative analyses. Forepaws and hindpaws were removed and immersed in fixative for at least 24 hours. In this study only glabrous skin from the ventral surfaces

of the paws was examined.

Blocks of tissue were taken from four locations: 1) forepaw digit 3 or 4 (digit 1 is greatly reduced in size and tree squirrels often damaged digits 2 and 5 while attempting to escape from live traps), 2) forepaw palmar tubercle 3, 3) hindpaw digit 3 or 4, and 4) hindpaw plantar tubercle 3. The side of the animal (left vs. right) and, where appropriate, the digit number for each block were completely randomized. Blocks of tissue were dehydrated through alcohols to xylene and embedded in paraffin (Paraplast). Serial sections were cut perpendicular to the skin surface at a thickness of 15 um and sections totalling 1 mm (67 sections) were affixed to slides with a gelatin-albumin solution (Harleco). Sections were then stained with a modified Bielschowsky silver stain (Sevier and Munger 1965) using 2 drops of 37-40% formalin instead of 10 drops of 4% formalin as originally indicated (Munger, personal communication).

Skin Shrinkage

Because of the quantitative and comparative nature of this study, shrinkage in tree squirrel and ground squirrel skin due to paraffin processing was compared. One randomly chosen tissue block was taken from each of 7 squirrels per species. The length of each block was measured with an ocular micrometer in a dissecting microscope and then with vernier calipers. Tissue blocks were dehydrated, cleared and infiltrated with paraffin according to a schedule used in the quantitative portions of this study. Each block was remeasured and percent shrinkage for ocular micrometer and vernier caliper measurements were calculated individually and then averaged together.

Percent shrinkage for the two species were then compared using a Mann-Whitney U test.

Skin shrinkage in tree squirrels (8 ± 1% for ocular micrometer and 6 ± 1% for vernier calipers; mean shrinkage = 7 ± 1%) and ground squirrels (8 ± 1% for ocular micrometer and 7 ± 1% for vernier calipers; mean shrinkage = 8 ± 1%) did not differ (Mann-Whitney U = 26.0, p = NS). To avoid inaccurate portrayal of variance in shrinkage by uniformly applying correction factors based on mean shrinkage estimates (based on an overlapping but different group of squirrels than used in the body of the experiment) and because shrinkage did not differ between species, the original uncorrected density estimates were used for all analyses.

Receptor Density

An estimate of the density of the following types of sensory endings (receptors) was made for each of the four pieces of skin taken from a squirrel: 1) corpuscular endings including Meissner, simple and Pacinian corpuscles and 2) non-corpuscular endings including dermal free nerve endings and intraepidermal endings (largely associated with Merkel cell-neurite complexes). Descriptions of these receptors are presented in the results section below.

Sections were viewed under the light microscope at 125X magnification and 0.7mm skin surface lengths were measured off using an ocular micrometer grid measuring 0.7mm x 0.7mm. The grid was then placed over one 0.7mm length that was randomly chosen using a "coin toss" procedure. All receptors falling at least partially within the grid and meeting the criteria described below were counted. For

corpuscular endings to be counted, the neurite within the corpuscle had to be visible and the section being examined had to contain at least as much of that neurite as the surrounding sections. Dermal free endings were included if the endings per se were visible or if the terminal neurite could be seen within the upper 1/2 of a dermal papilla. Intraepidermal fibers had to be seen approaching and crossing the dermal-epidermal (D-E) junction or coursing through the epidermis and had to have at least part of their length in the same focal plane as epidermal cells under 300X magnification to be counted. The latter criterion helped to exclude neurites running along the D-E junction without actually crossing into the epidermis in that section. These criteria should lead to relatively conservative estimates of receptor density and were applied uniformly to squirrels of both species.

The area of the actual skin surface under the grid was also determined (see Figure 4). The curvature of the skin surface required that it, along with the borders of the grid be traced onto a data sheet with the aid of a drawing tube. A map measuring wheel was then used to measure the length of skin surface under the grid and the grid length from the drawing. The area of the skin surface under the grid was calculated according to the following equation:

$$\frac{\text{Skin Surface length}_{\text{drawing}}}{\text{Grid length}_{\text{drawing}}} \times \text{Grid length}_{\text{known}}(0.7\text{mm}) \times$$

Skin surface width (15 um) = skin surface area.

The above procedures and calculations were repeated for six randomly chosen sections (section numbers were drawn from a random

Figure 4. The procedure for determining skin surface area. The skin surface length is determined by measuring the grid length from the drawing made on a data sheet. By multiplying the ratio of the skin surface length/grid length by the known length of the actual grid (0.7mm) the actual skin surface length is calculated. The section thickness (15um) is used as the skin surface width. Skin surface length X skin surface witdth = skin surface area.

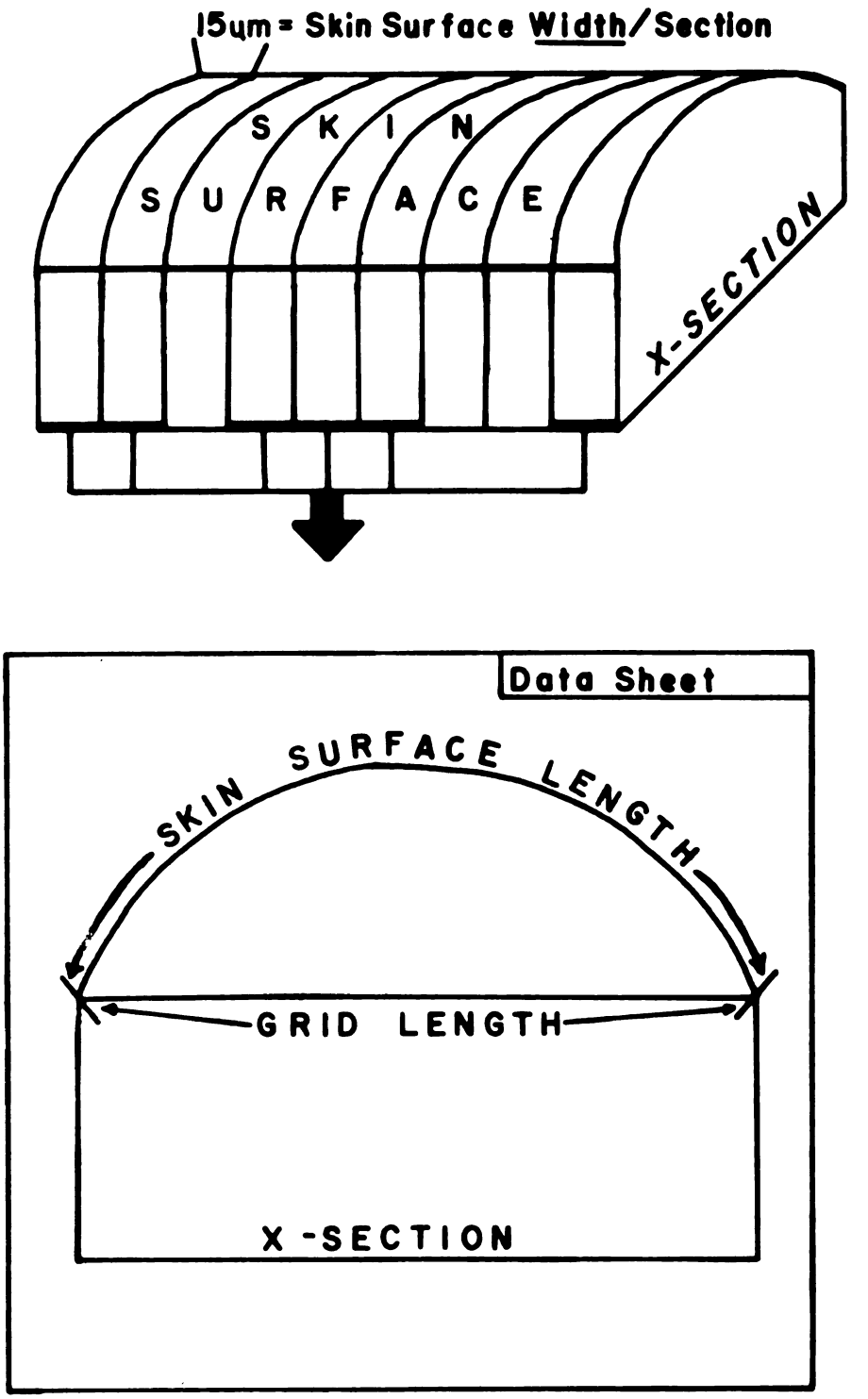

15μm = Skin Surface Width/Section
SKIN SURFACE
X-SECTION
Data Sheet
SKIN SURFACE LENGTH
GRID LENGTH
X-SECTION

Figure 4.

numbers table) from each tissue block. The number of sections to be used was determined by plotting the standard error of the mean receptor density for a given piece of skin (averaged across all members of a species) as a function of the number of sections from which that density estimate was derived (S.E. decreases as the number of sections used increases). The number of sections at which the slope of this curve approaches or fluctuates around 0 (4-6 sections for pieces of skin in this experiment) was then used for all tissue blocks. The number of receptors was summed over the six sections and then divided by the total skin surface area of the six sections to yield a single receptor density (receptors/mm^2) for each tissue block. This approach for estimating density was chosen over calculating a mean density estimate for the six sections because it preserves information about the actual amount of skin sampled until the final calculation of density.

The total density of receptors was analyzed by analysis of variance (ANOVA) with the following design: a three factor mixed design with repeated measures on two factors (location and paw)

Factor 1: species (Spermophilus vs. Sciurus)

Factor 2: paw (fore vs. hind)

Factor 3: location (digit vs. tubercle)

The prediction that tree squirrels would have a greater density of receptors in its forepaws than ground squirrels was tested with a planned comparison as well. Duncan multiple range tests were used for appropriate post-hoc comparisons. The ratio of forepaw receptor density to hindpaw receptor density was compared among species with a Mann-Whitney U test. The directional prediction is that tree

squirrels will have a greater forepaw receptor density/hindpaw receptor density ratio than ground squirrels.

The remaining analyses were restricted to the forepaw tubercles of the two species of squirrels where receptor density is sufficient. First the proportions of the two classes of receptors were determined by calculating corpuscular receptor density/non-corpuscular receptor density ratios. Ratios for the two species were compared using a Mann-Whitney U test.

Receptor Dispersion

The pattern of dispersion of receptors over the skin surface (randomly distributed, clumped or uniformly distributed) was examined by calculating Coefficients of Dispersion (CD's) for each animal. The sections used to estimate receptor densities also were used for this analysis. On the data sheet for each section, skin lengths of 0.70mm and 0.35mm, yielding skin surface areas of $11 \times 10^{-3}mm^2$ and $6 \times 10^{-3}mm^2$, were randomly chosen. The number of receptors in these large and small "quadrats" were counted. In all, 6 large and 6 small quadrats per animal were sampled. The mean number of receptors within a quadrat and the variance between quadrats were calculated for each quadrat size, for each animal. A CD was then calculated for each quadrat size, for each animal according to the following equation: CD = Variance/Mean (Pielou 1969, Sokol and Rohlf 1969). The relationship between CD and patterns of dispersion is discussed in the results section. Two quadrat sizes were examined, rather than one, because it is reported that the dispersion pattern observed is at least partially a function of the quadrat size used (Pielou 1969,

Smith-Gill 1975). The CD's for the two species of squirrels were then compared using Mann-Whitney U tests.

To study the pattern of dispersion (see Figure 6 for examples) of different types of receptors (corpuscular and non-corpuscular) in relationship to each other (rather than in relationship to the skin surface, as in CD), a Coefficient of Segregation (S) (Pielou 1969) was calculated for each animal (see Appendix B for additional information). The sections used for this analysis overlapped partially with sections used in previous analyses but additional sections were also used. Sections were scanned under 125X magnification until a "base receptor" was located. To be included the base receptor had to be surrounded by two other receptors or it had to have a receptor on one side and a length of skin at least as great as the distance between the base and second receptor on its other side. A receptor meeting these criteria had its type (corpuscular or non-corpuscular) and the type of the "Nearest Neighbor" (the receptor closest to it) recorded. The scanning then continued until a new receptor was located. It was designated a base receptor and its type, along with the type of its nearest neighbor, was recorded. In this case, the nearest neighbor could be a receptor examined earlier in the same section. This procedure was repeated until 10 base receptors of each type and their nearest neighbors were recorded.

The data were then arranged in a 2 X 2 table with the following format:

		Nearest Neighbor		
		Corpuscular	Non-corpuscular	
Base Receptor:	Corpuscular	a	c	m
	Non-corpuscular	b	d	n
		r	s	N

(a, b, c and d = cell frequencies; m and n = row totals; r and s = column totals; N = table total). S was then calculated for each animal according to the following equation:

$$S = 1 - \frac{\text{observed number of mixed pairs of receptors}}{\text{expected number of mixed pairs or receptors}} =$$

$$1 - \frac{N(b + c)}{ms + nr}$$ (Pielou 1969).

These procedures were adopted from Pielou (1969). The relationship between S and the relative distribution of different receptor types is discussed in the results section. The S calculated in this study is an estimate of the true population S and is, therefore, subject to sampling error. S's for tree squirrels and ground squirrels were compared using a Mann-Whitney U test.

Results

Receptor Density

On the basis of differences in the behavior and natural history of the squirrels, it was predicted that the forepaw receptor density/ hindpaw receptor density ratio would be higher for tree squirrels than for ground squirrels. The mean forepaw receptor density/ hindpaw receptor density ratio for tree squirrels is 3.3 ± 0.5 and only 1.3 ± 0.3 for ground squirels. As predicted, the ratio for the first species is significantly greater than that of the second species

(Mann-Whitney U = 45.5, $p < 0.005$).

Mean receptor densities (and their standard errors) are presented in Figure 5 and results of the 3-way analysis of variance and post-hoc comparisons are summarized in Table 1. Because Figure 5 shows actual densities and the ANOVA is based on transformed data, direct comparison of the two may be misleading. The analysis of variance shows that paw and position are significant main effects, and that species X paw and paw X position two way interactions are significant. There is no significant species effect, nor are the species X position or the three way interactions significant. Post-hoc comparisons indicate that the tree squirrel's forepaw tubercle has a significantly higher receptor density than its hindpaw tubercle. No other comparisons between paws are statistically significant. In all cases, the tubercle of a paw has a higher receptor density than its corresponding digit, but for both species, this difference is significant for the forepaw only. Significant interactions between species and paw variables and between paw and position variables appear to be based largely on comparison of the tree squirrel forepaw tubercle, with its exceptionally high density of receptors (95.4 ± 16.8 receptors/mm^2), and other locations. In a planned comparison of average forepaw receptor densities (digit + tubercle/2) the two species did not differ ($t = 0.8$, $df = 12$, $p = NS$).

The proportions of the two classes of receptors in the forepaw tubercles of the two species, expressed as corpuscular receptor density/non-corpuscular receptor density ratios, were compared. For tree squirrels this ratio is 0.5 ± 0.1 and for ground squirrels it is 0.9 ± 0.2. Whereas tree squirrels have proportionately more

Figure 5. Receptor densities in squirrel glabrous paw skin. Means (bars) plus one standard error (flags) are presented.

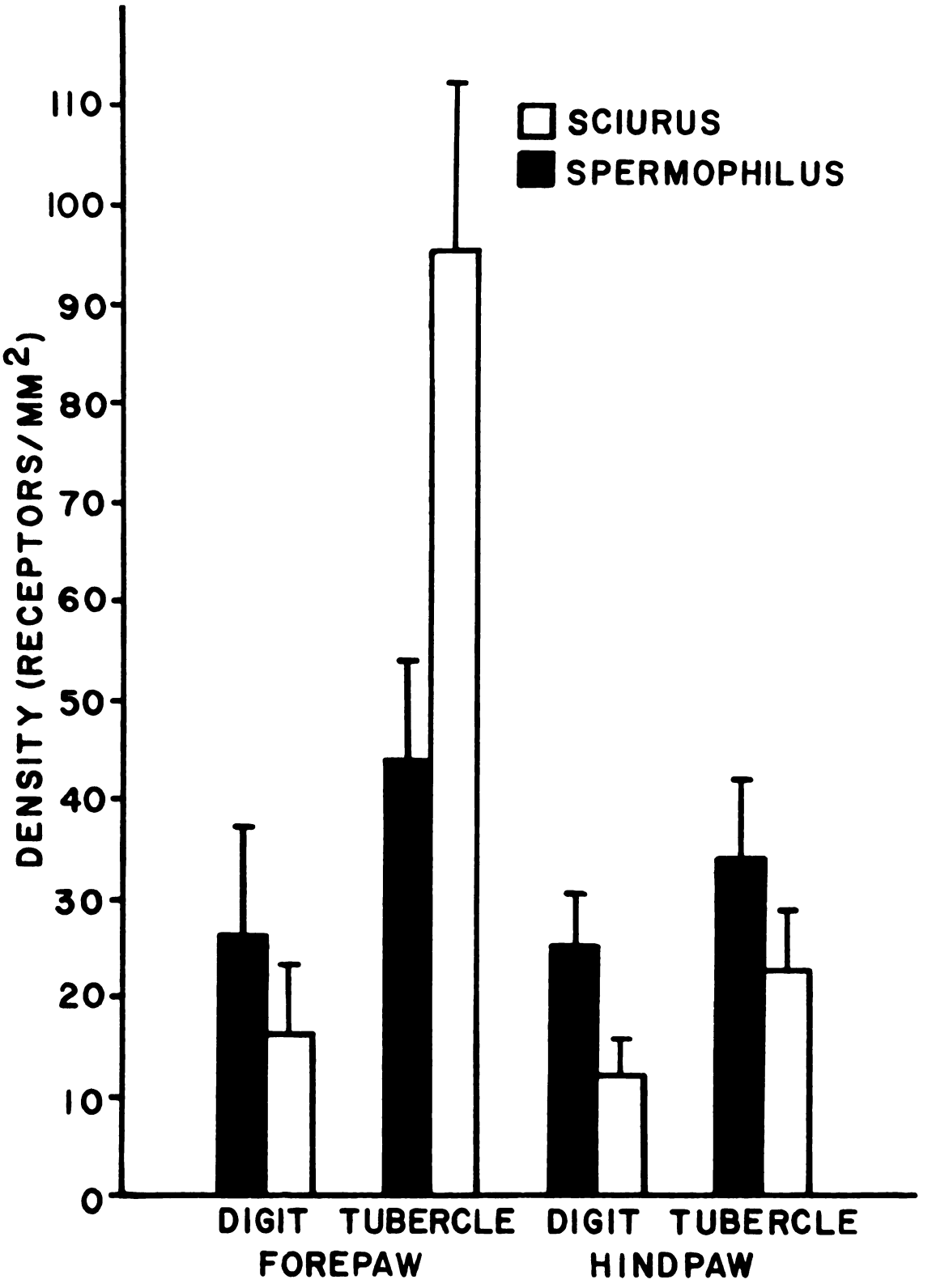

SCIURUS
SPERMOPHILUS
DENSITY (RECEPTORS/MM2)
0
10
20
30
40
50
60
70
80
90
100
110
DIGIT
TUBERCLE
DIGIT
TUBERCLE
FOREPAW
HINDPAW

Figure 5.

Table 1. Analysis of receptor densities

Anova Table

	SS	df	MS	F	P
Total	430.7	55	--	--	--
Between subjects	78.5	13	--	--	--
Species	1.4	1	1.4	0.2	NS
$Error_{between}$	77.2	12	6.4	--	--
Within subjects	352.2	42	--	--	--
Paw	28.7	1	28.7	9.6	**
Position	100.7	1	100.7	20.1	***
Speices x Paw	18.2	1	18.2	6.1	*
Species x Position	17.5	1	17.5	3.5	NS
Paw x Position	42.0	1	42.0	6.0	*
Sp. x Paw x Pos.	8.3	1	8.3	1.2	NS
$Error_1$	36.4	12	3.0	--	--
$Error_2$	60.4	12	5.0	--	--
$Error_3$	83.9	12	7.0	--	--

Post-hoc Comparisons

Spermophilus/forepaw/digit	vs.	Spermophilus/hindpaw/digit	: NS
Spermophilus/forepaw/tubercle	vs.	Spermophilus/hindpaw/tubercle	: NS
Sciurus/forepaw/digit	vs.	Sciurus/hindpaw/digit	: NS
Sciurus/forepaw/tubercle	vs.	Sciurus/hindpaw/tubercle	: *
Spermophilus/forepaw/digit	vs.	Spermophilus/forepaw/tubercle	: *
Spermophilus/hindpaw/digit	vs.	Spermophilus/hindpaw/tubercle	: NS
Sciurus/forepaw/digit	vs.	Sciurus/forepaw/tubercle	: *
Sciurus/hindpaw/digit	vs.	Sciurus/hindpaw/tubercle	: NS

*$p < 0.05$ **$p < 0.01$ ***$p < 0.001$

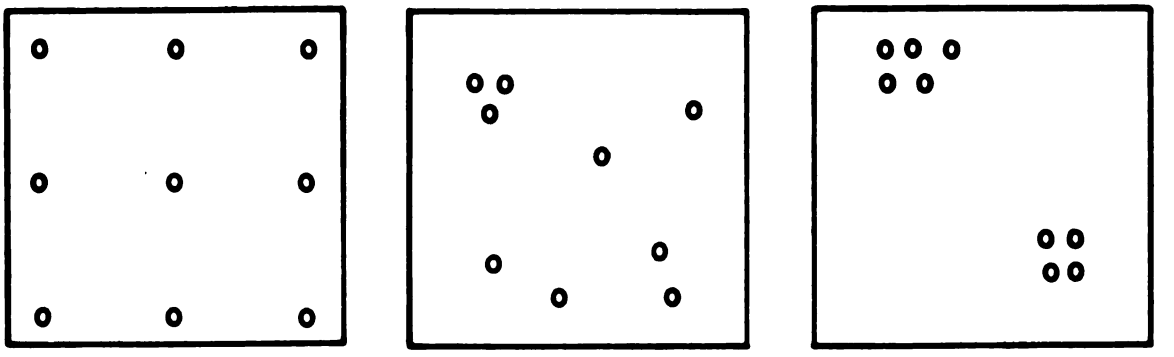
non-corpuscular receptors than ground squirrels, this difference is not statistically significant (Mann-Whitney U = 25.5, p = NS).

Receptor Dispersion

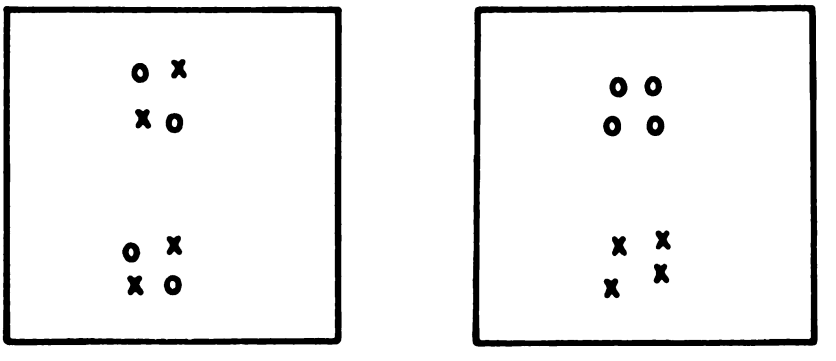
In a Poisson (random) distribution the mean number of receptors/plot equals the variance between plots and, by definition, CD = 1. When CD > 1 (variance > mean) receptors are clumped and when CD < 1 receptors are overdispersed or uniformly distributed (Pielou 1969, Sokol and Rohlf 1969). These three possible dispersion patterns are illustrated in Figure 6. The mean CD's for tree squirrels are 0.8 ± 0.2 for small plots and 1.1 ± 0.3 for large plots. For ground squirrels the mean CD's are 0.7 ± 0.1 and 0.9 ± 0.2, respectively. The CD's for the two speices did not differ regardless of the plot size considered (for small plots U = 27.0, p = NS; for large plots U = 27.5, p = NS). Receptors are randomly distributed across the skin surface in the glabrous palm of both species, for both of the plot sizes examined. These results indicate that of the potential sites for a receptor (e.g. a dermal papilla for a Meissner corpuscle), those sites actually occupied are randomly distributed. Alternatively, if every potential site is occupied, the sites themselves would have to be randomly distributed. In both species the first situation exists. These results do not imply that a receptor will be found outside its normal site (e.g. a Meissner corpuscle in a rete ridge).

It is also possible to study the distribution of one receptor type relative to another receptor type, rather than in relationship to the skin surface, as in the analysis above. When corpuscular and non-corpuscular receptors are randomly intermingled, each receptor

Figure 6. Receptor dispersion. a) Potential dispersion patterns and their relationships to the Coefficient of Dispersion (CD). b) Examples of segregated and unsegregated patterns and their relationships to the Coefficient of Segregation (S).



a. COEFFICIENT OF DISPERSION (CD)



b. COEFFICIENT OF SEGREGATION (S)

Figure 6.

type will have corpuscular and non-corpuscular receptors as nearest neighbors in the same proportions as they exist in the population of receptors in the skin (S = 0; Pielou 1969). Conversely, receptors can be segregated, forming "relative clumps" (Pielou 1969) where one receptor predominates. In this case the proportions of corpuscular and non-corpuscular receptors serving as nearest neighbors will differ from their proportions in the population of receptors in the skin. For instance, in a relative clump of corpuscular receptors, corpuscular receptors will be nearest neighbors a greater proportion of the time than their actual proportion in the population of receptors in the skin. When receptor types are fully segregated S = 1 (Pielou 1969). These two possible distributions are illustrated in Figure 6. S's for tree squirrels ($\bar{x}$ = 0.29 ± 0.1) and ground squirrels ($\bar{x}$ = 0.33 ± 0.1) do not differ (Mann-Whitney U = 24.5, p = NS). In both species corpuscular and non-corpuscular receptors appear to be largely intermingled. Because the sampling distribution of S in a randomly intermingled population has not been derived it is not possible to test the above values against a standard.

Receptor Morphology

To facilitate the quantitive analyses presented in this study, receptors were divided into two classes based on light microscopic characteristics. The first class consists of non-corpuscular endings and includes intraepidermal endings and dermal free endings. The second class consists of corpuscular endings and includes Meissner, simple and Pacinian corpuscles. Figure 7 shows a cross section from a ground squirrel's forepaw tubercle and illustrates the general

Figure 7. A cross section of squirrel glabrous skin. This section from a ground squirrel forepaw tubercle illustrates the general organization of squirrel glaborous skin. Simple corpuscle (C), dermis (D), epidermis (E), sweat gland (G), nerve fibers (N), dermal papilla (P), rete peg (R), sweat duct (S).

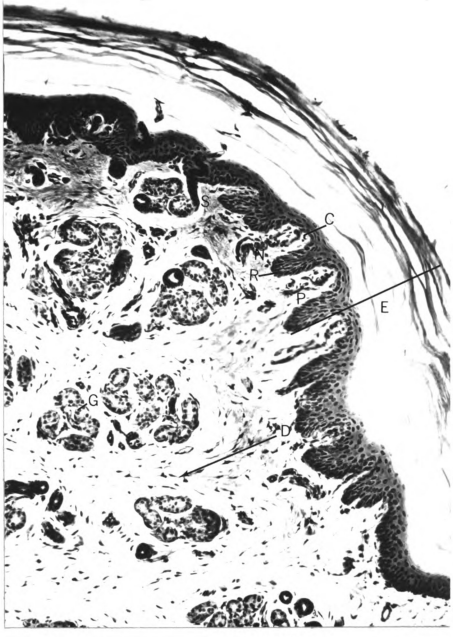


Figure 7.

organization of squirrel glabrous skin. Table 2 is a summary of the types of receptors found in the glabrous skin of the forepaws and hindpaws of tree squirrels and ground squirrels. Each type of receptor will be described below.

Intraepidermal Endings. Intraepidermal endings occur most frequently at the base of rete pegs (Figure 8) but are also found entering the epidermis above dermal papillae and in regions where the D-E junction is relatively featureless, such as in digits. They are common in all sites examined. In both species of squirrels large (4-8um) myelinated fibers originating in the corial plexus course up through the dermis and approach the dermal epidermal (D-E) junction. They lose their myelin sheaths shortly before crossing into the epidermis. Fibers often branch at least once before entering the epidermis. The branching appears to be more extensive in tree squirrels than in ground squirrels, although a rigorous analysis was not performed.

After entering the epidermis, fibers terminate in a short distance, frequently forming disc-like expansions. The latter are often difficult to see. In some cases Merkel cells, identified by their vacuolated cytoplasm and large elongated nucleus, are found adjacent to these intraepidermal endings (Figure 9). In material fixed with neutral buffered formalin, vacuolated cytoplasm is not a consistent feature of these cells and they are often hard to find. Most of these endings should be parts of Merkel cell-neurite complexes (Munger 1965, Halata 1975, Breatnach 1977). Physiologically, Merkel cell-neurite complexes are known to be Type I slowly adapting mechanoreceptors (Iggo and Muir 1969, Munger et al. 1971).

Table 2. Receptors Found in Squirrel Glabrous Paw Skin

	Intraepidermal endings	Dermal free endings	Pacinian corpuscles	Simple corpuscles	Meissner corpuscles
Tree Squirrel					
Forepaw Digit	X			X	
Tubercle	X	X	X	X	
Hindpaw Digit	X			X	
Tubercle	X	X		X	
Ground Squirrel					
Forepaw Digit	X	X		X	X
Tubercle	X	X		X	X
Hindpaw Digit	X	X		X	X
Tubercle	X	X		X	X

Figure 8a. Intraepidermal endings in tree squirrel tubercle skin. A large myelinated fiber sends out several primary branches which innervate an extensive area of epdiermis.

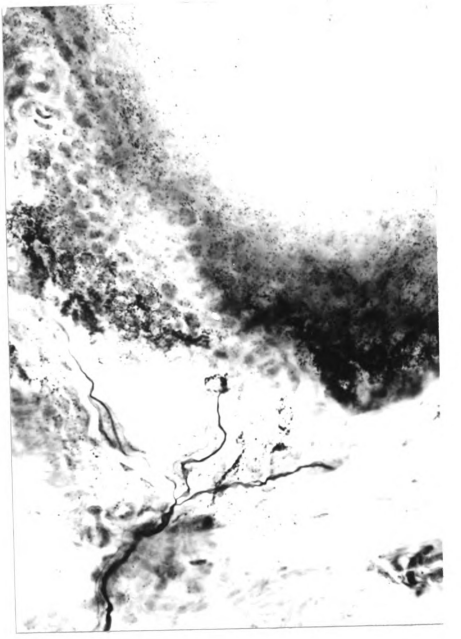


Figure 8a.

Figure 8b. Intraepidermal endings in ground squirrel tubercle skin. A large myelinated fiber courses up through the dermis, branches before reaching the dermal-epidermal junction, and sends small terminal branches (arrow) into the epidermis at the base of a rete peg.

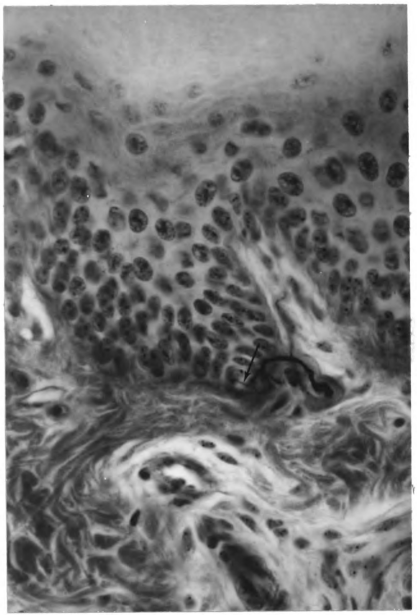


Figure 8b.

Figure 9a. A Merkel cell in tree squirrel digit skin. A Merkel cell (arrow) with vacuolated cytoplasm and an elongated nucleus is seen at the base of a rete peg.

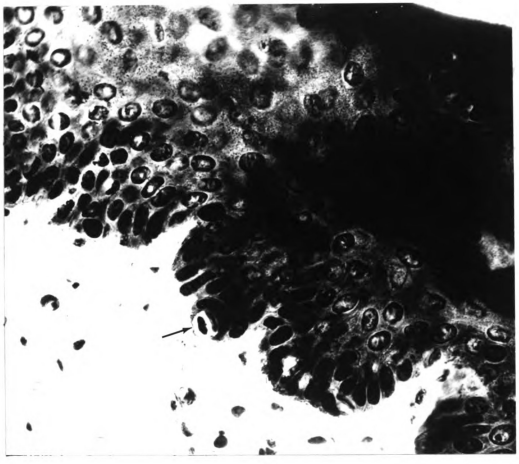


Figure 9a.

Figure 9b. A Merkel cell in ground squirrel tubercle skin. A Merkel cell (arrow) with vacuolated cytoplasm, and an elongated nucleus is seen within a rete peg. An intraepidermal fiber can be seen entering the same peg.

Figure 9b.

Dermal Free Endings. Dermal free endings are the least common receptor in both tree squirrels and ground squirrels. They were found in all sites examined in ground squirrels but were found only in the forepaw and hindpaw tubercles of tree squirrels. These results indicate that dermal free endings are rare in the digits of tree squirrels, and should not be taken as evidence that they do not occur there.

In both species, large (5-8um) myelinated fibers course up into the superficial dermis where they enter the bases of dermal papillae. The fibers extend up into the apical portion of the papillae and terminate close to the epidermis above it (Figure 10). They consistently branch within the papillae and the terminal portions of these fibers are either myelinated or unmyelinated. Sometimes, the fiber diameter increases before terminating, forming an expanded terminal. While the function of these endings is largely unknown, they are considered part of the somatic afferent system (Munger and Pubols 1972, Hensel et al. 1974) and possibly mechanoreceptors (Horch et al. 1977). Because of these points, especially the latter, dermal free endings were included in the quantitative analyses described above.

Meissner Corpuscles. Meissner corpuscles are bulb-like endings that occur in dermal papillae in glabrous skin. They were found only in ground squirrels. If they occur at all in tree squirrels they are exceedingly rare. In ground squirrels, large (4-8um) myelinated fibers originating deep in the dermis course up towards the skin surface and enter dermal papillae. Within a papilla 1-2 fibers enter an ellipsoid shaped corpuscular structure and follow a tortuous

Figure 10a. A dermal free ending in tree squirrel tubercle skin. A myelinated fiber courses up into a dermal papilla and terminates close to the epidermis above it. The fiber forms a branched terminal (arrow). A single Schwann cell nucleus (S) can be seen close to the terminal.

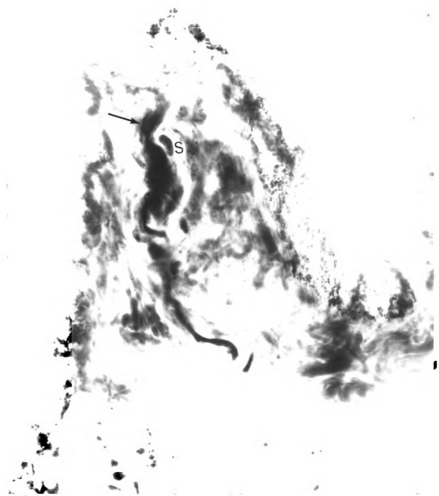


Figure 10a.

Figure 10b. A dermal free ending in ground squirrel tubercle skin. A myelinated fiber enters a dermal papilla and branches before terminating high in the papilla.

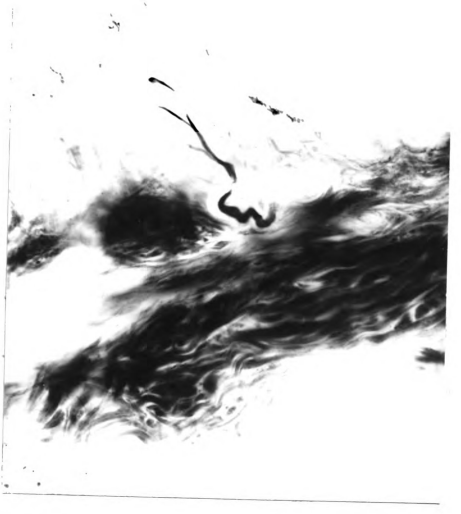


Figure 10b.

course winding around within it (Figure 11). For most of their length these fibers are oriented parallel to the skin surface. They form ramified terminals which have either expansions or free ramifications.

As a fiber enters a corpuscle, the myelin and Schwann sheaths give way to lamellar cell processes which surround the fibers as they proceed through the corpuscle. The lamellar cells are thought to be modified Schwann cells (Idé 1977). Meissner corpuscles are not surrounded by distinct capsular structures as are simple corpuscles. The perineural cup around the base of the corpuscle which has been reported in mice (Idé 1976) was not positively identified in ground squirrels. Connective tissue elements from within the corpuscle are frequently continuous with those from within the dermal papillae. Meissner corpuscles generally measure 25-40um by 50-75um with the long axis oriented perpendicular to the skin surface. While the physiological properties of Meissner corpuscles are not well known, considerable inferential evidence suggests that they are rapidly adapting mechanoreceptors (Munger 1971, B. Pubols, personal communication).

Simple Corpuscles. Simple corpuscles with inner cores (Halata 1975) are a second type of bulb-like ending common in all sites examined in both species of squirrels. Their morphology is more variable than that of Meissner corpuscles but there are no clearcut species differences. One or more (up to four) large (4-8um) myelinated fibers course up through the dermis into the papillary layer where they enter distinct encapsulated structures (Figure 12). Simple corpuscles most frequently occur in dermal papillae but can be found in the dermis

Figure 11. A Meissner corpuscle in a dermal papilla. In this section from a ground squirrel hindpaw tubercle, a single mylinated fiber (N) can be seen entering a corpuscular structure. The fiber forms branches which swirl around within the lamellar matrix of the corpuscle. These branches terminate in small digitate ramifications (arrow). Lamellar cell bodies (L) lie toward the periphery of the corpuscle.

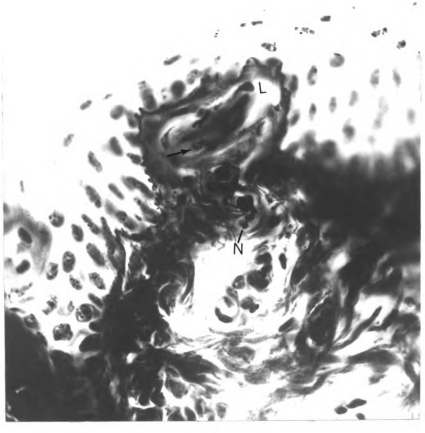


Figure 11.

Figure 12a. A simple corpuscle with inner core. In this section from a tree squirrel tubercle, a large myelinated fiber enters the base of a corpuscle, follows a relatively straight course towards its apex and bends over at the terminal segment. The fiber branches within the corpuscle and terminates in club-like expansions (E). The corpuscle consists of an inner core (arrow) and an outer capsular structure (C). On the left side of the capsule, a single capsular cell can be seen (*).

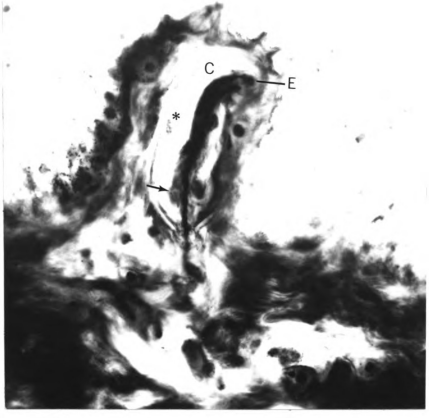


Figure 12a.

Figure 12b. A simple corpuscle in ground squirrel tubercle skin. The arrow points to the capsule.

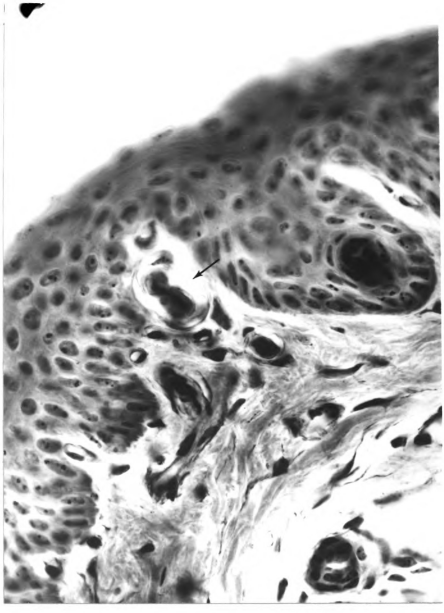


Figure 12b.

deep to papillae or immediately below rete pegs.

Within a corpuscle, the myelin and Schwann sheaths give way to an inner core which completely surrounds the fibers. The inner core is composed of tightly packed lamellar processes of cells that resemble Schwann cells. Capsule cells invest these corpuscles with distinct capsules that separate them from the surrounding connective tissue. The capsule is thought to be perineural in origin (Saxod 1973, Halata 1975). Between the inner core and the capsule there is a subcapsular (capsular) space.

The nerve fibers follow a relatively straight course within the inner core and course up towards the far end of the corpuscle. They frequently branch within the core, especially in tree squirrels. In corpuscles which have their longitudinal axis oriented perpendicular to the skin surface (particularly those within dermal papillae) the fibers generally bend over so that their terminal segments are parallel to the skin surface. As implied, the orientation of these corpuscles does vary. The fibers terminate in club-like expansions.

In both species of squirrels simple corpuscles are 20-40um by 50-90um. Occasionally two corpuscles innervated by the same parent fiber are found next to each other in a single dermal papilla. Malinovský (1966a) considers these to be branches of a single large corpuscle. Physiologically, simple corpuscles with inner cores have been shown to be rapidly adapting mechanoreceptors (Pubols et al, 1971, Munger and Pubols, 1972, Iggo and Ogawa 1977).

Pacinian Corpuscles. Pacinian corpuscles are found only in the forepaw tubercles of tree squirrels and are rare. They are found in the subcutaneous tissue deep to the level of the sweat glands (Figure 13). It is likely that these receptors are more common in the deeper lying periosteal tissue. The corpuscles found in tree squirrels had ellipsoidal fibers located inside inner cores. The inner core of a Pacinian corpuscle is composed of lamellae which are processes of cells whose cell bodies are located around the periphery of the core. These lamellae are arranged in a fashion that results in the presence of a bilaterally symmetrical cleft on either side of the nerve fiber. There is then a subcapsular space filled with many, less tightly packed lamellae and it appears that in some instances more than one lamellar cell contribute processes to form a single lamella. This entire structure is then enclosed within a capsule. Pacinian corpuscles in tree squirrels are approximately 160um in diameter at their largest point. Physiologically, they are very rapidly adapting mechanoreceptors that act as vibration detectors (Sato 1961, Loewenstein 1966, 1971, Ilyinsky 1976, Iggo and Ogawa 1977).

Discussion

Testing a Neuroethological Hypothesis

As stated at the outset, the main purpose of this study has been to test the hypothesis that the distribution of mechanoreceptors in the skin of an animal is related to its behavioral-ecological specializations. This hypothesis derives from evidence that in mammals the relative sizes of central somatic sensory projections reflect a species' behavioral specializations (Welker 1976, Johnson 1978) and

Figure 13. A Pacinian corpuscle in tree squirrel tubercle skin. In this section from a tree squirrel forepaw tubercle, a Pacinian corpuscle with an ellipsoid nerve fiber (arrow), inner core (I), sub-capsular space with loosely packed lamellae (L) and outer capsule (C) can be seen.

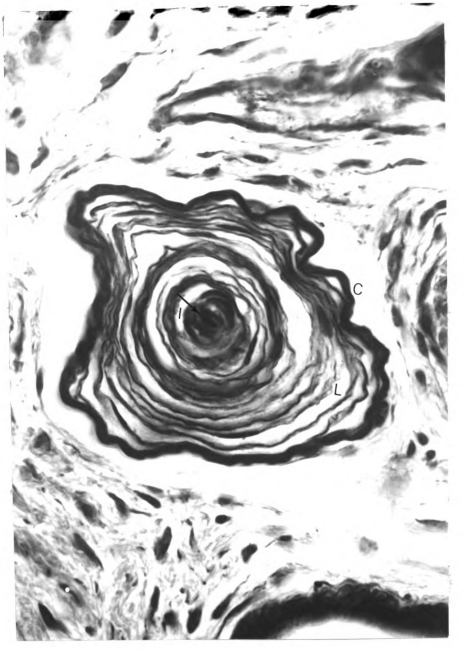


Figure 13.

the hypothesis that relative projection size is dependent upon relative receptor density peripherally (Mouncastle and Henneman 1952, Welker 1973, 1976, Johnson 1978). Based on behavioral and natural historical data it was predicted that tree squirrels would have a greater density of receptors in the glabrous skin of their forepaws than would ground squirrels. Because of the emphasis placed on relative receptor density (Mountcastle and Henneman 1952, Welker 1976), it was suggested that looking at forepaw receptor density/hindpaw receptor density ratios represents a more direct test of the hypothesis than looking at forepaw density alone.

As predicted, the forepaw receptor density/hindpaw receptor density ratio is significantly greater in tree squirrels than in ground squirrels. To the contrary, the average forepaw receptor densities (digit + tubercle/2) for the two species do not differ. These results support the hypothesis that there is a relationship between an animal's behavioral and ecological specializations and the distribution of receptors in its skin. They demonstrate that behavioral and natural historical data can be used to predict the relative densities of receptors in the glabrous skin of different parts of animals' bodies. These results clearly show that one can not predict the relative densities of receptors in a single part of the body, between species.

The results and theoretical considerations of cortical mapping studies provided the background for the hypothesis and predictions discussed above. The majority of central mapping studies indicate that receptive field size is "inversely related to distality" (Rubel 1971), digits having smaller receptive fields than palms

(Pubols et al. 1965, Pubols and Pubols 1972, Sur et al. 1978). According to the "map theoretic" this would indicate that receptor density increases going distally and one would predict that the digits of the forepaw would have a greater receptor density than the palm. In both species of squirrels the opposite was found; receptor density in the palm is significantly greater than in the digits. This same general trend is true for their hindpaws although it is not statistically significant there. It is possible that the squirrel's palm has a larger cortical representation than its digits. However, a recent cortical mapping study of the gray squirrel (Sur et al. 1978), another tree squirrel, suggests that this result is unlikely.

One could explain this apparent contradiction by hypothesizing that proportions in cortical maps are determined by relative numbers of primary afferent fibers, not receptors, and that receptor convergence onto single afferent units differs between palm and digits. Lee and Woolsey (1975) have reported that cortical representation of individual vibrissae is highly correlated with the number of fibers (it is likely that these are branches of fibers) innervating the follicles of those vibrissae, supporting the first point. I have planned experiments to examine the convergence of receptor input onto afferent fibers in the palms vs. the digits of squirrels.

As described in the introduction, tree squirrels use their forepaws in a broader range of behaviors than do ground squirrels. Results presented above suggest that with respect to their pattern of innervation, the tree squirrel's forepaw is composed of two highly differentiated regions. These same results suggest that the ground squirrel's forepaw is relatively less differentiated. In ground

squirrels, which use both digits and palms in excavating burrows (Hildebrand 1974), the mean receptor density in palm skin is only twice as high as in digital skin. These two regions of the forepaw also contain the same complements of receptors (see Table 2). The mean density of receptors in palm skin in tree squirrels is 6 times as high as in digital skin. Additionally, the complements of receptors in these two regions are different. Pacinian corpuscles were found only in the palmar tubercle (and only rarely there) and dermal free endings were restricted to the tubercles of both paws. In these two respects, the palm and digit regions of the tree squirrel's forepaw are strikingly different from each other. The differences between the palm and digits of the ground squirrel's forepaw are minor by comparison.

These results suggest that the tree squirrel's palm and digits may play different roles in the performance of specific behaviors or in different phases of a single behavior. Behavioral observations described later in this dissertation support this hypothesis. When a food item is relatively large it is held between the digits of both forepaws and is manipulated frequently. As it gets smaller, it is moved up to a position between the edges of the palms and is manipulated less frequently. One might speculate that this highly differentiated forepaw evolved as an alternative to a more generalized forepaw that would otherwise be necessary for the performance of a wide range of skilled motor patterns. By definition, such a paw would not be as well suited for any single behavior.

Receptor Arrays

Quilliam (Quilliam and Armstrong 1963a, Quilliam 1966) developed the concept of the receptor array to describe highly specialized and localized aggregations of different types of receptors. He reasoned that these different types of receptors act in combination and thereby respond to a broad range of environmental stimuli to produce cutaneous sensation. More recently, he broadened the concept to include the somewhat more diffuse aggregations of receptors found in the ridged digital skin of primates (Quilliam 1975). One can extend his logic and consider the receptors in any patch of skin to be an array, although defining units in the array and the patterns of the array are more difficult when receptors are not organized into striking, highly localized clusters.

The importance of the array concept lies in the fact that natural tactile stimuli such as food items, mates and burrow entrances excite entire arrays, not single receptors. Whereas a detailed understanding of the nature of individual receptors is extremely important (Munger 1971), understanding any neural system requires detailed information about the interaction of elements within it. One of the first steps to understanding complex interactions between individual elements in a system, such as receptors within arrays, is to define the spatial relationships between them (Freeman 1976).

In addition to testing the neuroethological hypothesis discussed above, this study has concentrated on defining and comparing the spatial distribution of receptors within arrays in the palmar tubercles of tree squirrels and ground squirrels. By calculating Coefficients of Dispersion it was possible to define the dispersion patterns within

these arrays. Coefficients of Dispersion did not differ between species and in both cases receptors appeared to be randomly distributed. By calculating Coefficients of Segregation it was possible to define the extent to which corpuscular and non-corpuscular receptors are intermingled or segregated within arrays. Coefficients of Segregation did not differ among species and in both cases the two classes of receptors in arrays were largely intermingled.

Whereas the receptor arrays in the palmar tubercles of tree squirrels and ground squirrels are similar in several respects, individual elements within the arrays differ. In both species they contain intraepidermal endings, dermal free endings and simple corpuscles. Only in ground squirrels do they contain Meissner corpuscles and only in tree squirrels do they contain Pacinian corpuscles. Assuming that differences in corpuscle morphology translate into physiological differences (Munger 1971, Ilyinsky 1976) there should be functional differences between arrays.

In summary, several characteristics of receptor arrays are defined in this study. Statistics like the Coefficient of Dispersion and Coefficient of Segregation provide a language with which to discuss array properties, although there are still unsolved problems concerning their use. The quantitative description of array properties is an invaluable means of comparing the innervation of the skin in different species and in different locations within a single animal. These quantitative descriptions are not suggested as an alternative to descriptions of single receptor types but as a means of complementing them and providing information about the spatial relationships between individual receptors.

Receptor Morphology

Intraepidermal endings in tree squirrels and ground squirrels are similar. There is some indication that the degree of branching and the area over which these branches ramify may be greater in tree squirrels than in ground squirrels. This impression is not based on a rigorous analysis. It is likely that the majority of these endings are associated with Merkel cells (Munger 1965, Halata 1975, Breathnach 1977). Their basic morphology and their relationships to other skin structures are similar to endings that are parts of Merkel cell-neurite complexes in the glabrous skin of other mammalian species (Munger 1965, Munger et al. 1971, Munger and Pubols 1972, Halata 1975). Merkel cells with vacuolated cytoplasm and large, elongated nuclei are sometimes found near the basal layer of the epidermis but vocuolation of the cytoplasm is not a regular feature of squirrel skin fixed in neutral buffered formalin.

Simple corpuscles in the two species of squirrels are composed of one or more large diameter fibers, an inner lameller core (undivided), subcapsular space and an outer capsule. The most common configuration in both species is a single fiber that ramifies into two terminal branches within a single inner core. These corpuscles are strikingly similar to corpuscles found in the glabrous snout skin of rats (Mac Intosh 1975). They also resemble corpuscles found in cats (Malinovský 1966a, b, c), raccoons (Munger and Pubols 1972), platypuses (Bohringer 1977), moles (Halata 1972b, 1975) and in the eyelid skin of hens (Malinovský 1968). Munger and Pubols (1972) and Halata (1975) discuss several additional corpuscles that resemble simple corpuscles, ultrastructurally.

The Meissner corpuscles found in ground squirrels are similar to those found in mice (Idé 1976, 1977), humans (Cauna 1956, Cuana and Ross 1960, Hashimoto 1973) and other monkeys (Sevier and Munger 1965, Halata 1975). The presence of this ending in the skin of a second rodent species indicates that its phylogenetic distribution is not restricted to primates, as Quilliam (1975) suggested. In some corpuscles, the terminal portion of the neurite is composed of small, free ramifications (Cauna 1956) rather than an expansion as is common in other species (Hashimoto 1973, Idé 1976). This observation will have to be confirmed at the ultrastructural level.

Observations on Pacinian corpuscles in tree squirrels are limited. Their basic organization, consists of an ellipsoid shaped fiber within an inner core, a subcapsular space and an outer capsule. The corpuscles in squirrels resemble those found in cats (Pease and Quilliam 1957), raccoons (Munger and Pubols 1972), humans (Cauna 1958, Cauna and Mannan 1959) and opossums (Brenowitz 1978). To my knowledge, this is the first report of a Pacinian corpuscle in the glabrous paw of a rodent.

CHAPTER II

BEHAVIOR EXPERIMENTS

Purpose

The main purpose of this study was to test the prediction that tree squirrels would depend upon somatic sensory (tactile) input from the volar surface of the forepaw to a greater extent than ground squirrels in food handling behavior. Several, more general questions about the role of sensory input in controlling food handling were also examined.

Methods and Materials

Subjects

Subjects were 10 adult ground squirrels and 10 adult tree squirrels live trapped in south central Michigan. Ground squirrels were housed in clear plastic cages with wood shavings and tree squirrels were kept in metal wire cages with plexiglass fronts and wood shavings. All animals were kept in the lab for a minimum of two weeks prior to testing. Ground squirrels and tree squirrels were given water and Purina mouse breeder blocks chow ad lib prior to testing. Because tree squirrels frequently did not eat lab chow, their diet was supplemented with raw peanuts. The same food and water regimes were followed while testing except particularly obese ground squirrels (greater than 175 g) were placed on a reduced diet.

Surgical Procedures

Five randomly chosen individuals per species were assigned to the sham operated group and the remaining 5 constituted the lesioned group. Squirrels were anesthetized with an intraperitoneal injection of sodium pentobarbital at an initial dose of approximately 50 mg/Kg. Supplementary doses were given as needed. The hair on the flexor surface of the forearm and wrist was shaved and an incision was made on the lower forearm. The skin and underlying subdermal tissue were dissected away, exposing the median nerve. Animals receiving lesions had their median nerves freed from surrounding connective tissue and a section of nerve 3-5 mm long in ground squirrels and 6-10 mm long in Fox squirrels was removed. The cut ends of the nerve were deflected from their normal course and the wound was flushed with saline and sutured. Sham operated individuals underwent the same procedures except the nerve was not cut, only freed from surrounding connective tissue. Animals were then given a prophylactic injection of antibiotics (Combiotic) and returned to their home cages. They were allowed to recover for 10-14 days before being used in experiments.

Preparation of Food Items

The food items presented to squirrels were cylinder shaped pieces of winesap apples cut to desired sizes with a cork-boring set. The large food items were cylinders with both diameter and height equal to 0.7 x total length of the forepaw (minus claws) and small food items were cylinders with both diameter and height equal to 0.5 x total length of the forepaw. The mean forepaw length of tree squirrels = 30.7 ± 0.87 mm (n = 7) and the mean forepaw length of

ground squirrels = 15.0 ± 0.24 mm (n = 14). Therefore, a large food item had a diameter and height of 20 mm for tree squirrels and 10 mm for ground squirrels and a small food item had a diameter and height of 14 mm for tree squirrels and 7 mm for ground squirrels. The volume of the large food item is 2.9 x the volume of the small food item.

Testing Procedures

At the beginning of a test session a squirrel in its home cage was placed in front of a closed circuit video camera in an observation room. A trial began when a squirrel picked up a food item, introduced into the home cage with a semi-automatic dispenser, and terminated when the squirrel finished the food item (or dropped it without picking it up again within 5 sec). A test session consisted of a maximum of 4 trials (2 large and 2 small food items) but often subjects did not eat all four food items. The order in which food items were presented and the order in which animals were tested on a given day were randomized. Squirrels were given 1 test session a day until they accumulated a total of 10 trials for each size food item (5-8 days). Actual testing was preceded by 3 days of pre-tests (one per day) to familiarize squirrels with the apparatus and procedures.

Squirrels were observed on a video-monitor in another room and data were recorded by pressing appropriate microswitches on a keyboard, thereby registering events on an Esterline Angus event recorder and on a series of counters. For a trial to be included, both forepaws had to be visible. The following data were recorded:

1) Total Time from when a squirrel picked up a food item until it finished it or dropped it without picking it up within 5 sec. If

an individual "froze" for 5 sec during a trial, the trial was terminated and 5 sec deducted from total time.

2) Pre-eating Time started when the food item was first picked up and ended when the first bite was taken from it. Eating Time is determined by subtracting Pre-eating Time from Total Time.

3) Bouts of Manipulation during Eating Time. Manipulation is defined as a change in position of a single paw (or part of a paw) or both paws on a food item. A bout is defined as a single manipulation or a group of virtually continuous manipulations separated from another such group by an interval equal to the time it took to release a microswitch to its resting position and press it again (approximately 0.25 sec). Instances in which the paws were held stationary and the position of the food item was changed with the teeth were difficult to differentiate from bites and were therefore not counted. When a food item was dropped and picked up again within 5 sec it was recorded as one bout and the trial continued.

Data Analysis

Eating time was divided by the number of bouts of manipulation to yield an Interbout Interval (1/interbout interval = rate of manipulation). A mean Interbout Interval, mean Total Time and mean Pre-eating Time were calculated (over 10 trials) for each individual. These three dependent variables were then analyzed by ANOVA with the following design: A three factor mixed design with repeated measures on one factor (food size).

Factor 1: Species (Spermophilus vs. Sciurus)

Factor 2: Condition (lesioned vs. sham operated)

Factor 3: Food size (large vs. small)

Duncan multiple range tests were used to make appropriate post-hoc comparisons between group means.

The Eating Time for a large food item was divided into quarters and interbout intervals were calculated for each quarter. Mean interbout intervals for each quarter were then calculated for each individual. Interbout intervals were then analyzed in a three factor mixed design ANOVA identical to that above but with quarter of Eating Time (1^{st}, 2^{nd}, etc.) substituted for food size. The specific prediction is that if animals continue to monitor food items as they eat them, there should be differences in interbout intervals between quarters.

Autopsies

Lesioned animals were killed with an overdose of chloroform and the sites of their lesions were checked for possible regeneration under a dissecting microscope. No regeneration of connections between cut ends of the median nerve was observed in any of the squirrels. Generally, the proximal end of the nerve was swollen into a neuroma.

Inter-Observer Reliability

Inter-observer reliability for scoring bouts of manipulation was tested in 10 trials on two different tree squirrels (it is harder to detect individual forepaw movements in tree squirrels than in ground squirrels). The correlation coefficient (r) for these trials = 0.971.

Results

Description of Food Handling

Tree squirrels and ground squirrels initially contact food items with their snouts and then pick them up with the upper and lower incisors. Typically, squirrels of both species transfer their weight back over their hind limbs and rock back so that they are eventually sitting up. This move frees the forelimbs so that the food item can be transferred to the forepaws. Pre-eating Time continues with a period during which the animals rapidly rotate the food item towards them with alternating movements of the forepaws. At some point the food is brought to the mouth and the first bite is taken. This period of extensive manipulation ends with the first bite.

In almost all cases ground and tree squirrels begin eating food items along an edge, rather than in the middle of the cylinder. The food item is cradled in the forepaw digits and is frequently repositioned by rapid flipping movements. The goal of these manipulations appears to be to find another edge from which to chip off another piece of food (Lockner 1970). In ground squirrels the food item remains cradled in the digits until it is finished. Tree squirrels differ in this stage. As a food item gets very small, they move it up to a position between the edges of the palms near the first digits. Most of the time the food item is held there until finished but on several occasions it was moved back and forth between the rest of the digits and this position between the edges of the palms.

Individual manipulations are of two basic types. The first consists of the movement of one forepaw relative to the food item. The forepaw is quickly lifted from the surface of the food item and then

repositioned on it. The second type of manipulation involves movement of both forepaws. These, in turn, can be either synchronous (both moving in the same direction) or asynchronous (both moving in opposite directions). Lesioning produces no noticable (with the techniques employed) qualitative changes in the nature of these manipulations or the organization of the sequence described above. The differences observed appear to be largely quantitative in nature.

Interbout Interval

The interval between bouts of food manipulation (1/Interbout Interval = rate) is the most direct measurement of the amount of manipulating done and has the advantage of being independent of the time actually spent eating a food item. Results are summarized in Figure 14 and Table 3. Interbout Interval is significantly affected by both food size and the subject's condition, for both species. Large food items are handled more than small food items and lesioning increases food handling. If the change in behavior was due to a motor deficit resulting from the lesion, one would expect lower motor neuron lesion effects, namely a decrease in motor output, not an increase. Thus, the change in behavior due to the lesion would appear to be the result of the alteration of sensory input. The analysis of variance also indicates that there is a significant interaction between food size and condition. Post-hoc comparison of group means (Table 3) shows that whereas the lesion significantly affects the handling of small food items for both species, it does not affect the handling of large food items for either one. There is a significant interaction between size and species as well. As would be predicted,

Figure 14. Interbout Intervals in tree and ground squirrels. Means (bars) plus one standard error (flags) are presented.

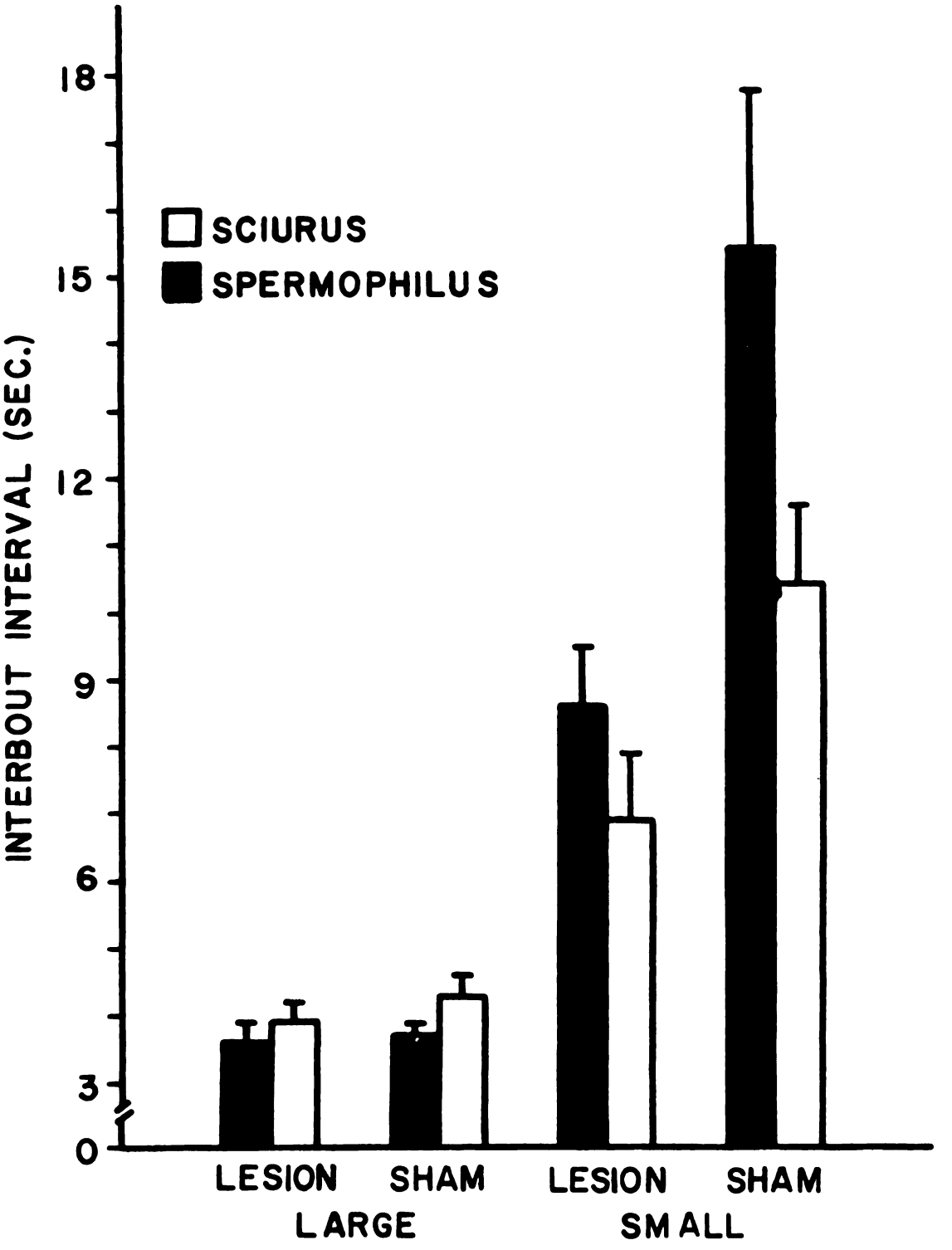

INTERBOUT INTERVAL (SEC.)
18
15
12
9
6
3
0
SCIURUS
SPERMOPHILUS
LESION
SHAM
LESION
SHAM
LARGE
SMALL

Figure 14.

Table 3. Analysis of Interbout Intervals

ANOVA Table

Source	SS	df	MS	F	P
Total	806.4	39	--	--	--
Between subjects	197.4	19	--	--	--
Species	21.3	1	21.3	3.49	NS
Condition	72.9	1	72.9	11.94	**
Species x Condition	5.2	1	5.2	0.85	NS
$Error_{between}$	98.0	16	6.1	--	--
Within subjects	609.0	20	--	--	--
Size	413.4	1	413.4	72.53	***
Size x Species	36.5	1	36.5	6.40	*
Size x Condition	60.1	1	60.1	10.54	**
Size x Sp. x Cond.	7.9	1	7.9	1.39	NS
$Error_{within}$	91.1	16	5.7	--	--

Post-hoc Comparisons

Spermophilus/Lesion/Large Food	vs.	Spermophilus/Lesion/Small Food:	*
Spermophilus/Sham/Large Food	vs.	Spermophilus/Sham/Small Food :	*
Sciurus/Lesion/Large Food	vs.	Sciurus/Lesion/Small Food :	NS
Sciurus/Sham/Large Food	vs.	Sciurus/Sham/Small Food :	*
Spermophilus/Lesion/Small Food	vs.	Spermophilus/Sham/Small Food :	*
Sciurus/Lesion/Small Food	vs.	Sciurus/Sham/Small Food :	*

*$p < 0.05$ **$p < 0.01$ ***$p < 0.001$

Interbout Interval is significantly less for the tree squirrel, the expected manipulator, than for the ground squirrel, for the small food item. From examining Figure 14, it is obvious that the large food items are treated the same by both species. There is no main effect of species on Interbout Interval, nor are the species by condition or three-way interactions significant.

Figure 14 indicates that there is a greater absolute difference in Interbout Interval between lesioned and sham operated ground squirrels than between lesioned and sham operated tree squirrels. However, when these differences are treated as proportional changes from the sham group mean, there is no difference in the extent to which the lesioned and sham groups differ ($t = 0.86$, $df = 8$). In ground squirrels the difference between large and small food sizes in sham animals is maintained in the lesioned animals (see Table 3). In tree squirrels, however, lesioned animals do not differ in their handling of large and small food items while sham animals do. These results indicate that sensory input from the volar surface of the forepaw is necessary for tree squirrels to adjust food handling according to food size. In this respect, the alteration of input from the forepaw affects tree squirrels more than it does ground squirrels.

The above results show by two different experimental manipulations that the handling of food items is subject to control by sensory input. To determine whether this control is exerted solely via an initial evaluation of the food item or via continued sensory feedback, separate Interbout Intervals were calculated for each quarter of the Eating Time for large food items. Results are summarized in Figure 15 and Table 4. Graphs of Interbout Interval vs. time

Figure 15. Interbout Intervals by quarters of Eating Time. Means (bars) plus one standard error (flags) are presented.

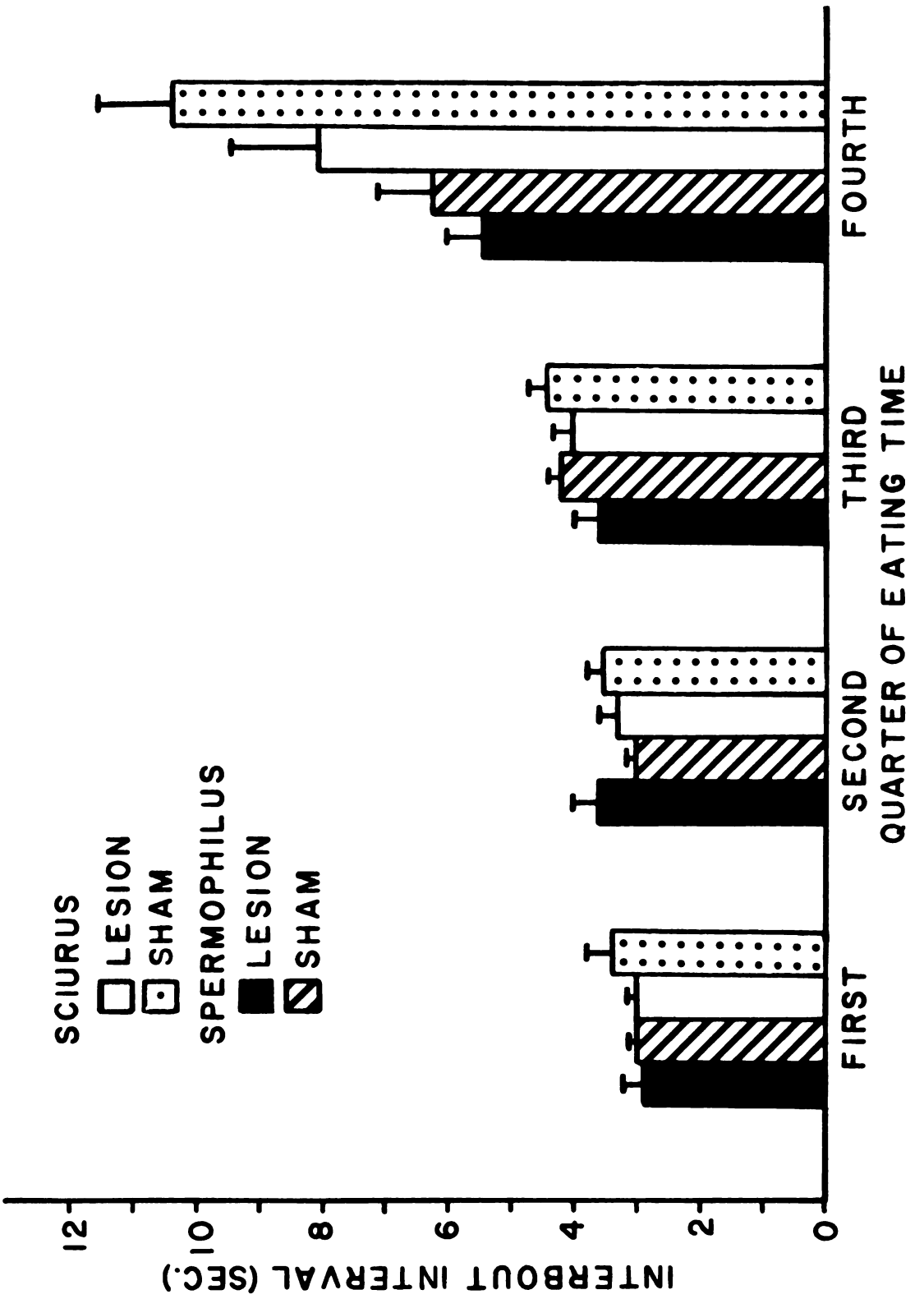

INTERBOUT INTERVAL (SEC.)
0
2
4
6
8
10
12
FIRST
SECOND
THIRD
FOURTH
QUARTER OF EATING TIME
SCIURUS
LESION
SHAM
SPERMOPHILUS
LESION
SHAM

Figure 15.

Table 4. Analysis of Interbout Interval by Quarters

Source	SS	df	MS	F	P
Total	430.2	79	--	--	--
Between subjects	73.6	19	--	--	--
Species	19.6	1	19.6	6.76	*
Condition	5.5	1	5.5	1.90	NS
Species x Condition	1.7	1	1.7	0.59	NS
$Error_{between}$	46.8	16	2.9	--	--
Within subjects	356.6	60	--	--	--
Quarter	245.7	3	81.9	63.00	***
Quarter x Species	37.5	3	12.5	9.62	**
Quarter x Condition	8.2	3	2.7	2.08	NS
Quart. x Sp. x Cond.	1.9	3	0.6	0.46	NS
$Error_{within}$	63.3	48	1.3	--	--

*$p < 0.05$ **$p < 0.01$ ***$p < 0.001$

(quarter of Eating Time) have positive slopes for all groups and the analysis of variance of these data shows that Interbout Interval changes significantly among quarters. These results are consistent with the hypothesis that there is continued feedback. It is not possible to attribute these results exclusively to a change in food size over quarters, for as a food item is eaten and its edges are chipped off it becomes more spherical in shape, a change that Lockner (1970) has shown to affect food manipulation in squirrels. Because this variable was not controlled across quarters of Eating Time, and because of its possible interaction with size, condition and species (as well as higher order interactions), further analysis and interpretation of these results seems unwarranted.

Pre-Eating Time

The only factor that plays a significant role in the control of Pre-eating Time is food size (see Figure 16 and Table 5). There are no significant differences between individual group means.

Total Time

As would be expected, it takes both species longer to eat a large food item than a small one (Figure 17 and Table 6). There is also an interaction between size and species which appears to be due to differences in the time taken to eat the large food items. Condition of squirrels does not affect the time it takes to eat a food item of either size. Individual group means were not compared.

Figure 16. Pre-eating Time in tree and ground squirrels. Means (bars) plus one standard error (flags) are presented.

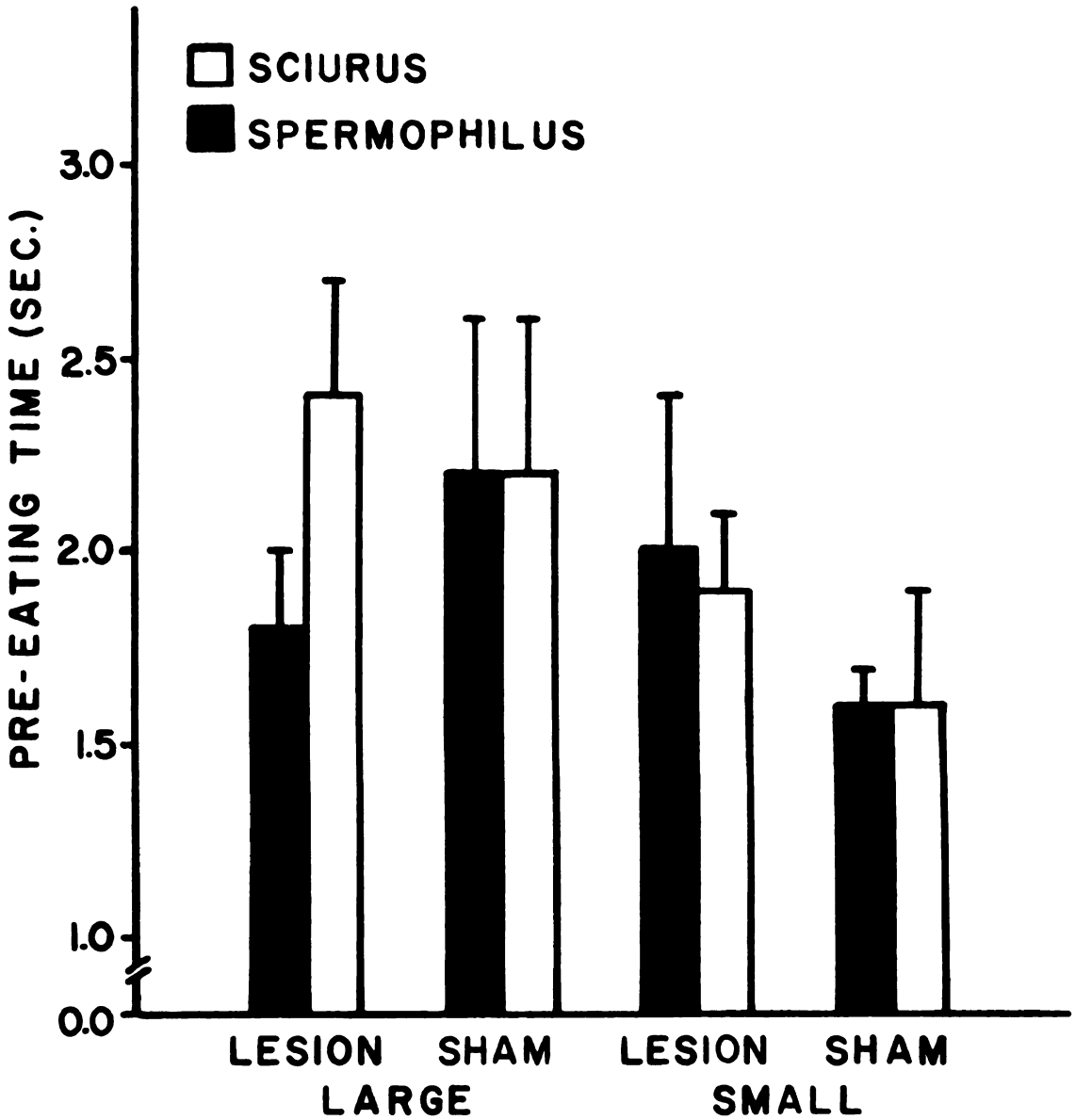

SCIURUS
SPERMOPHILUS
PRE-EATING TIME (SEC.)
3.0
2.5
2.0
1.5
1.0
0.0
LESION
SHAM
LESION
SHAM
LARGE
SMALL

Figure 16.

Table 5. Analysis of Pre-eating Time

ANOVA Table

Source	SS	df	MS	F	P
Total	17.8	39	0.5	--	--
Between subjects	12.4	19	0.7	--	--
Species	0.2	1	0.2	0.29	NS
Condition	0.1	1	0.1	0.14	NS
Species x Condition	0.2	1	0.2	0.29	NS
$Error_{between}$	11.9	16	0.7	--	--
Within subjects	5.4	20	0.3	--	--
Size	1.2	1	1.2	6.00	*
Size x Species	0.2	1	0.2	1.00	NS
Size x Condition	0.5	1	0.5	2.50	NS
Size x Sp. x Cond.	0.3	1	0.3	1.50	NS
$Error_{within}$	3.2	16	0.2	--	--

Post-hoc Comparisons

Spermophilus/Sham/Large Food	vs.	Spermophilus/Sham/Small Food:	NS
Sciurus/Lesion/Large Food	vs.	Sciurus/Lesion/Small Food :	NS

$^{*}p < 0.05$ $^{**}p < 0.01$ $^{***}p < 0.001$

Figure 17. Total Time in tree and ground squirrels. Means (bars) plus standard one error (flags) are presented.

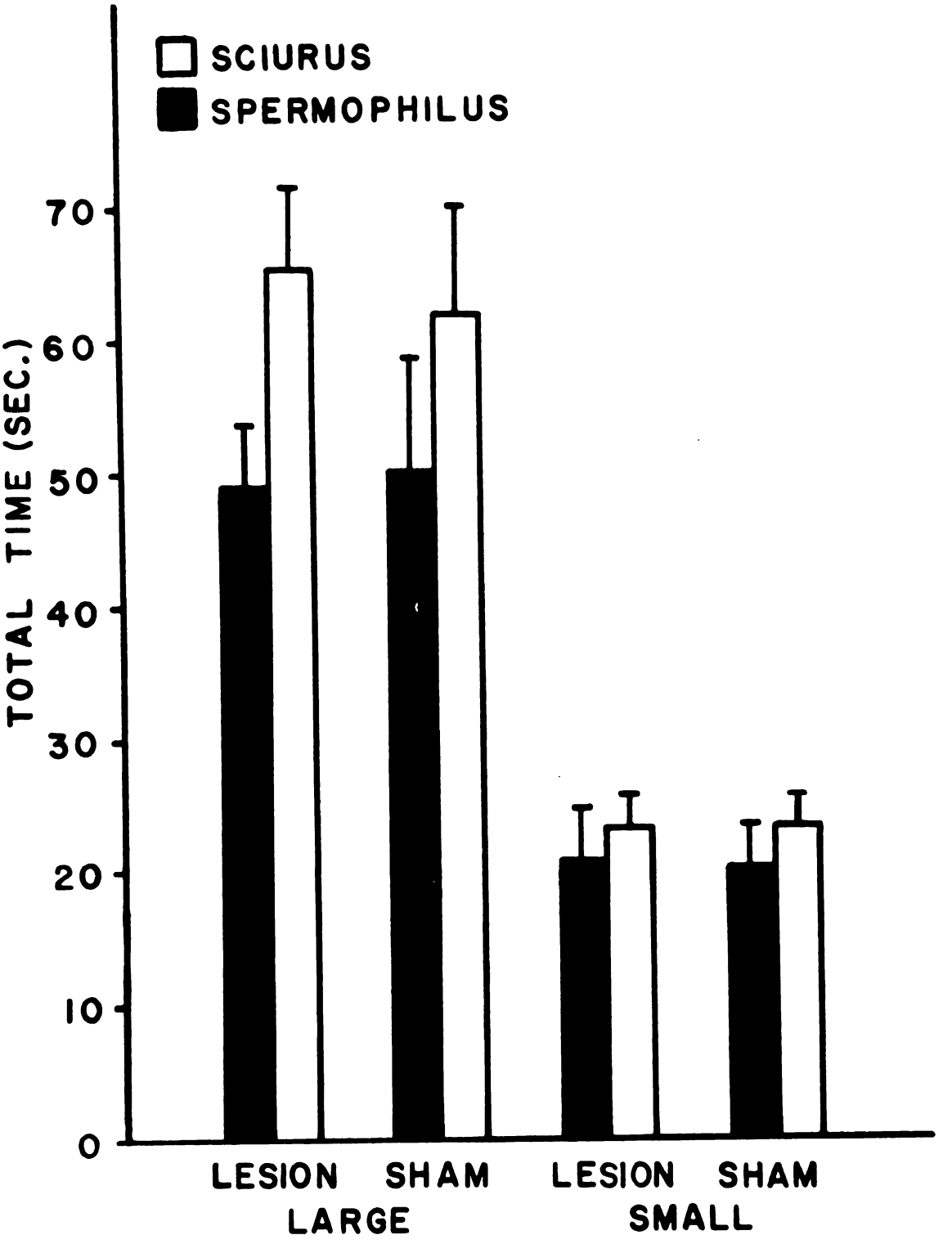

SCIURUS
SPERMOPHILUS
TOTAL TIME (SEC.)
70
60
50
40
30
20
10
0
LESION
SHAM
LESION
SHAM
LARGE
SMALL

Figure 17.

Table 6. Analysis of Total Time

Source	SS	df	MS	F	P
Total	17,849.9	39	--	--	--
Between subjects	4,885.6	19	--	--	--
Species	717.4	1	717.4	2.76	NS
Condition	4.2	1	4.2	0.02	NS
Species x Condition	12.3	1	12.3	0.05	NS
$Error_{between}$	4,151.7	16	259.9	--	--
Within subjects	12,964.3	20	--	--	--
Size	11,957.8	1	11,957.8	281.36	***
Size x Species	306.9	1	306.9	7.22	**
Size x Condition	2.1	1	2.1	0.05	NS
Size x Sp. x Cond.	16.9	1	16.9	0.40	NS
$Error_{within}$	680.6	16	42.5	--	--

*$p < 0.05$ **$p < 0.01$ ***$p < 0.001$

Discussion

In a complementary neuroanatomical study, natural history and behavioral data were used to predict that tree squirrels would have a relatively greater density of cutaneous mechanoreceptors in the glabrous skin of their forepaws than would ground squirrels. This prediction was supported by data showing that the tree squirrel's forepaw receptor density/hindpaw receptor density ratio (3.3 ± 0.5) is significantly higher than the ground squirrel's (1.3 ± 0.3). Based on these neuroanatomical data, it was predicted that tree squirrels would depend upon somatic sensory input from the volar surface of the forepaw to a greater extent than would ground squirrels in food handling behavior. The main purpose of this study was to test this prediction. In addition, a series of more general questions about the sensory control of food handling were examined.

The fact that manipulation of food items (as measured by the interval between bouts of manipulation) is affected by food size is evidence that it is controlled by sensory input. The changes in behavior produced by depriving squirrels of somatic sensory input from the glabrous forepaw (on small food items) indicates that somatic sensory input does contribute to that control in both species. The observation that Interbout Interval changes over the time taken to eat a large food item supports the hypothesis that there is continued sensory feedback from the food item. While lesioning the median nerve bilaterally produces similar quantitative changes in food handling in the two species, they differ in the extent to which their perception of food size depends upon somatic sensory input (according to the measure used here). Several of these results warrant further discussion.

Food Size

Based on Lockner's (1970) work on chipmunks it was predicted that large food items would be manipulated more (per unit time) than small ones. This prediction was supported by the Interbout Interval data, however, it is surprising that Pre-eating Time is not affected within a single species. Initially, it appeared that the function of the extensive manipulating that occurs during this period is tactile evaluation of the food item. These results do not appear to be consistent with this hypothesis, for it should take longer to evaluate large food items than small ones. It was not surprising to find that it takes longer to eat a large item than a small one.

Median Nerve Lesions

Bilaterally lesioning the median nerve in both species of squirrels did not appear to qualitatively affect manipulation of food items. Within 24 hours of surgery it was virtually impossible to tell the difference between lesioned and control (sham operated) animals in any behaviors. I have planned experiments to attempt to verify this finding with greater resolution by using high speed cinematography. For tree squirrels and ground squirrels median nerve lesions increased food manipulation (lowered Interbout Interval), but only for small food items. These data indicate that the role of somatic sensory input in controlling these motor patterns differs depending on food size. The importance of this result will be discussed below.

Recording experiments (see Appendix A) showed that sectioning the median nerve blocks all tactile input from the volar surface of the forepaw but leaves proprioceptive input almost completely intact.

Moist food items were used to compensate for a potential decrease in sweat gland activity, the most important change in autonomic function that might occur. Median nerve lesions produced increases in motor output in both species. If these behavioral changes were due to a deficit in motor function, decreases in motor output, the primary result of such Lower Motor Neuron Lesions, would have been expected. In conclusion, bilateral median nerve lesions produce a relatively selective loss of somatic sensory input from the volar surface of the forepaw. Changes in behavior resulting from that procedure can be attributed predominantly to that loss.

Species Comparison

Ariëns Kappers et al. (1936; pp. 261-262) suggested that the number and diversity of sensory endings in an animal's skin and its dependence (behaviorally) upon input from those receptors are closely related. Historically, this hypothesis has played a central role in understanding relationships between an animal's behavior and the organization of its central somatic sensory system (Welker 1976, Johnson 1978). Comparing the effects of median nerve lesions in the two species was designed as a test of that hypothesis. The prediction that tree squirrels would be more affected by median nerve lesions than ground squirrels provided the primary impetus for this entire study.

The results presented here show that the quantitative change in the handling of small food items that results from this lesion is proportionately the same in both species. However, these results also suggest that the two species differ in the extent to which they depend

on somatic sensory input from the glabrous forepaw in controlling food handling. Both normal and lesioned ground squirrels handle large food items significantly more than small food items. To the contrary, normal tree squirrels handle the two sized items differently, but lesioned tree squirrels no longer show a significant difference between food sizes (see post-hoc comparisons, Table 3). This finding suggests that the tree squirrel's ability to adjust food manipulation behavior according to food size (as indicated by measurement of Inter-bout Interval) is dependent upon somatic sensory input from the volar forepaw to a greater extent than is the ground squirrel's. These results support the predicted species difference in at least one important respect. They indicate that it is possible to make predictions about an animal's behavior based on detailed understanding of the organization of its somatic sensory system, supporting Ariëns Kappers et al.'s (1936; pp. 261-262) suggestion.

As a food item gets small a tree squirrel moves it from the digits to the palm, while a ground squirrel leaves it cradled in the digits. In tree squirrels the mean density of cutaneous receptors in the palm is 6 times as great as in the digits. The mean density of receptors in the palm of a ground squirrel is only twice as great as in the digits. Moving a food item up to the palm should increase the tree squirrel's ability to obtain somatic sensory input from it considerably more than it would the ground squirrel's. Although this correlation was not predicted it further supports a relationship between relative receptor density and behavioral dependence upon somatic sensory input.

The Role of Somatic Sensory Input in Controlling Behavior

According to Bullock (1961) sensory input can trigger behavior or it can modulate ongoing behavior. The first alternative resembles both the ethologisis' "releaser" (Lorenz 1950, Tinbergen 1951) and the physiologists' "reflex" (Sherrington 1906, 1910, Gray 1950). In both species of squirrels somatic sensory input modulates ongoing behavior. As a food item changes size as it is eaten, feedback from the food item enables a squirrel to adjust the interval between successive bouts of manipulations. Eliminating normal input from the glabrous forepaw adversely affects a squirrel's ability to make these adjustments, resulting in increased manipulation of small food items. There is no evidence that somatic sensory input from the glabrous forepaw skin plays a role in triggering food handling. As described above, food items are first contacted with the snout or teeth and only later are transferred to the forepaws.

The role of somatic sensory input in controlling food handling by squirrels is similar to its role in controlling mounting in male rats (Carlsson and Larsson 1964, Sachs and Barfield 1970) and sensorimotor components of feeding in pigeons (Zeigler 1974, 1975a, b, Zeigler et al. 1975). In both cases, somatic sensory input (plus proprioceptive input in pigeons) modulates ongoing behavior. Blocking this input by deafferentation or application of local anesthetics produces an increase in motor output, but a decrease in the efficiency of any single movement. For instance, in pigeons the number of pecks/grain of food increases when they undergo trigeminal deafferentation, but cinematographic analysis reveals that they fail to properly adjust their beak movements as the food item is grasped and

moved to the rear of the buccal cavity (Zeigler et al. 1975).

The role of somatic sensory input in controlling food handling in squirrels differs from its role in controlling lordosis in female rats (Gerall and McCrady 1970, Diakow et al. 1973, Pfaff et al. 1974, Kow and Pfaff 1976), predatory attack in cats (MacDonnell and Flynn 1966, Flynn 1967, Flynn et al. 1971, Bandler and Flynn 1972) and inter-male aggression in rats and mice (Flory et al. 1965, Bugbee and Eichelman 1972, Thor and Ghiselli 1973a, b, 1974, Katz 1976). In all of these situations eliminating somatic sensory input from facial regions results in a decrease in motor output. The role of somatic sensory input is one of triggering behavioral sequences, although Thor and Ghiselli (1973a) suggest that it may play an orienting (modulating) role in inter-male aggression in rats. In summary, there is a general correlation between the role of somatic sensory input in controlling behavior and the effects of eliminating that input. Where it triggers behavior, blocking that input produces a net decrease in behavior and where it modulates ongoing behavior, this procedure results in an increase in motor output, with an apparent decrease in efficiency.

As indicated above, median nerve lesions do not appear to qualitatively change food handling behavior. If this result is confirmed it would appear that a decrease in efficiency is an unlikely explanation for the observed increase in motor output. One alternative explanation is that squirrels adjust their motor output in an attempt to produce a level of stimulation similar to that which would normally be produced in a particular situation (e.g., in the process of eating a food item). When an individual bout of

manipulation fails to produce an expected level of stimulation, the next bout follows in a shorter time than would be normal. Bermant and Westbrook's (1966) study on the peripheral control of sexual contact in rats lends support to this suggestion. By swabbing the genital regions of female rats with a local anesthetic, they were able to significantly reduce the interval between a completed mating sequence and a female's subsequent attempt to gain sexual contact. Moreover, the further through a mating sequence a normal female was allowed to proceed, the longer this interval became. This hypothesis is analagous to, and partially based on, Konishi's sensory template model of song development in birds (Konishi 1965, Marler 1970). The first step, however, is to determine at a higher level of resolution whether there are any qualitative changes in food handling that result from median nerve lesions.

Dynamic Weighting of Sensory Inputs

Fentress (1976) recently suggested that the relative contributions of peripheral (sensory) and central factors to the performance of a behavior can change in response to changes in a host of intrinsic and extrinsic parameters. Essentially, the boundaries between the peripheral and central control of behavior are dynamic rather than static. These arguments can be extended to include dynamic roles for inputs from different sensory modalities. Under a particular set of stimulus parameters input from different sensory modalities will be weighted in a particular fashion before a final adjustment of behavior occurs. When these stimulus parameters change, the relative weighting of these inputs may change as well. There are

data to support this argument.

Pigeons will use the sun to navigate with when it is visible, however, when it becomes clouded over, they are still able to navigate (Keeton 1974). These facts indicate that pigeons can readily shift the weighting of solar cues such that other sensory inputs predominate. While male sticklebacks use visual cues to approach intruding males, in the final "release" of biting attacks the role of visual input decreases and tactile input predominates (Tinbergen 1951). Also, in selecting shells hermit crabs use visual cues for initial location and choice of shells but switch over to tactile and proprioceptive cues once initial contact with a shell occurs (Reese 1962, 1963).

When tree squirrels and ground squirrels are manipulating large food items, somatic sensory input from the volar surface of the forepaw plays a relatively minor role in controlling manipulation parameters. However, with small food items this same source of input makes a significant contribution to the control. While a food item is large, a squirrel's forepaws and forearms are apart and changing position as the food item decreases in size, providing proprioceptive feedback. When the food item is reduced to a given size the forepaws will be close together and the position of the forearms will no longer change, making proprioceptive cues harder to follow. Also, observations indicate that an animal's snout blocks a clear view of the food item when it is very small. As these sources of input become less useful, the relative weighting of somatic sensory input should increase. The results of this study support this hypothesis.

Conclusions

In conclusion, the motor patterns used in the handling of food items by tree squirrels and ground squirrels are modulated by continued sensory feedback which provides information about a food item as it is eaten. The contribution of somatic sensory input from the glabrous skin of the forepaw to the control of manipulation behavior is relatively minor with large food items, however, its role increases in importance with small items. While somatic sensory input is important to both species, tree squirrels appear to depend on it to a greater extent than ground squirrels. This result was predicted on the basis of neuroanatomical data concerning the relative distribution of cutaneous mechanoreceptors in the two species.

APPENDICES

APPENDIX A

RECORDING EXPERIMENTS

APPENDIX A

RECORDING EXPERIMENTS

Methods and Materials

Microdissection of the median nerve in both species indicated that this nerve innervates the skin of the entire volar surface of the forepaw, including the digits. Recording experiments were done on two male ground squirrels and a female tree squirrel to determine the receptive fields of the sensory components of their median nerves and the extent to which movement of their forepaws is controlled by the motor components of this nerve (done by stimulating the nerve). Animals were anesthetized with approximately 50 mg/Kg of sodium pentobarbital given intraperitoneally. Two incisions were made: one on the flexor surface of the forearm, exposing the median nerve at the level at which lesions would be made for behavioral experiments; the second was made on the upper arm and trunk, exposing the brachial plexus. All forearm nerves pass through this plexus en route to and from the CNS.

All of the nerve trunks contributing to the brachial plexus were ligated and then cut proximal to that point. The skin was sutured to form a reservoir which was filled with warm mineral oil. The nerve trunks were then layed across a tungsten wire hook electrode and lowered into the mineral oil. Light tactile stimuli were applied to the entire volar forepaw surface with a small camel's hair brush

and responses to deep punctate stimuli and joint rotation were also explored. After the responses in the brachial plexus were examined, the median nerve was sectioned as it would be for behavior experiments. The forepaw was stimulated again and the extent of any remaining input from it was determined. Responses were monitored on an oscilloscope and an audiomonitor.

Next, a bipolar silver wire stimulating electrode was placed under the distal portion of the cut median nerve and stimuli were given at 3-10 pulses/sec with durations of 1-10 msec and intensities of 0.03 to 1.23v. Movements of the forepaw were recorded. Quantitative physiological data such as thresholds were not systematically collected. Finally, the receptive field of the median nerve was double checked by placing the recording electrode under the distal portion of the median nerve and stimulating the forepaw once again.

Results

Tactile stimulation of any point on the volar surface of the forepaw of the tree squirrel and this entire area, with the possible exception of the lateral-most part of the fifth digit of the ground squirrels produced responses in brachial plexus units. Joint rotation and deep punctate stimulation also produced responses. Following sectioning of the median nerve, no responses to light tactile stimulation could be elicited from any portion of the volar surface of the forepaw in either species. Joint rotation and deep punctate stimulation (possibly intense enough to stimulate the back of the paw) still produced responses. After the lesion was performed, recordings taken from the distal portion of the cut median nerve

confirmed the above findings. Joint rotation elicited some response, however, this was minor in comparison to the response that the same stimulation produced at the level of the brachial plexus. Tactile stimulation of any point on the volar surface of the forepaw of either species (with the possible exception of the lateral fifth digit in ground squirrels) produced responses in median nerve units. In the two ground squirrels, stimulation of the median nerve distal to the cut produced only low amplitude (less than 1 mm displacement) twitching in the two hindmost tubercles on the palm. In the tree squirrel these two tubercles did not move when the nerve was stimulated, instead, there was an almost undetectable movement of the reduced first digit. To summarize, the median nerve in both species appears to be predominantly sensory (plus autonomic) in its functioning. Lesioning wipes out all tactile input from the volar surface of the forepaw but leaves proprioceptive input almost completely intact. Little motor deficit results from the lesion.

APPENDIX B

COEFFICIENT OF SEGREGATION

APPENDIX B

COEFFICIENT OF SEGREGATION

The Coefficient of Segregation (S) (Pielou 1969) is a statistic that can be used to examine the dispersion of objects of one category in relationship to objects of a second category. These objects could be two species of trees in a woodlot, two types of mechanoreceptors in glabrous skin, two types of cells in a nuclear region of the CNS, or any other discrete entities that can be assigned to one of two categories. At one extreme (when S = 0) objects in the two categories can be randomly intermingled and at the other extreme (when S = 1) they can be fully segregated (see Figure 6 for examples of both extremes).

The data used to calculate S come from a "nearest neighbor" analysis. A "base" object is located (e.g., a receptor in a section of tissue) and two questions are asked about it: 1) To what category does it belong? 2) To what category does its nearest neighboring object (e.g., another receptor) belong? In this dissertation, this approach was used to examine the dispersion of corpuscular and non-corpuscular receptors. First, sections of skin were scanned under 125x magnification until a "base receptor" was located. To be included in this analysis the receptor had to be surrounded by two other receptors or it had to have a receptor on one side and a length of skin at least as great as the distance between the base and second

receptor on its other side. A receptor meeting these criteria had its category (corpuscular or non-corpuscular) and that of its nearest neighbor recorded. The scanning of a section continued until a new receptor (one not previously examined) was located. It was designated a base receptor and its category, along with that of its nearest neighbor, was recorded. In this case, the nearest neighbor could be a receptor examined earlier in the same section. When a section was completed, another section was examined in a similar fashion. This procedure was repeated until 10 base receptors (this number was arbitrarily chosen) of each category and their nearest neighbors were recorded. This particular sampling procedure was adopted for counting receptors in sections of skin. Other applications of the technique may require a different sampling procedure.

Once these data are obtained, S is calculated according to the following logic:

$$S = 1 - \frac{\text{observed number of mixed pairs of objects}}{\text{expected number of mixed pairs of objects}} .$$

A mixed pair is one in which the base object and its nearest neighbor belong to different categories. The expected number of mixed pairs is based on the proportions of objects in the two categories found in the area being sampled, although this does not have to be calculated separately. S is most easily calculated by first tabulating the data in a 2x2 table with the following format:

		Nearest Neighbor		
		Category 1	Category 2	
Base Object:	Category 1	a	c	m
	Category 2	b	d	n
		r	s	N

(a, b, c, d = cell frequencies; m, n = row totals; r, s = column totals; N = table total). Next, S is calculated for each individual being examined according to the following equation:

$$S = 1 - \frac{N\,(b + c)}{ms + nr}$$ (Pielou 1969).

S was used as a population parameter to compare the dispersion of two categories of objects (receptors) among two species of mammals. S's were calculated for each animal in question and then S's were compared among the two species using a Mann-Whitney U test.

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