A BEHAVIOURAL EXAMINATION OF THE INTRAMODAL
AND INTERMODAL CONSEQUENCES OF LONG-TERM
TACTILE RESTRICTION BY VIBRISSAE REMOVAL IN RATS

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Despite the extensive work done on the neural consequences of tactile restriction very little is known about the behavioural consequences of this manipulation. In the present investigation, an assessment was made of the effects of early, long-term tactile restriction by bilateral removal of the mystacial vibrissae on the subsequent somatosensory capacities of rats (i.e. the intramodal consequences) as well as its effects on visual and spatial capacities (i.e. the intermodal consequences). As well, rearing environment (enriched vs. normal) and type of surgery (vibrissae removal by cauterization of follicles or by plucking) were examined to determine specific factors that might influence the effect of early, long-term vibrissae removal.

Five tasks were used to assess these effects. The first two tasks assessed the intermodal consequences of vibrissae removal. Visual competence was assessed by measuring the habituation of orientation to repeated visual stimuli and the
dishabituation to subtle changes in these stimuli. A version of the Morris (1981) water maze was used to assess the rats' spatial abilities.

The results of these two tasks revealed limited evidence for intermodal effects. In terms of habituation to visual orientation, rats that had had their vibrissae removed by cauterization and were subsequently reared with daily access to an enriched environment required more trials to habituate to the presentation of repeated visual stimuli. As well, these rats were the only group to dishabituate to a subtle change in the stimuli. No effect of vibrissae removal was found in the spatial task, and environmental enrichment during development enhanced performance on this task, apparently through increased attention to distal cues by rats reared in this condition.

The remaining three tasks assessed the motoric and somatosensory effects of tactile restriction. No effect was found on the performance of the Puzzle Latch Box test in which the rats were required to manipulate various latches to obtain a food reward. As well, no significant effect was observed in reactions to the tying of pieces of wire to the rats' wrists. However, early, long-term vibrissae removal (by cauterization of follicles or by plucking) attenuated orientation to contacts of the mystacial pad itself. This effect was dissociated from tactile reactivity; all rats exhibited eye-flinch responses to taps on this area.

These results suggest that early, long-term tactile restriction has significant behavioural consequences for the
somatosensory system as well as the visual system. These data also provide limited evidence for theories of modality interdependence as well as yielding basic information concerning the role of the mystacial vibrisse in the behaviour of the rat.
# TABLE OF CONTENTS

- Introduction .................................................. 1
- Rationale ...................................................... 15
- Methods .......................................................... 21
  - Visual Orientation Task .................................... 26
  - Spatial Memory Task ....................................... 32
  - Manipulatory Behaviour .................................... 36
  - Bracelet Task ................................................. 38
  - Snout Contact Orientation .................................. 38
- Results ............................................................ 39
  - Visual Orientation Task .................................... 39
  - Spatial Behaviour .......................................... 44
  - Puzzle Latch Box ........................................... 52
  - Bracelet Task ................................................. 52
  - Snout Contact Orientation .................................. 59
- Discussion ....................................................... 62
- Conclusions ..................................................... 71
- References ....................................................... 74


LIST OF TABLES

Table A  The number of subjects assigned to each condition..................................................25

Table B  Description of the trials in the water maze task.
(Cue postion and platform position are described. A schematic drawing showing the quadrant positions appears in upper right corner)...............................35

Table C  Mean number of trials in which orientation occurred for the three visual stimuli. Solid display in trials 1-10; rapidly flashing display in trials 11-20; slowly flashing display in trials 21-30.................................43

Table D  Percentage of enriched and normally reared animals that contacted the cue in the "incorrect" quadrant on trials 7 and 8...............................51

Table E  Method of manipulation used to open the three latch types (A=butterfly latch; B=bolt latch; C=shielded butterfly latch--see Fig. 7. Numbers represent percentage of animals using that manipulation.).................................56
LIST OF FIGURES

Figure 1 The ontogenetic sequence of emergence of four sensory systems. (From Gottlieb, 1983)............7

Figure 2 Diagram of the apparatus used to test visual orientation...............................................28

Figure 3 Schematic of the presentation of visual stimuli during the thirty trials in the visual orientation task..........................................................30

Figure 4 Mean suppression ratios for rats in all conditions. Trials 1-10: solid display. Trials 11-20: rapidly flashing display. Trials 21-30: slowly flashing display. (A suppression ratio of zero indicates complete suppression of licking whereas a suppression ratio of 0.5 represents no suppression of licking)................................................41

Figure 5 Latency in seconds to find the submerged platform across trials for all conditions.............47

Figure 6 Latency in seconds to find the submerged platform across trials for all enriched and normally reared animals.................................................49
Figure 7 Latencies in seconds to open latches. ("ENRICHED" and "NORMAL" refer to rearing environment; "C" and "P" refer to cauterized surgical procedure and plucked surgical procedure respectively.) 54

Figure 8 Panel A: Latency in seconds to contact the wire bracelets.  
Panel B: Latency in seconds to remove one of the wire bracelets. ("ENRICHED" and "NORMAL" refer to rearing environment; "C" and "P" refer to cauterized surgical procedure and plucked surgical procedure respectively.) 58

Figure 9 Frequency of orientations to light taps on the snout with a surgical swab according to condition. ("ENRICHED" and "NORMAL" refer to rearing environment; "C" and "P" refer to cauterized surgical procedure and plucked surgical procedure respectively.) 61
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Introduction

The effects of early sensory experience on the development of perceptual capabilities and their neural substrates has long been one of the most important and active topics of study for investigators interested in the general principles underlying neural and behavioural plasticity (Greenough, 1976; Mistretta & Bradley, 1978; Tees, 1976; 1986). In most cases the focus has been on the examination of the impact of early and/or long-term deprivation of a sensory modality on subsequent intramodal competencies (e.g., Mitchell & Timney, 1984). As well, examination has been made of the effects of early or long-term multimodal sensory enrichment on brain and behaviour (e.g. Greenough & Green, 1981).

For a variety of reasons, including the relative ease with which one can alter early visual stimulation history, the role played by experience in the development of the visual system and related behaviours has been a prime target of most of the investigative activity (Tees, 1976). This work has been reviewed extensively ( Boothe, Vassdal, & Schenk, 1986; Mitchell and Timney, 1984; Tees, 1986). The most common method of manipulating early visual experience has been binocular visual deprivation by eyelid suturing or dark-rearing. The general finding is that visual experience during a "sensitive period" early in ontogeny is necessary for normal visual competence in terms of specific neural (e.g. Blakemore & Van Sluyters, 1975) and behavioural
measures (e.g., Tees, 1979).

Another area of recent interest is the part played by stimulation history in the development of the somatosensory system (Kaas, Merzenick, & Killackey, 1983). While a considerable amount of work has been done on the effects of deafferentation of body surface areas of limbs or hands (e.g. Johnson, Hamilton, Hsung, & Ulinski, 1972), most of the research has focused on the manipulation of sensory input to the mystacial vibrissae of rodents (Gustafson & Felbain-Keramidas, 1977).

The vibrissae-tactile system appears to be an extremely important source of environmental information for rodents and many other mammals. In the rat, the mystacial pad represents the single largest portion of the somatotopic map of the somatosensory cortex (Keramidas, 1976). As well, the vibrissae-tactile system is highly receptotopically organized from the periphery through to the cortex (Welker, 1971; 1976). The vibrissae are arranged in rows along the snout of rodents. This organization is followed almost exactly from the peripheral innervation to the contralateral thalamus and to area 1 of the contralateral somatosensory cortex (SmI) (Belford & Killackey, 1979). At the level of the cortex (and, to a lesser extent, in the thalamus), each vibrissae projects to an individual field of cells referred to as a 'barrel' because of its distinctive shape (Woolsey & Van Der Loos, 1970).

As is the case with the visual system, early deprivation has severe effects on the development of the
somatosensory system. In terms of neuroanatomical development, many of the effects of early restriction are analogous to the effects of binocular deprivation of the visual system (Weller & Johnson, 1975). Destruction by cauterization of the vibrissae and their receptor organs before postnatal day 5 (Weller & Johnson, 1975; Woolsey, Anderson, Wann, & Stanfield, 1979) leads to a disruption of the barrel formations in the cortex (Van Der Loos & Woolsey, 1973). While the number of neurons in the barrel field remains the same, the 'barrel' organization of the cells is completely abolished (Kaas et al., 1983). A reduction in dendritic spine density in this area is also seen (Ryugo, Ryugo, & Killackey, 1975). Peripheral destruction after day 5 has been reported to have no disruptive effects on these barrel formations (Weller & Johnson, 1975).

Interestingly, the effects of early tactile deprivation on the presence or absence of barrel formations appears to be entirely dependent on the destruction of the receptor organs in the vibrissae follicles. Long-term clipping (see Hand, 1982) or removal by depilatory (Weller & Johnston, 1975) of the vibrissae does not lead to disruption of the barrel formations. However, Simons and Land (1987) recently reported that although clipping does not disrupt the cytoarchitectonic structure of the barrel formations, it does lead to 'functional' disruption. Chronic trimming of vibrissae virtually abolished electrophysiological responding of cells in the barrel formations corresponding to those
vibrissae.

While the study of the neuroanatomical effects of early tactile restriction has become a major area of research, our knowledge of the 'functional' behavioural significance of this manipulation is virtually non-existent (see Gustafson & Felbain-Keramidas, 1977). A major reason for this ignorance is the result of our lack of understanding of what the vibrissae system actually does. Beyond speculation that the vibrissae may provide sensory information for nocturnal animals or animals with poor vision (Boudreau & Tsuchitani, 1972) very little systematic research has been performed on this system. Gustafson and Felbain-Keramidas (1977) do make a number of undocumented observations on the effects of early vibrissectomy on behaviour. Vibrissectomized animals show faster transits of a balance beam and decreased thigmotaxic behaviour compared with controls. These authors speculate that these effects may result from a shift to the use of visual cues in the tactile-restricted animals.

While it might be expected that sensory input plays an important role in normal intramodal development, some theorists have recently suggested that differential experience in one modality might also have consequences for the development of other sensory systems (e.g. Burnstine, Greenough, and Tees, 1984; Gottlieb, 1971; Tees, 1976; Turkewitz and Kenny, 1982). The concept of modality interdependence is by no means new, however. Berkeley described the necessity of intermodal experience for the development of spatial perception in 1709. As well, there
are numerous apocryphal reports of heightened auditory or tactile abilities in blind individuals (see Burnstine et al., 1984). This second area of interest—the impact of stimulation history in one modality on the capabilities of another—has been the brunt of the more recent writings concerning modality interdependence. Much of this interest by developmental psychobiologists has been spurred by the writings of Gottlieb and of Schneirla.

Gottlieb's (1971;1976) seminal works described the pattern of ontogeny of mammalian and avian sensory functions. In all cases examined he found an invariant sequence of emergence of the onset of function of the modalities: tactile development occurred first followed, in order, by vestibular, olfactory, auditory, and visual development (see fig. 1). It may be the case that this sequence of emergence allows for the independent and isolated development of each sensory system, making modality interdependence in development unlikely. However, Schneirla (1965) proposed that continuities in development exist; the organization of one modality may be dependent upon the level of organization of an already established modality.

Turkewitz, Gilbert, and Birch (1974) and Turkewitz and Kenny (1982) have proposed that the widespread appearance of this sequential development of sensory systems might have emerged because, as a result, competition is reduced between sensory systems, allowing each system to develop in relative independence. As well, this sequence of development allows later-maturing systems to utilize information from those
Figure 1. The ontogenetic sequence of emergence of four sensory systems. (From Gottlieb, 1983).
ONTOGENETIC SEQUENCE OF DEVELOPMENT OF FOUR SENSORY SYSTEMS

- **Period of Development?**
  - ONSET of Entire System
  - range of individual variability unknown

- **Visual**
  - ONSET
  - termination unknown
  - orientation, inhibition or excitation of ongoing activity
  - tracking discrimination etc.

- **Auditory**
  - ONSET
  - localization discrimination etc.
  - orientation, inhibition or excitation of ongoing activity

- **Vestibular**
  - ONSET
  - post-rotational head nystagmus
  - ocular nystagmus etc.
  - orientation or righting

- **Cutaneous**
  - ONSET
  - spread of sensitivity to rest of body etc.
  - oral or nasal region sensitive

AGE
already developed (Turkewitz & Kenny, 1982).

The underlying assumption of this position is that competition between modalities can, and does occur. The sequential development of systems allows earlier developing systems to organize themselves in relative (but not complete) independence and later systems to be assimilated into the now established frameworks. Based on this argument, disruption of one modality can have consequences for the development of another. Reduction of input to one modality should lead to decreased competition for a spared modality, thus leading (possibly) to increased competence of the latter. Another possibility is that restriction of an early developing modality will disrupt the "organizational framework" that a later emerging modality may need for its own development. In this second case, a decline in competence of the later developing system would be predicted.

There is some evidence that competition is a powerful force in ontogeny. In terms of the intramodal consequences of deprivation, Hubel and Wiesel (1963) showed that monocular deprivation had a much more severe and long-lasting effect than binocular deprivation. These researchers and others have since shown that this effect is due to decreased competition from the deprived eye, thus allowing the non-deprived eye to 'gain control' of the other's cortical areas (cf. Cynader, 1979). Monocular deprivation has been shown to give the non-deprived eye a perceptual advantage as well—at least in terms of vernier acuity (Freeman & Bradley, 1980). Intramodal competition is also found in the development of
the somatosensory system of mice. As mentioned previously, removal of select vibrissae from the mystacial pad of mice leads to the disruption of their barrel formations in the somatosensory cortex (Van Der Loos & Woolsey, 1973). The remaining vibrissae's "barrel" formations move into the regions that would have been occupied by the deprived vibrissae (Harris & Woolsey, 1981; Killackey & Erzurumlu, 1982).

Evidence is also available that intermodal competition is also a significant factor in neural development. For example, Cynader (1979), in examining single unit recordings of cells in the superior colliculus (SC) of cats, found that dark-rearing had a significant effect on some visually-driven cells. Cells in the superficial layers of the SC continued to be driven by visual input. However, in the deeper regions, where multimodal units are mostly found, dark-rearing virtually abolished the presence of visually driven cells while the percentage of cells driven by other modalities increased (Rauschecker & Harris, 1983). Cynader (1979) interpreted this finding as resulting from a competitive advantage gained by the auditory and somesthetic inputs to the region as a function of the loss of visual stimulation. Ryugo, Ryugo, Globus, and Killackey (1975) found similar effects at the level of the cortex. For example, blinding rats at birth yielded an increased density of dendritic spines in the auditory cortex of those animals 25 days later.

Ryugo et al. (1975) also found evidence of intermodal
consequences resulting from tactile restriction. Cauterization of vibrissa follicles at birth led to augmented dendritic spine density in the auditory cortex but not the visual cortex. While Ryugo et al. (1975) proposed that these intermodal effects may be initially limited to the auditory cortex due to its earlier development, Burnstine et al. (1984) have speculated that their results might be due to the relatively slow development of compensatory effects. Since Ryugo et al examined their animals at a very young age (25 days), the effects on visual cortex may well have been seen in the case of older tactile-deprived rats. Indeed, visual cortex thickening has been seen in adult rats (270 days of age) subjected to long-term dewhiskering (Keramidas, 1976)

The behavioural evidence for intermodal competition is somewhat less convincing. Burnstine et al (1984) in an extensive review of both the human and animal literature, found that, in general, the hypothesis of intermodal competition after early unimodal deprivation is borne out. For instance, rats blinded at birth have been shown to perform better on a non-spatial auditory learning task than rats blinded at adulthood or sighted control animals (Spigelman & Bryden, 1967). However, Tees and Cartwright (1972) found that dark-reared rats were not significantly handicapped nor any better at learning a simple conditioned avoidance response to auditory stimuli. As well, others have reported no visual deficits or enhancements due to auditory deprivation (MacDougall & Rabinovitch, 1971). The range of
tests employed in studying these effects, however, leaves a lot to be desired.

There is also fragmentary behavioural evidence concerning the intermodal influence of tactile deprivation. Keramidas (1976) in accordance with the visual cortex data discussed previously, found that long-term dewhiskering of rats led to faster learning of a visual form discrimination (triangle vs square) and a grating discrimination (2.2 cm vs 1.6 cm stripes) on a jumping stand task. As well, Turkewitz, Gilbert, and Birch (1974) found earlier and superior performance on a visual cliff task in cats that had had their vibrissae clipped from birth. However, as Turkewitz et al note, since a control group of animals that was clipped at the time of testing was not run, the results may be due to the intact cats choosing to use tactile before visual information (cf. Schiffman, Lore, Passafuime, and Neeb, 1970). Thus the results may be attributed to differences in the information available at the time of testing rather than to actual differences in attention or competency.

Approaching the issue from a somewhat different angle, Kenny and Turkewitz (1986) examined the effects of premature visual stimulation on the homing behaviour of rat pups. Their reasoning was that since homing behaviour came under the control of different sensory systems as they emerged, premature visual stimulation (through surgically-induced eyelid opening) may lead to a disruption in the behaviour due to precocious competition with the senses normally used to guide the behaviour. Early eye-opening led to an earlier use
of visual cues and a decrease in olfactory abilities. Thus, in terms of the intermodal competition hypothesis, early eye-opening has significant effects in the development of other modalities.

There is, then, some evidence for one of the hypotheses regarding modality interdependence (Turkewitz & Kenny, 1982). Reduction of input in one modality, does, in most cases, lead to increased competence in the processing abilities of other modalities. This effect appears to be mediated by competitive interactions. However, the evidence is incomplete and sometimes contradictory.

Fragmentary evidence also exists for the second hypothesis of Turkewitz and Kenny's (1982) proposition. Based on Schneirla (1965), they proposed that disruption of a modality necessary for the initial development of an "organizational framework" for a behaviour might adversely affect the subsequent level of competence of that behaviour even in response to signals in other modalities (Burnstine et al., 1984). An important assumption of this model is that disruption would presumably be most effective early in ontogeny, before an organizational framework is fully established. The evidence for this hypothesis comes primarily from studies of spatial behaviour.

Spigelman demonstrated that early-blinded rats performed more poorly than sighted or late-blinded rats in an auditory localization task (Spigelman, 1969; Spigelman & Bryden, 1967). Similar results have been found for performance on the Hebb-Williams maze (Hebb, 1947). Tees, Midgley, and
Nesbit (1981) also found that dark-rearing had an adverse effect on learning in a 17-arm radial maze. Burnstine et al's (1984) review of the human literature also follows the same theme: early blind are poorer at spatial tasks than late blind or sighted subjects.

Some inconsistencies do exist, however. Gamboni (1964) found that dark-reared rats perform better on a Krech hypothesis maze than light-reared controls. Also, Sutherland and Dyck (1984) found that early blinding led to improved learning of an auditory version of the Morris (1981) water maze. Finally, Meyer, Feo Ramos, and Ferres-Torres (1976) reported increased dendritic spine density in the CA1 hippocampus and dentate gyrus of dark-reared rats. Both these areas have been implicated in spatial behaviour (O'Keefe & Nadel, 1978).

It is interesting to note that there are virtually no studies concerning the effects of deprivation of modalities other than vision on spatial behaviour. This may be due to the importance most theorists place on vision for the development of spatial abilities (e.g. Gibson, 1969). Also the adverse effects due to visual deprivation seen by some researchers is somewhat contradictory to the hypothesis proposed by Turkewitz and Kenny (1982). In this case, a late developing modality appears to be providing information for earlier ones (Burnstine et al., 1984). Most researchers attribute the effects of visual deprivation on spatial behaviour to the attenuation of cortical development seen in visually deprived animals (see Tees et al., 1979). However,
the hypothesis of Turkewitz and Kenny (1982) is that disruption of an earlier developing system (and, therefore, its organizational framework) should lead to disruptions in later developing systems. While it certainly may be the case that appropriate visual functioning is the necessary precursor to normal spatial behaviour, no systematic study of the effects of earlier developing modality restriction on spatial behaviour has been performed.

Another aspect of intermodal competition that has not been systematically explored is the role that behavioural demand might play (Burnstine et al., 1984). In most of the animal studies, the animals were reared in relatively environmentally impoverished conditions. As Burnstine et al. (1984) note, the laboratory cage does not correspond very well with the complex world encountered by deaf or blind humans. Behavioural demand is an important requisite of normal sensorimotor development (Hein, 1980; Held and Hein, 1963). As well, increased demand, through environmental enrichment, has significant effects on cortical cell development (Greenough & Green, 1981), overall brain size, and cortical activity (Rosenzweig & Bennett, 1978). These effects occur only after actual behavioural interaction with the enriched environment. Ferchmin, Bennett, and Rosenzweig (1975) found no significant cortical activity differences between animals placed inside enclosures in enriched environments and normally cage reared animals.

There is some evidence that behavioural demand may play a role in intermodal competition. Krech, Rosenzweig, and
Bennett (1963) found that neonatally blinded rats raised in complex environments had a heavier somesthetic cortex and increased acetylcholinesterase activity in non-visual cortical areas than sighted rats raised in similar environments. The behavioural significance of this result is speculative, but given the evidence from other sources that environmental enrichment leads to improved performance in a variety of tasks (e.g. Forgus, 1954; Greenough, Madden, & Fleischmann, 1972; Juraska, Henderson, and Muller, 1984), it seems likely that the effects found by Krech et al. (1963) may be of some functional importance. Interestingly, Krech et al (1963) also found that the enucleated enriched, animals had heavier visual cortices than the restricted, non-sighted controls. This finding suggests that some 'functional reallocation' (Burnstine et al, 1984) may be occurring. The visual areas may be processing information from other modalities. Finally, Burnstine et al. (1984) reported an unpublished study that found that blinded mice raised in enriched environments showed a whisker-triggered placing response at a further distance than sighted controls.

Rationale

The evidence for the modality-interdependence model proposed by Turkewitz, Gilbert, and Birch (1974) and Turkewitz and Kenny (1982) is suggestive but incomplete. The present study is a direct test of the two main hypotheses arising from this model: 1) that early restriction of one
modality will lead to compensation (Burnstine et al., 1984) in another modality; and 2) that early restriction of sensory input in one modality might disrupt the 'organizational framework' of a behaviour that is required for appropriate subsequent competence in another modality.

The test involves examining the effects of early tactile restriction through disruption of the mystacial vibrissae of rats. Vibrissae are present in all rodents and many other mammals, suggesting its important contribution to the fitness of these species. As mentioned previously, the mystacial pad is the single largest part of the somatotopic map of the somatosensory cortex of the rat (Keramidas, 1976), and the vibrissae tactile system is highly organized at all levels of projection from the periphery to the cortex (Welker, 1971; 1976). These facts illustrate the extreme (albeit poorly understood) importance of this system to the rat. Given this evidence, the excellent physiological evidence and the fragmentary behavioural evidence, it seems likely that disruption of this system would have important consequences for developing rats.

Also, the tactile system is the earliest emerging sensory modality (Gottlieb, 1971). Thus, disruption of this system directly examines the second (i.e. 'organizational framework') hypothesis of Turkewitz and Kenny (1982). Presumably, if disruption of the tactile system hinders the development of some framework (e.g. for spatial behaviour--Bogardus & Henke, 1911) then performance in subsequently emerging modalities should be impaired. Also, since it is
established that peripheral tactile restriction leads, at the very least, to abolished neural activity (Simons & Land, 1987), it seems likely that this manipulation will give other modalities a 'competitive advantage' if the intermodal-competition hypothesis is tenable.

In accordance with the speculations of Burnstine et al. (1984), the present study also examines the role of behavioural demand in intermodal competition. Behavioural demand is augmented by allowing some animals daily access to an enriched environment. Finally, a preliminary examination is made of the behavioural consequences of tactile restriction resulting from receptor disruption (by follicular cauterization) as opposed to restriction of tactile input (by long-term clipping).

In order to assess the consequences of these manipulations, a battery of tests was used. The advantages of such an approach have been outlined previously (Kolb & Whishaw, 1983; Whishaw, Kolb, & Sutherland, 1983) and its effectiveness illustrated in the work of these researchers in their assessment of the effects of brain damage in rats. Briefly, the premise of such an approach is that several different tests of behaviours that animals are likely to engage in spontaneously are more likely to yield interpretable results than would a single test. The present study employed five tasks.

1. A task developed by Midgley and Tees (1981; 1983) to assess orientation to visual stimuli was used as a test of the
intermodal-competition hypothesis. This task measures habituation to the repeated presentation of visual stimuli and dishabituation to subtle changes in these stimuli. Performance on this task appears to be mediated by attentional factors rather than processing capabilities—dark-reared rats do show orientation to the visual stimuli, but habituate more quickly and are less likely to dishabituate to stimulus changes (Midgley & Tees, 1983). It has been suggested that intermodal compensation is most likely to be an attentionally based phenomenon rather than an actual augmentation of processing capabilities (Burnstine et al, 1984; Tees, 1976). Thus, this task is an excellent measure of potential visual compensation for tactile restriction. As well, this task examines visually-guided orientation solely, excluding the use of other cues (e.g. auditory, tactile) that may have confounded other studies of intermodal competition (Turkewitz, Gilbert, & Birch, 1974).

2. The 'organizational framework' hypothesis of Turkewitz and Kenny (1982) was examined by testing spatial behaviour using the water maze developed by Morris (1981). In this task animals are required to find a submerged platform hidden in a pool full of water using available distal or proximal cues (Kolb & Walkey, 1987; Sutherland and Dyck, 1984). Variations of this task have been used to test the ontogeny of spatial behaviour (Rudy, Stadler-Morris, & Albert, 1987) and the effects of various brain lesions (Morris, 1983; Kolb & Walkey, 1987). Again, this task is entirely visually
based, thus accurately assessing any differences in visual spatial behaviour due to tactile restriction.

3. A puzzle latch box was used to assess the fine motor behaviours of the tactile-restricted animals. In this task, the animals are required to open latches of various types in order to receive a food reward. This task has been used previously as a measure of brain damage effects (Gentile, Green, Nieburgs, Schmelzer, & Stein, 1978; Kolb & Whishaw, 1983).

4. Another test of sensorimotor control, as well as a measure of laterality, is the bracelet test developed by Schallert and his colleagues (e.g. Schallert & Whishaw, 1984). In this task, pieces of wire are tied to the wrists of the rats, and their reactions to it are recorded. Performance on this task has been shown to be sensitive to cortical damage (Schallert & Whishaw, 1983) and is also used here as an assessment of tactile reactivity.

5. Orientation to snout contact was also used as a measure of tactile responsiveness. SC lesions impair performance on this task (Kirvel, Greenfield, & Meyer, 1974), thus this test was used as a measure of the efficacy of the tactile restriction techniques. As well, a second related test of tactile reactivity was administered. In normal rats, a sharp tap to the mystacial pad evokes an eye-flinch response. This test was used to determine differences between general
tactile sensitivity and orientation to tactile stimuli.
Methods

Subjects

The subjects were 88 male rats of the Long-Evans (Rattus Norvegicus) strain, born and reared in the Biopsychology colonies at the University of British Columbia. The general rearing conditions have been described previously (Tees, 1968). The rats were all raised in 25 x 47 x 20 cm plastic maternity bins until 21 days of age at which time they were placed in groups of 4 to 6 in hanging wire mesh cages (66 x 25 x 18 cm). Food (Purina Rat Chow) and water were available ad libitum until the time of testing. All rats remained on a 12:12 hr light/dark schedule throughout the experiment, and all testing was performed during the rats' light cycle. At the time of testing the rats were separated and housed individually in hanging wire mesh cages (20 x 25 x 18 cm). The rats were between 350 and 600 g at the time of testing.

Surgery

One half of the rats underwent complete removal of their mystacial vibrissae shortly after birth. In order to ensure that vibrissae removal occurred before the initial development of the posteromedial barrel field, all of the experimental rats were operated on within 3 days of birth (Keramidas, 1976). Two manipulations were performed: (1) plucking of the vibrissae or (2) cauterization of the
vibrissae follicles. Assignment to each condition was determined by litter, and at least three litters were randomly assigned to each condition. All rats were separated from their dams and anaesthetized with a combination of cold (ice) and Halothane vapour. The rats were maintained on ice during surgery. For the plucked group, the vibrissae were located with a dissecting microscope and individually pulled from the follicles. For the cauterization groups, each vibrissa was located, and a thin (98 micrometer) wire connected to a dc lesion maker (Grass) was inserted into the follicle. The follicle was lesioned using a 150 V current with an intensity of 2 ma (Van Der Loos & Woolsey, 1973). The wire represented the positive source while the plate the rat rested on during the surgery was the negative source. Control rats were treated in a similar manner; however, in the case of the 'cauterization controls', a similar current was passed through the upper snout or pinnae of the rats.

The plucking procedure typically inhibited regrowth of vibrissae in the young rats for approximately 1 week. At this time, in order to avoid repeated anaesthetization, the rats' vibrissae were shaved using an Oster small animal shaver with a size 40 head. Shaving continued twice weekly until the time of testing.
Environments and Rearing Conditions

Starting at the age of 21 days, the litters assigned to the enriched condition were given daily access in groups of 7 to 12 for 1 to 2 hours to an elaborate open field. This daily period of enriched environment exposure has been reported to have an effect equivalent to continuous exposure, at least in terms of some brain size measures (Rosenzweig, Love & Bennett, 1968). The open field was a tall, wire-mesh box (180 x 92 x 62 cm) with a Sanicel-covered floor and two Sanicel-covered bridges located approximately 19 and 39 cm above the bottom. Wire-mesh ramps connected the bridges with one-another and with the bottom of the apparatus. The open field was filled with an assortment of toys some of which were changed daily (cf Greenough and Green, 1981). The control rats were also handled daily and maintained in normal group cages.

Design and Behavioural Tasks

The general design of the study was a 2 x 2 x 2 factorial. The two environment types (enriched and normal) represented one factor, tactile restriction (vibrissae present or absent during development) the second factor, and type of restriction (receptor destruction vs tactile restriction by clipping) the third. The number of subjects in each group is shown in Table A. The five tasks chosen
Table A. The number of subjects assigned to each condition.
<p>| | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Enriched</td>
<td>9</td>
</tr>
<tr>
<td>Cauterized</td>
<td></td>
</tr>
<tr>
<td>Enriched</td>
<td>7</td>
</tr>
<tr>
<td>C. Controls</td>
<td></td>
</tr>
<tr>
<td>Enriched</td>
<td>11</td>
</tr>
<tr>
<td>Plucked</td>
<td></td>
</tr>
<tr>
<td>Enriched</td>
<td>14</td>
</tr>
<tr>
<td>P. Controls</td>
<td></td>
</tr>
<tr>
<td>Normal</td>
<td>9</td>
</tr>
<tr>
<td>Cauterized</td>
<td></td>
</tr>
<tr>
<td>Normal</td>
<td>18</td>
</tr>
<tr>
<td>C. Controls</td>
<td></td>
</tr>
<tr>
<td>Normal</td>
<td>11</td>
</tr>
<tr>
<td>Plucked</td>
<td></td>
</tr>
<tr>
<td>Normal</td>
<td>9</td>
</tr>
<tr>
<td>P. Controls</td>
<td></td>
</tr>
</tbody>
</table>
tested a variety of perceptual and motor behaviours. In order to avoid a possible sequencing effect confound, rats in all groups proceeded through the tasks in the same order. The order of task presentation was as follows.

Apparatus and Procedure

Visual Orientation Task

The apparatus used to examine visual orientation behaviour has been described previously (Midgley & Tees, 1981, 1983) and is presented in Figure 2. Nine 4.7 mm diameter green light-emitting diodes (LEDs) were positioned in an arc 12 cm above the floor of the apparatus. All of the LEDs were 9 cm from the tip of the metal water spout subtending an arc of 130 degrees from this point. The water spout was attached to the center of the Plexiglas panel, at 5 cm above the brass rod floor. The light intensity of the LEDs at the spout was approximately 4.8 cd/m². The entire apparatus was housed within a 66.2 x 66 x 50.8 cm light- and sound-attenuating box with a ventilation fan that produced 60 dB (SPL) background noise.

The presentation of lights and the counting of the number of licks was controlled by an Comtex PC XT microcomputer using a QNX operating system. A computer program written in C language monitored the licking and presented the visual stimuli through a 96-line digital IO board. Water was presented through a metal tube, which was
Figure 2. Diagram of the apparatus used to test visual orientation.
Figure 3. Schematic of the presentation of visual stimuli during the 30 trials in the visual orientation task.
TRIALS 1-10

ON
LEDS
OFF

TRIAL N 15 LICKS 5 SEC BASELINE 5 SEC TEST TRIAL N+1

TRIALS 11-20

ON
LEDS
OFF

TRIAL N 15 LICKS 5 SEC BASELINE 5 SEC TEST TRIAL N+1

TRIALS 21-30

ON
LEDS
OFF

TRIAL N 15 LICKS 5 SEC BASELINE 5 SEC TEST TRIAL N+1
connected by a rubber tube to a teflon solenoid valve. (General Valve Corp.). Each lick completed a circuit that opened the valve for 0.1 secs allowing approximately 0.02 ml water to pass from a reservoir into the tube and registered the lick with the computer.

Five days prior to testing, the rats were water deprived for 24 hr and then individually allowed 15 min access to the apparatus with the lick tube circuit connected. During this acclimatization period, the LEDs were disconnected. After each acclimatization period the rats were returned to their home cages and given an additional 15 min access to water. The rats were acclimatized for three days and were then tested (Midgley & Tees, 1983).

Testing consisted of three blocks of ten trials. Each trial began with the rat making 15 licks to initiate a 5 s baseline period. During this baseline period, the number of licks was recorded. The fifteenth lick following the baseline period initiated the display of lights for 5 s. The number of licks was also counted during this 5 s test period (see Fig. 3 for schematic). The nine lights (solid display) were turned on for the entire 5 s on trials 1 to 10. On trials 11 to 20 the lights flickered on and off every 0.1 s (rapidly flickering display). The lights flickered on and off every 0.2 s (slowly flickering display) on trials 21 to 30. This pattern of displays was chosen because it had previously been shown to be the most subtle in terms of habituation and recovery of orientation (Midgley & Tees, 1983). Thus, it is less likely that these displays would
produce a floor effect and more likely that differences in orientation might be found.

Orientation to the light displays was determined by the suppression of ongoing licking during the presentation of the stimuli. Suppression ratios were calculated using the formula: TEST LICKS / (TEST LICKS + BASELINE LICKS). TEST LICKS was the number of licks during the 5 s "stimulus on" phase of a trial and BASELINE LICKS is the number of licks during the preceding 5 s "stimulus off" baseline phase. Thus a value of zero indicated complete suppression of licking, while a value of 0.5 represented no suppression.

Rate of habituation and recovery of orientation to the light display was determined by analysing the number of trials in which the number of licks during the test period represented 10% or less than the number of licks during the previous baseline period. The number of trials in which this criterion was met for each of the three sets of ten trials represented the number of trials for each stimulus (i.e. solid display, rapid flashing, slow flashing) that the rats oriented to the stimulus.

**Spatial Memory Task**

Spatial memory was evaluated using a variation of the water-maze procedure developed by Morris (1981). The apparatus consisted of a circular plastic pool (Coleco) with a diameter of 1.3 m and a height of 28cm. The pool was filled to 21 cm with cool water (approximately 22 C) rendered
opaque with black watercolour paint powder (Alphacolor). The platform was a large plastic jar 19 cm tall and 9 cm in diameter at the lid, covered in black plastic film. Painted wire mesh was attached to the top of the jar and the jar was filled with stones for weight. A blue racquet ball (Deuce Court) painted with white stripes was used as a proximal cue and was attached by a 20 cm string to a sheet-metal anchor. This allowed the cue to be placed on the platform or to float freely depending on the nature of the trial. The entire apparatus resided in an IAC sound attenuating chamber (Model 402-A) with a number of conspicuous distal cues available.

The testing consisted of 16 trials conducted over 3 days. On the first day, each rat was given two 90-s habituation trials with no platform or cue present. On the second day testing began. The second day consisted of eight trials (see Table B for a summary of the trials). For the first four trials, the platform was located in quadrant I (see top of Table B) and the proximal cue was placed on top of it. On trials 5 and 6, the cue was placed in quadrant III while the platform remained in quadrant I. And on trials 7 and 8 the platform was moved beneath the cue in quadrant III.

On the second day test trials 9 to 14 were run. Trials 9 and 10 were a replication of trials 7 and 8 after a 24 hour retention interval. On trials 11 and 12 the cue was removed form the pool. And on trials 13 and 14, the platform was moved to quadrant IV.

The rats were released on each trial from one of the four poles in a pseudorandom sequence. Escape latency in
Table B. Description of the trials in the water maze task. 
Cue position and platform position are described. 
A schematic drawing showing the quadrant positions appears in upper right corner.
<table>
<thead>
<tr>
<th>Trial #</th>
<th>Trial Type</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>C1/P1</td>
<td>Cue located on top of platform in quadrant 1.</td>
</tr>
<tr>
<td>2</td>
<td>C1/P1</td>
<td>Cue located on top of platform in quadrant 1.</td>
</tr>
<tr>
<td>3</td>
<td>C1/P1</td>
<td>Cue located on top of platform in quadrant 1.</td>
</tr>
<tr>
<td>4</td>
<td>C1/P1</td>
<td>Cue located on top of platform in quadrant 1.</td>
</tr>
<tr>
<td>5</td>
<td>C3/P1</td>
<td>Cue located in quadrant 3. Platform located in quadrant 1.</td>
</tr>
<tr>
<td>6</td>
<td>C3/P1</td>
<td>Cue located in quadrant 3. Platform located in quadrant 1.</td>
</tr>
<tr>
<td>7</td>
<td>C3/P3</td>
<td>Cue located on top of platform in quadrant 3.</td>
</tr>
<tr>
<td>8</td>
<td>C3/P3</td>
<td>Cue located on top of platform in quadrant 3.</td>
</tr>
<tr>
<td>9</td>
<td>C3/P3</td>
<td>Cue located on top of platform in quadrant 3. 24 hour delay from T8.</td>
</tr>
<tr>
<td>10</td>
<td>C3/P3</td>
<td>Cue located on top of platform in quadrant 3.</td>
</tr>
<tr>
<td>11</td>
<td>-/P3</td>
<td>No Cue. Platform located in quadrant 3.</td>
</tr>
<tr>
<td>12</td>
<td>-/P3</td>
<td>No Cue. Platform located in quadrant 3.</td>
</tr>
</tbody>
</table>
seconds was recorded. It was also noted whether or not the rats touched the cue during trials 5 and 6, when the cue was located in an "incorrect" quadrant.

When a rat encountered the platform, it was permitted to remain there for 60 s. If the platform was not located within 90 s, the rat was removed and given a score of 90 s. The rats were run individually in squads of 3 to 6.

This sequence of trials allowed the testing of a number of different aspects of spatial memory and perception. First, trials in which the cue was present tested the rats' attention to local and distal visual aspects of the environment. The shifting of the cues tested the rats' reliance on the local cue for finding the platform. The 24-hr delay represented a test of long-term retention, and the repositioning of the platform tested the extent to which distal visual cues were being utilised to complete the task.

**Manipulatory Behaviour**

Fine motor control was assessed using a latch box similar to that used by Gentile, Green, Nieburgs, Schmelzer, and Stein (1978) and Kolb and Walkey (1987). The apparatus was a 43 x 25 x 18 cm hanging "double" wire cage with a Plexiglas partition mounted at 16 cm of the length. A hinge-mounted 9 x 8 cm Plexiglas door was located in the centre of the partition. On this door a variety of latches could be mounted (see below). In the smaller section of the box a small food dish was located.
The rats were food deprived for 24 hr before testing and were given sufficient food each day to maintain 85 percent of their normal body weight. The testing consisted of four phases. The first phase was a pretraining period during which the rats were adapted to the apparatus and their behaviour shaped to push open the Plexiglas door to receive a Honeynut Cheerio (General Foods) reward. Once the rats reliably opened the door within 10 s, testing commenced.

The remaining three phases of testing consisted of latch manipulation. The first latch was a butterfly wing-nut (see Fig. 7). A downward or upward displacement of the latch by 2 cm opened the door. The next phase involved a bolt latch which required a sideward movement of the bolt or handle to open the door. The final latch was a butterfly latch similar to the first except that it was partially covered with a 8 x 5 cm piece of Plexiglas. Only the end of the latch was manipulable by the rats.

On each trial, the rats were required to open the door within 120 s to gain access to the Cheerio reward. The rats were required to complete 5 trials in one day in order to move on to the next latch. The rats were run individually in their colony room. Total duration of manipulation of the door or latch was used as the primary dependent variable rather than latency to open the door (cf. Kolb & Walkey, 1987), since it represented a more accurate measure of the rats' motor behaviour. As well, the predominant method of manipulating the latch (i.e. by snout, mouth or paws) was also recorded.
Sensorimotor Tasks

Bracelet Test

Two tasks were used to assess the sensorimotor abilities of the rats. The first task, the wrist-bracelet test, is a derivation of the dot test used by Schallert and his colleagues (e.g. Schallert & Whishaw, 1984). The task was used as a measure of sensorimotor asymmetry as well as a general measure of tactile reactivity and fine manipulatory abilities.

All rats were individually tested in their home cages. Each rat was removed from the cage and 8 cm pieces of 22 ga. wire were tied around each wrist using half-hitch knots. The wires were tied tightly enough to prevent them from falling off easily and the ends of the wire were cut nearly flush to the knot. The rats were then returned to their home cages. Latency to contact the wires, side of first contact, total duration required to remove one of the wires and the side of first removal were all recorded. If the wire was not removed within 4 min, the rat was given a score of 240 s and the trial was terminated.

Snout Contact Orientation

The second task—a measure of orientation to snout
contact (Whishaw, O'Connor & Dunnett, 1985)--is also a measure of tactile responsiveness and was used as an assessment of the efficacy of the tactile deprivation techniques.

All rats were tested individually in dim red light (Kodak safelight filter No. 16). Each rat was taken from its home cage and placed in a 40 x 48 x 20 cm plastic bin in the testing room. After a 1-min habituation period, the rat's snout was touched with a cotton-tipped surgical swab. Six trials were run and the number of orientations to the probe was recorded. At the end of the six trials, the rat was held by the experimenter and tapped sharply on the mystacial pad with a surgical swab, and eye-flinch responses were recorded.

Results

Visual Orientation Task

A repeated measures ANOVA was performed on the suppression ratio data generated by the eight groups of rats across the 30 presentations of visual stimuli. This analysis revealed a significant Rearing Environment x Surgery x Vibrissae interaction, $F(1,80)=4.01$, $p<.05$. As well, a significant Trials effect was found, $F(29,2320)=30.14$, $p<.01$. No other significant effects were observed. A summary of the suppression ratios for all groups is found in Fig. 4. Unfortunately, the variances of the suppression ratio data was heterogeneous across group thus making these repeated-
Figure 4. Mean suppression ratios for rats in all conditions. Trials 1 to 10: solid display. Trials 11 to 20: rapidly flashing display. Trials 21 to 30: slowly flashing display. A suppression ratio of zero indicates complete suppression of licking whereas a suppression ratio of .5 represents no suppression of licking.
Table C. Mean number of trials in which orientation occurred for the three visual stimuli. Solid display in trials 1 to 10; rapidly flashing display in trials 11 to 20; slowly flashing display in trials 21 to 30.
<table>
<thead>
<tr>
<th></th>
<th>Trials 1-10</th>
<th>Trials 11-20</th>
<th>Trials 21-30</th>
</tr>
</thead>
<tbody>
<tr>
<td>Enriched</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cauterized</td>
<td>5.24</td>
<td>1.22</td>
<td>0.78</td>
</tr>
<tr>
<td>Enriched C. Controls</td>
<td>3.00</td>
<td>0.29</td>
<td>0.57</td>
</tr>
<tr>
<td>Enriched Plucked</td>
<td>4.09</td>
<td>0.364</td>
<td>0.55</td>
</tr>
<tr>
<td>Enriched P. Controls</td>
<td>3.93</td>
<td>1.00</td>
<td>0.50</td>
</tr>
<tr>
<td>Normal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cauterized</td>
<td>3.00</td>
<td>0.78</td>
<td>0.56</td>
</tr>
<tr>
<td>Normal C. Controls</td>
<td>3.94</td>
<td>0.89</td>
<td>0.33</td>
</tr>
<tr>
<td>Normal Plucked</td>
<td>4.09</td>
<td>1.01</td>
<td>0.36</td>
</tr>
<tr>
<td>Normal P. Controls</td>
<td>4.12</td>
<td>0.67</td>
<td>0.44</td>
</tr>
</tbody>
</table>
measures ANOVA results somewhat suspect. Thus, the further analysis of the number of trials in which significant orientation based on the criterion of test licks being less than 10% of baseline licks was used to analyse habituation and dishabitation to the three stimulus patterns.

In this regard, a summary of the trials on which statistically significant interruption of licking occurred is found in Table C. An analysis of variance of these data found a significant effect for display pattern, ($F(2,160)=129.8$, $p<.01$), as well as a significant Rearing Environment x Surgery x Vibrissae interaction, $F(2,160)=3.12$, $p<.05$). As can be seen on this Table and in Fig. 4, the number of trials in which significant suppression of licking occurred differed according to group. Most notably, the enriched/dewhiskered/cauterized rats appeared to be more attentive to the LED displays than rats in the other groups. Post-hoc analysis of these data (Tukey's) indicated that the enriched/dewhiskered/cauterized rats oriented on significantly more trials than any of the other groups to the presence of the solid display of lights in the first 10 trials ($p<.05$). No other significant difference was found.

**Spatial Behaviour: Water Maze Task**

A repeated measures ANOVA was used to assess the significance of differences in escape latencies between the eight groups of rats across the 14 test trials. Long-term dewhiskering, by cauterization or by plucking, had no effect
on spatial behaviour as measured by the water maze task, $F(1,72)=.307, p>.05$. However, a significant main effect for Trial ($F(13,936)=27.05, p<.01$) as well as a Rearing Environment x Trial interaction ($F(13,936)=1.992, p<.05$) were observed. No other significant effects were found. The data for all groups are summarized in Fig. 5.

Post-hoc testing revealed that, overall, the enriched rats had significantly faster escape latencies on trials 1, 5, 7, and 8 and a slower escape latency on trial 13 than did the normally reared rats (Tukey's HSD, all $p$'s <.05) (see Fig. 6 for a summary of the data based on rearing environment). It appears that the normally reared rats were disrupted by the movement of the cue to the quadrant opposite the platform on trials 5 and 6. This effect is corroborated by an analysis of the percentage of rats that made contact with the cue placed in the "incorrect" quadrant on trials 5 or 6. Significantly more normally reared rats contacted the cue on trials 5 or 6 than did enriched rats, $X^2(1)=8.851, p<.01$ (see Table D). The probability of touching the cue did not vary with any other factor.

The normally reared rats were significantly disrupted on trials 7 and 8. On these trials the platform was shifted from the quadrant without the cue to the quadrant with the cue. Finally, the enriched rats were more disrupted by the "probe" trial (trial 13) than the were normally reared rats. This could be viewed to be a result of their perseveration of searching the formerly correct quadrant (quadrant 3).
Figure 5. Latency to find the submerged platform on each trial for all conditions.
Figure 6. Latency to find the submerged platform on each trial for all enriched and normally reared rats.
TRIAL
CUE POSITION/PLATFORM POSITION

MEAN ESCAPE LATENCY (SECS)

- ENRICHED
- NORMAL

0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
1/1 1/1 1/1 1/1 3/1 3/1 3/3 3/3 3/3 -3 -3 -3 -4 -4

49
Table D. Percentage of enriched and normally reared rats that contacted the cue in the "incorrect" quadrant on trials 7 and 8.
<table>
<thead>
<tr>
<th>Touched cue</th>
<th>Enriched</th>
<th>Normal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>29.41%</td>
<td>63.04%</td>
</tr>
<tr>
<td>Did not touch cue</td>
<td>70.59%</td>
<td>36.96%</td>
</tr>
</tbody>
</table>

**REARING ENVIRONMENT**
Puzzle Latch Box

The latency of the rats to open the each of the three latches was analysed using a repeated-measures ANOVA. All three latches were learned relatively quickly by all rats. An effect for Latch Type ($F(2,138)=64.68, p<.01$) as well as an interaction between Rearing Environment and Surgery ($F(1,69)=11.37, p<.05$) and a Latch x Surgery interaction ($F(2,138)=3.73, p<.05$) were found. Post-hoc comparisons (Tukey's HSD) found the enriched/dewhiskered/cauterized rats and their controls took significantly longer to open the door with the bolt latch than did any of the other groups (see Fig. 7, panel B). The results for all three latches are summarized in Fig. 7.

The method of manipulation used to open the latches was entirely dependent upon the type of latch being used and did not vary with any of the experimental factors (see Table E for summary). The snout was used predominantly for opening the butterfly latch and the shielded butterfly latch, while the mouth was used for the bolt latch. Based on these results, it seems unlikely that the presence of vibrissae during development is necessary for fine manipulations of the kind measured by the puzzle latch box.

Bracelet Test

An analysis of variance was used to analyse each of the four measures generated from the rats' reactions to wire
Figure 7. Latencies in seconds to open latches. "ENRICHED" and "NORMAL" refer to rearing environment; "C" and "P" refer to cauterized surgical procedure and plucked surgical procedure respectively.
Table E. Method of manipulation used to open the three latch types. A=butterfly latch; B=bolt latch; C=shielded butterfly latch--see Fig. Numbers represent percentage of rats using that manipulation.
### Method of Manipulation

<table>
<thead>
<tr>
<th></th>
<th>Snout</th>
<th>Mouth</th>
<th>Paws</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>57%</td>
<td>14%</td>
<td>29%</td>
</tr>
<tr>
<td>Enriched B</td>
<td>14%</td>
<td>57%</td>
<td>28%</td>
</tr>
<tr>
<td>Cauterized C</td>
<td>71%</td>
<td>14%</td>
<td>15%</td>
</tr>
<tr>
<td>A</td>
<td>60%</td>
<td>20%</td>
<td>20%</td>
</tr>
<tr>
<td>Enriched B</td>
<td>20%</td>
<td>40%</td>
<td>40%</td>
</tr>
<tr>
<td>C. Controls C</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>A</td>
<td>37%</td>
<td>0%</td>
<td>62%</td>
</tr>
<tr>
<td>Enriched B</td>
<td>25%</td>
<td>25%</td>
<td>50%</td>
</tr>
<tr>
<td>Plucked C</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>A</td>
<td>58%</td>
<td>8%</td>
<td>34%</td>
</tr>
<tr>
<td>Enriched B</td>
<td>42%</td>
<td>25%</td>
<td>33%</td>
</tr>
<tr>
<td>P. Controls C</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>A</td>
<td>90%</td>
<td>0%</td>
<td>10%</td>
</tr>
<tr>
<td>Normal B</td>
<td>20%</td>
<td>40%</td>
<td>40%</td>
</tr>
<tr>
<td>Cauterized C</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>A</td>
<td>37%</td>
<td>13%</td>
<td>50%</td>
</tr>
<tr>
<td>Normal B</td>
<td>35%</td>
<td>47%</td>
<td>17%</td>
</tr>
<tr>
<td>C. Controls C</td>
<td>89%</td>
<td>0%</td>
<td>11%</td>
</tr>
<tr>
<td>A</td>
<td>67%</td>
<td>0%</td>
<td>33%</td>
</tr>
<tr>
<td>Normal B</td>
<td>22%</td>
<td>56%</td>
<td>22%</td>
</tr>
<tr>
<td>Plucked C</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>A</td>
<td>44%</td>
<td>11%</td>
<td>45%</td>
</tr>
<tr>
<td>Normal B</td>
<td>0%</td>
<td>56%</td>
<td>44%</td>
</tr>
<tr>
<td>P. Controls C</td>
<td>100%</td>
<td>0%</td>
<td>0%</td>
</tr>
</tbody>
</table>
Figure 8. Panel A: Latency to contact the wire bracelets.

Panel B: Latency to remove one of the wire bracelets. "ENRICHED" and "NORMAL" refer to rearing environment; "C" and "P" refer to cauterized surgical procedure and plucked surgical procedure respectively.
bracelets. The four measures were: (1) latency to contact one of the wires; (2) latency to remove one of the wires; (3) the paw initially contacted; (4) and the paw from which the first wire was removed. The only significant effect found was a main effect for Surgery type on the Contact Latency measure, $F(1,76)= 4.10, p<.05$. The dewhiskered cauterized rats and their controls had a significantly longer latency than the plucked rats and their controls (Cauterized mean=8.31 s; Plucked mean=5.44 s). The contact latency and removal latency data are summarized in Fig 8. Based on these data, it appears that long-term dewhiskering plays no role in the fine motor behaviours involved in removing the wire bracelets.

**Snout Contact Orientation**

An analysis of variance was performed on the frequency of orientations across 6 trials to a light tap on the snout with a surgical swab. Long-term dewhiskering, whether by plucking or cautery, had a significant and disruptive effect on orientation to contacts of the snout. As shown in Fig. 9, the dewhiskered rats in all conditions oriented significantly less to snout contacts than did any of the control rats ($F(1,76)=36.48, p<.01$). No significant interactions were observed. This effect does not appear to be due to a loss of all tactile capabilities; all rats exhibited eye-flinch responses when tapped sharply on the snout.
Figure 9. Frequency of orientations to light taps on the snout with a surgical swab according to condition. "ENRICHED" and "NORMAL" refer to rearing environment; "C" and "P" refer to cauterized surgical procedure and plucked surgical procedure respectively.
DE WHISKERED
CONTROL

MEAN
FREQUENCY OF ORIENTATIONS
(6 TRIALS)

ENRICHED NORMAL

DEWHISKERED
CONTROL
Discussion

One of the purposes of the present study was to examine the intermodal consequences of early, long-term somatosensory restriction and some of the factors that might effect them. As mentioned previously, there are numerous theoretical arguments (e.g. Gottlieb, 1971) to suggest that intermodal effects would be found. A related goal of the present investigation was to broadly test the motoric and perceptual effects of this early, long-term dewhiskering in rats. It was hoped that observing the effects of the manipulations of sensory experience on a battery of tests (Kolb and Whishaw, 1983) would increase our understanding of the role that the mystacial vibrissae play for rats in their interactions with their environments.

Limited evidence for modality interdependence was found. Long-term dewhiskering through cauterization led to increased orientation to visual stimuli. This only occurred for those animals given access to an enriched sensory environment during rearing. This finding is consistent with two hypotheses about early experience and perceptual development: 1) decreased competition during development from an early developing system (in this case, the somatosensory system) leads to increased competency in a later emerging system—in this case vision (Burnstine et al, 1984; Turkewitz & Kenny, 1982); and 2) that behavioural demand is a significant factor in the determining the impact of early somatosensory restriction on this competency (Burnstine et al, 1984). As
well, given in part the nature of this visual orientation task, and the finding that animals in all conditions habituate to repeated presentations of the visual stimuli, these data best support the contention that the compensation seen here is primarily a shift in attentional rather than processing capabilities (Burnstine et al, 1984; Tees, 1976).

An interesting aspect to this observation is that no effect was found for the animals given access to an enriched environment but whose vibrissae were merely plucked during development. As mentioned previously, while this procedure does not appear to disrupt the cytoarchitectonic structure of cortical neurons related to the vibrissae receptors (Weller & Johnson, 1975), it does abolish electrophysiological responding of these same cortical cells (Simons & Land, 1987). Parenthetically, as data from the Snout Contact Orientation task in the present study indicate, long-term plucking does attenuate orientation to tactile cues providing behavioural evidence that this manipulation does have some specific intramodal consequences. However, it appears from the results of the visual orientation task that even though the cortical units corresponding to the vibrissae are presumably unresponsive, they are still providing some kind of intermodal influence with respect to the visual system.

There are some differences between the results of the study and those found in previous work using this visual orientation paradigm (e.g. Midgley & Tees, 1983). In previous studies, significant dishabitation was observed in normal light-reared animals with the shift from the solid
display to the rapidly flashing display on trial 11. In the present study, no reliable dishabituation was observed on trials 11-20. This is most likely attributable to the differences in intensity of the light displays used in the past and in the present experiment. The illuminance of the LEDs in the display used in the present study was 4.8 cd/m², whereas in the previous work, the light displays have been somewhat brighter—5.25 cd/m² (Midgley & Tees, 1983). As indicated by Midgley and Tees (1983), light intensity of displays can be a significant factor in determining rates of habituation and dishabituation. The less intense displays used in the present study most likely rendered the shifts from display to display less salient than in early reports (e.g. Midgley & Tees, 1983), thus making dishabituation to shifts in the stimuli less likely.

Performance on the water maze was used to examine a second proposal of Turkewitz & Kenny, (1982). Their "organizational framework" proposal stated that if experience related to an earlier developing system is necessary to establish a framework for a behaviour, that is then assimilated by later developing systems, then a reduction in competency related to the later developing system would be expected. In spatial behaviour as assessed by the present version of the water maze, early tactile restriction had no effect on performance. This result can be interpreted in a number of different ways. First, it may be that tactile input is unnecessary for normal spatial behavior. Many authors have suggested that visual input is of primary
importance for appropriate spatial behaviour (Burnstine et al, 1984; Gibson, 1969; Tees et al, 1981). Thus it may be that the "organizational framework" for spatial behaviour is for the most part dependent on appropriate visual capabilities; tactile restriction is of no consequence to spatial behaviours. There is some evidence to support this hypothesis (e.g. Tees et al, 1981).

A second possibility is that since tactual cues or signals are not necessary to solve the water maze problem, tactile restriction might be of no consequence. Early reports (Bogardus & Henke, 1911) espoused the necessity for normal tactile input in appropriate spatial behaviours in rats. Bogardus and Henke (1911) examined acutely dewhiskered animals in an alley-way type maze. Thus, it may be that, in a spatial task that incorporated some potential local tactile cues (e.g. Hebb-Williams maze or radial arm maze), different results might have been found for the long-term dewhiskered animals.

A final possibility is that the water maze is too simple a task for the potentially subtle differences that dewhiskering might be causing. This possibility seems unlikely given the differences found with respect to enrichment. This effect of early rearing environment on water maze performance was to be expected, given the superior performance of enriched animals in other spatial tasks (e.g. Greenough & Juraska, 1979; Juraska et al, 1984). However, a number of interesting results emerged from the use of the version of the water maze task employed in the present study.
Specifically, the manipulation of the local visual cue in the present study had significant effects for the behaviour of the normally reared animals.

First, the normally reared animals were significantly poorer than their enriched counterparts at finding the platform on the first trial. This may be a result of less attention being paid by the normally reared animals to the presence of the local visual cue. Neither the submerged platform nor the cue was present during the pre-trial habituation phase of the study, thus the cue represents a novel visual stimulus on the first trial. It may be that the enriched rats were more attentive to the presence of the cue. Another possibility is that the enriched rats were just more likely to explore or approach the cue; the normally reared animals may also have seen the cue but may have preferred to scrabble against the wall of the pool. Previous research has shown that animals reared in enriched environments tend to be more likely to explore unfamiliar objects (Renner, 1987).

The normally reared animals were disrupted by the shift of the local cue on trial 5 and by its movement to the quadrant with the platform on trial 7 and 8. From these findings, it appears that the normally reared animals were less attentive to the available distal cues in the testing room than the enriched animals. The normally reared animals seemed to be relying on the (presumably) more salient proximal visual cue (i.e. the racquet-ball) than the enriched animals.

The differential performance on the "probe" trial (trial
13) of the animals reared in the two environments provides support for the interpretation that the normally reared animals showed decreased attentiveness to distal cues. The enriched animals were more disrupted by the shifting of the platform to a novel quadrant than the control animals. This appears to be a result of the enriched animals being more likely to perseverate in searching the previously correct quadrant. It may be that the normally reared animals are less likely to perseverate in using distal cues if they don't find the platform and thus switch to a general maze searching strategy earlier than the enriched animals.

The results of the visual orientation task and the water maze provide limited but important evidence of intermodal effects due to long-term tactile restriction. Tactile restriction in combination with access to an enriched environment lead to changes in orientation to repeated visual stimuli but had no effect on spatial behaviour. Thus, the present investigation provides support for the first proposition of Turkewitz & Kenny (1982)--that decreased competition from an early developing system leads to increased competency in a later developing system. However, the present study does not support the "organizational framework" hypothesis of Turkewitz & Kenny (1982). Early tactile restriction played no role in spatial competency, at least in the test used in the present study.

The remaining three tasks (Puzzle Latch Box, Wrist Bracelet Task, and Snout Contact Orientation) were primarily used as assessments of the intramodal effects of long-term
dewhiskering. The results of the Puzzle Latch Box test indicate that fine manipulations of the type necessary for this task do not require the presence of vibrissae during development. The absence of vibrissae appeared to be of no consequence even in cases (e.g. the shielded butterfly latch) where snout use was predominant (see Table E and Figure 7).

However, in most cases, the top of the snout was used to open all the latches, thus it may be that these latch types were not sufficiently challenging to reveal differences due to dewhiskering. Another possibility is that the dewhiskered animals had switched to the use of visual cues to guide their behaviour. This seems unlikely, however, since, for rats, visual cues within 7 cm of their eyes are not in focus (Powers & Green, 1978), and all manipulations occurred at considerably less distance from the rats' eyes.

Dewhiskering also played no significant role in performance on the Wrist Bracelet task. Since the primary method of removal was by chewing the wire, it seems unlikely that vibrissae play an important role in manipulations involving the mouth area. Also, the lack of difference between dewhiskered and control animals in contacting the wire bracelets indicates that there is likely no significant change in tactile sensation in the paw area due to long-term dewhiskering.

Interestingly, no effects were observed with respect to any of the experimental factors in terms of side of first contact or side of first removal. If one assumes this test as a measure of laterality as expressed by
pawedness, then stimulation history appears to play little role in the development of population-based laterality in rats. This idea is not consistent with the hypothesis of Denenberg (1981) that exposure to enriched environments during rearing should increase laterality in rats, strengthening the control of many behaviours in the right hemisphere. This presumably, would lead to an increased incidence in population-based left-pawedness. The present study does not support this hypothesis. First, the enriched animals showed no significant paw preference, neither in first contact nor first removal. Secondly, long-term tactile restriction did not effect paw preference for either of the measures in the present study. This is consistent with previous reports (e.g. Tees, 1984) which indicate that limiting early visual stimulation had no effect on several measures of laterality.

The results of the Snout Contact Orientation Test indicate that the presence of vibrissae during development appear to be important for normal orientation to tactile stimuli. This is true both for animals with receptor destruction (the cauterized animals) and those that had been plucked. This is in accordance with the findings of Simons & Land (1987) that long-term tactile restriction (by shaving) abolishes responding of cortical vibrissae receptor cells; destruction of the peripheral receptors is not necessary for functional disruption of this system.

The results of the final three tasks indicate that vibrissae play little role in fine manipulations involving
the mouth, snout or paws, but are very important in terms of orientation to tactile contact. Since vibrissae activity (i.e. whisking) increases during exploration in rats (Woolsey and Van Der Loos, 1970) it appears likely that they play a significant role in exploration and orientation to tactile stimuli. Given the rats' nocturnal lifestyle and its poor short-range (i.e. less that 7 cm) visual capacities (Powers & Green, 1978), it may be that the vibrissae are used to orient the animal to objects for further olfactory or gustatory investigation.

A comment should be made about the effects of the cauterizing procedure on the behaviour of rats. In the case of the Latch Puzzle Box and the Bracelet task, it was found that the cauterizing procedure significantly disrupted performance. This diminished competency might be due to an increase in the emotionality of the cauterized animals due to the relatively traumatic effect of the surgical procedure. Previous reports (Keramidas, 1976; Vincent, 1912) have indicated that vibrissae removal leads to increased emotionality. Although this alternative explanation might be plausible with respect to the results obtained by the enriched/dewhiskered/cauterized animals in the visual orientation task, this seems unlikely given that the normally reared/dewhiskered/cauterized animals did not respond in a similar fashion.
Conclusions

Gibson (1969) describes the case of a young boy in Boston who has been blind since birth. Although blind, this boy is capable of riding his bike through the streets of Boston without much difficulty. The boy apparently uses auditory cues not only to navigate throughout the city but also, presumably, to avoid various obstacles. An intermodal consequence of early visual deprivation has presumably occurred; the boy has presumably compensated through increased attention to non-visual cues.

While, intermodal compensation after unimodal restriction is the most commonly cited form of modality interdependence (Burnstine et al, 1984), it is not the only form. Modality interdependence can also be said to occur if unimodal deprivation changes performance on a task in which signals involving many modalities may be participating (e.g. spatial behaviour). As well, if competency in one modality for a behaviour is based on the integrity of an "organizational framework" for another modality, then modality interdependence should be demonstrable after disruption of that framework by evidence of reduced competency.

The present study examined both of these propositions concerning modality interdependence. In accordance with past behavioural (e.g. Keramidas, 1976; Turkewitz et al, 1982) and neuroanatomical (e.g. Ryugo et al, 1975) evidence, it was
found that long-term tactile restriction (through dewhiskering) had significant effects for the development of other modalities. Thus, in the examination of the role of experience in the development of perceptual competency, a broad view of the kinds of experience that might be affecting specific competencies must be adopted by developmental psychobiologists interest in the role of experience. Examining the effects of unimodal deprivation on the development of that modality is not sufficient for a complete account of the role experience plays in development.

As well, as the present study demonstrates, the use of several different tasks to assess the behavioural consequences of a manipulation can yield more interpretable findings than the use of a single task. In the present examination, a battery of tests specified which behaviours are most affected by changes in stimulation history, better illuminating the role played by experience in the normal development of vibrissae-environmental interactions of the rat.

The present study, however, is by no means an exhaustive examination; a number of issues still remain to be explored. For instance, the effect of long-term somatosensory restriction on complex social interactions might be explored using a paradigm similar to Whishaw and Tomie (1988), wherein the motor patterns of food stealing and dodging from intruders are examined. As well, other species-specific behaviours such as the defensive burying of dangerous objects (e.g. Pinel and Treit, 1978) might be examined to better
clarify the role vibrissae play in other complex motor behaviours. Finally, it might be interesting to examine the effects of early vibrissectomy on the patterns of emergence of behaviours mediated by other sensory systems. Kenny and Turkewitz (1986) found an interesting shift in the early development of homing behaviour of rats due to premature eyelid opening. Moreover, Moye and Rudy (1985) found that rats early in development exhibit reflex reactions to visual stimuli before they are capable of forming conditioned associations to these stimuli. One might examine the effect of early somatosensory restriction on the emergence of behaviours of this nature.

The presence of the mystacial vibrissae during ontogeny are important to the rat not only in terms of normal somatosensory perception and development but also in terms of the emergence of competencies related to other perceptual systems. While stories of blind, bike-riding boys are bountiful, the present study contributes to a growing but still limited body of laboratory evidence for modality interdependence.
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