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Perceptual context-dependent remodeling of the forepaw map in the SI cortex of rats trained on tactile discrimination

Research report

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Abstract

We combined behavioral assessment of texture discrimination and electrophysiological mapping of concomitant reorganization in the forepaw representation within the SI cortex. Rats were housed in enriched (EE) or impoverished (IE) environments which have been shown to remodel the forepaw map and possibly alter discriminative abilities. In addition, animals were trained to discriminate homogeneous floorboards of invariant roughness from heterogeneous floorboards of gradually decreasing roughness contrasts during locomotion. As reported recently, differences in perceptual abilities were not related to housing conditions, but to a predilection for a floorboard type [Bourgeon S, Xerri C, Coq JO. Abilities in tactile discrimination of textures in adult rats exposed to enriched or impoverished environments. Behav Brain Res 2004;153:217–231]. Consistently, the present study shows that cortical map remodeling resulting from short-duration daily experience can prevail over changes induced by housing conditions. The relative area of glabrous skin representation was related to the discrimination performance and learning abilities in the rats (H) with a predilection for heterogeneous floorboards, i.e. in the animals performing discrimination in the most challenging perceptual context. By contrast, this cortical area was influenced by the duration of sensory experience in rats (h) with a predilection for homogeneous floorboards. Both EE condition and training to discrimination selectively decreased the sizes of the SI neurons' receptive fields (RFs) located on glabrous skin. Smaller RFs and larger cortical areas serving glabrous skin were correlated with better perceptual performances and learning abilities in the H rats only. The present study shows that representational reorganization related to tactile discrimination performances depends upon the perceptual context.

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1. Introduction

Diamond et al. [20] proposed that somatotopic maps constitute structural frameworks for tactile information processing, perceptual learning and neural plasticity. Indeed, an increasing number of experiments reveal that sensory experience reconfigures somatotopic maps through alterations in the properties of neuronal receptive fields (RFs). In contrast, few studies have investigated the use-dependent reorganization of these cortical maps which is concomitant with changes in perceptual abilities [53,54,57,58,64]. Combining behavioral studies with electrophysiological mapping allows for a better understanding of the functional implications of topographic map remodeling in perceptual learning, as revealed in mapping studies in monkeys [35,57,58,65,73] and rats [17,70], as well as brain imaging studies in humans [10,11,24,31,32,50,52,54]. These studies have shown significant expansions in area of SI serving intensely stimulated skin surfaces and/or those surfaces involved in a discrimination behavior. Moreover, the animal studies cited above have revealed that the topography, size and overlap of the neurons' RF were highly dependent

Abbreviations: EE, enriched environment; IE, impoverished environment; H, heterogeneous; h, homogeneous; RF, receptive field; GABA, gamma aminobutyric acid

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on the spatiotemporal structure of the sensory stimulation delivered to the skin (see also [3,14,16]). It is generally assumed, although direct evidence is scarce, that these experience-dependent alterations in RF properties contribute to improvement in tactile discrimination [57].

In previous experiments, we have shown that rats housed with conspecifics and numerous objects to explore (enriched environment, EE) and rats housed singly without object (impoverished environment, IE) exhibited specific alterations in the forepaw representation of the SI cortex. In the EE rats, the protuberant glabrous skin surfaces (digit tips and palmar pads) preferentially used during object palpation and manipulation were represented over larger cortical sectors than those in IE rats, contrary to other glabrous or hairy skin surfaces. Moreover, the SI neurons in these expanded representational zones displayed smaller RFs that were clustered on the digit tips and palmar pad skin surfaces [17]. In contrast, housing in IE decreased and fragmented the forepaw cutaneous area, as noncutaneous zones emerged, and enlarged glabrous skin RFs [18]. We postulated that changes in the SI cortex observed in the EE rats would facilitate tactile discrimination, whereas alterations in the IE rats would result in impaired discrimination. Therefore, we trained EE and IE rats to use the glabrous skin surfaces of their paws in a texture-discrimination task during locomotion on floorboards of homogeneous or heterogeneous roughness [9]. In that earlier study, we showed that the EE rats performed better than the IE rats during the early learning sessions, revealing an effect of housing conditions upon the early stages of tactile learning. Surprisingly, both groups of animals developed similar discriminative abilities later in the training and testing sessions. Data analysis revealed that some rats performed significantly better when confronted with homogeneous floorboards (h rats) of invariant roughness, while some others performed better when confronted with the heterogeneous floorboards of gradually diminished roughness contrasts (H rats). Others showed no predilection (Hh rats). Furthermore, regardless of the environmental conditions, H rats and Hh rats on average made a finer discrimination of roughness contrasts than did h rats [9].

In the present study, we addressed the question of how tactile experience related to short-duration daily training to texture discrimination and to floorboard type predilection would impact organizational features of the SI map of the forepaw used in the discrimination task in rats housed in EE or IE conditions.

2. Experimental procedures

All experiments have been carried out in accordance with the National Institute of Health Guide for Care and Use of Laboratory Animals (NIH Publication number 80-23) revised 1996 for the UK animals (Scientific Procedures) act 1986 and associated guidelines, or the European Communities Council Directive of 24 November 1986 (86/609/EEC).

2.1. Housing conditions

After weaning, 1-month-old female Long-Evans rats (CERJ; Le Genest St Isle, France) were housed in an enriched (EE) or impoverished (IE) environment [6,29]. Rats housed in EE lived in a group of 12-15 in two spacious cages $(76 \text{ cm wide} \times 76 \text{ cm deep} \times 40 \text{ cm high})$ connected by two tunnels. To promote tactile experience, these cages contained mobile and immobile objects of various shapes and textures. Each day, the EE cages were furnished with a new set of objects to stimulate the exploratory behavior of the rats. Daily observation of the EE rats indicated that the animals actively touched, palpated, and manipulated these objects. Moreover, exploratory behavior was found to alternate with grooming and mutual cleaning [17]. IE rats lived singly in small cages $(23.5 \text{ cm} \times 35.5 \text{ cm} \times 19 \text{ cm})$ without any objects. The floor of all cages was covered with sawdust. All animals had water ad libitum and were maintained on a 12-h light-dark cycle.

2.2. Behavioral training

After 2 months of housing, 10 EE and 10 IE rats were trained to perform roughness discrimination during locomotion on textured floorboards (for details, see [9]). All of their mystacial vibrissae on both sides of the face were clipped every 2 days to within 2–3 mm of the skin surface in order to enhance the contribution of their paws in the discrimination task. The rats were placed on a food-restriction schedule before the experimental sessions. Each animal was trained for about an hour in a daily morning session, 6 days a week, then replaced in its respective environment. During training sessions, the rats were placed in a modified Skinner box located in a sound- and light-proof box (Imétronic, France) (Fig. 1). A floorboard was placed on a sliding plate and inserted in



Fig. 1. Experimental device used to evaluate texture discrimination abilities in rats. Inner view of the Skinner box contained in a sound- and light-proof box. The figure shows the holes for nose pokes (1), the food tray (2), the food pellet dispenser (3), a heterogeneous floorboard (4) and the infrared video camera (5).

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