

Geraniol ( $C_{10}H_{17}OH$ ) ließen sich starke zyklusabhängige Schwankungen der olfaktorischen Sensitivität nachweisen.

Während im Proöstrus noch  $5 \times 10^8$  Moleküle Geraniol/cm<sup>3</sup> Luft erkannt wurden, wählten die Mäuse im Metöstrus selbst bei einer Konzentration von  $5 \times 10^{11}$  Molekülen Geraniol/cm<sup>3</sup> Luft nicht mehr signifikant positiv.

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## Olfaction in pregnant and lactating albino mice

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### Abstract

Studied were the alterations of the neural olfactory threshold during pregnancy and lactation in albino mice (NMRI-strain) by means of evoked potential measurements from the Bulbus olfactorius. After copulation the threshold to geraniol is raised from the low proestrus level to a medium level that remains stable during most of the gestation period. Two to three days before parturition the olfactory acuity increases, till immediately after giving birth a sensitivity peak is reached. In the presence of a male this hyperosmia lasts a maximum of 4 days, in isolated females up to 8 days. The biological significance of this effect is discussed.

### Introduction

During the sexual cycle of females, the olfactory sensitivity changes to a very high degree. This has been found in humans (LE MAGNEN 1952; KÖSTER 1965; VIERLING and ROCK 1967; DOTY et al. 1981), as well as in rats (PIETRAS and MOULTON 1974; PHILLIPS and

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VALLOWE 1975) and in mice (SCHMIDT and SCHMIDT 1980; RITTNER and SCHMIDT in press). In humans the span between lowest and highest sensitivity was up to the factor  $10^5$ , in laboratory mice the neural olfactory thresholds in metestrus were up to factor  $10^6$  higher than in proestrus. Only very few observations indicate alterations of the olfactory acuity during pregnancy and in the post-partum-period in humans (HANSEN and GLAS 1936; LUVARA and MOURIZI 1961; GUERRIER 1964; GOOD et al. 1976); in animals no investigations have been found in the literature.

### Material and methods

The experiments were carried out with 21 ♀♀ albino mice (NMRI-strain), 4 to 5 months old, all of them experienced mothers. An isolated tungsten electrode ( $50\text{ }\mu\text{m}\text{ }\varnothing$ ) was permanently implanted into one of the olfactory bulbs under anesthesia; the electrical activity of the olfactory bulb was recorded from the waking animals (for details see SCHMIDT 1978). The electrodes remained in function between 5 days and 5 weeks. Each day the neural olfactory threshold for geraniol ( $\text{C}_{10}\text{H}_{17}\text{OH}$ ) was established by means of evoked potential measurements. The intensity of the stimulus was graduated in steps of factor 10.

The mice, which were kept in individual cages, were divided into three groups: Group 1 was isolated before the experiments; two days after the operation a male was placed into the cage. In this group the days before copulation and the first days of pregnancy were investigated. In group 2 each female was constantly kept with a male. The operation was performed at the second half of gestation or shortly after parturition. The females of group 3 were isolated after copulation (olfactory contact to males, who lived in the same room, was maintained); all of them were operated the day after giving birth.

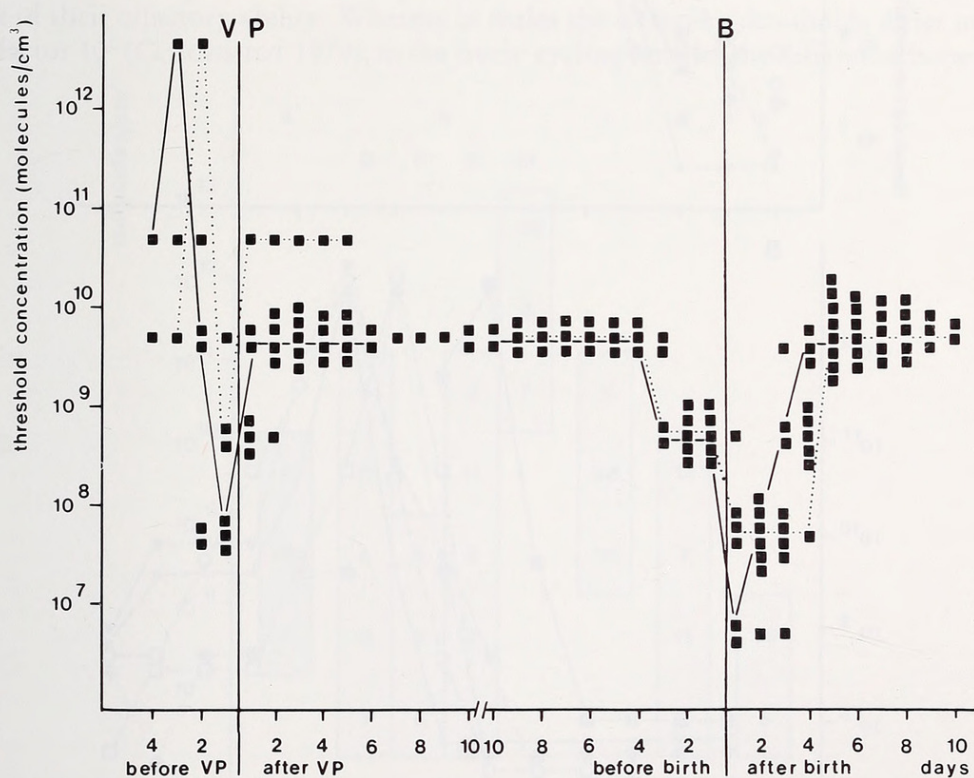


Fig. 1. Olfactory thresholds for geraniol of female mice before and after copulation (group 1, left half) resp. before and after parturition (group 2, right half). Each square represents the threshold value of one animal at a given day; in both groups the values of two mice are connected. Ordinate: threshold concentration (molecules geraniol/ $\text{cm}^3$  air); the concentrations investigated differ at the factor 10 (always  $10^n$  molecules/ $\text{cm}^3$ ). To indicate the number of females with the same threshold value, the squares are arranged vertically at each concentration. Abszissa: days before or after vaginal plug (VP) resp. birth (B)



## Results

### Olfactory thresholds of the females kept constantly with a male

Before copulation the females of group 1 showed the normal cycling alterations in their olfactory sensitivity with a high threshold in metestrus (up to  $5 \cdot 10^{12}$  molecules geraniol/cm<sup>3</sup> air) and a low threshold in proestrus ( $5 \cdot 10^7 - 5 \cdot 10^8$  molecules/cm<sup>3</sup>). As soon as the vaginal plug was observed the threshold values remained at a medium level, in most of the cases  $5 \cdot 10^9$  molecules/cm<sup>3</sup>. This level persisted during most of the time of pregnancy. Only two to three days before parturition the sensitivity increased slightly (factor 10). In fig. 1 the data of group 1 and 2 are combined.

A considerable improvement of olfactory acuity was reached immediately after giving birth. The threshold values of all females decreased at a factor of 100 to 1000 compared with the long lasting gestation level. This sensitivity peak only lasted for up to 4 days. Then copulation occurred and all animals regained the constant level typical for pregnancy. 6 out of the 8 females of group 2 got their next litter 25 to 28 days after the first parturition. In two females the next birth took place not until 42 resp. 43 days. Nevertheless they showed

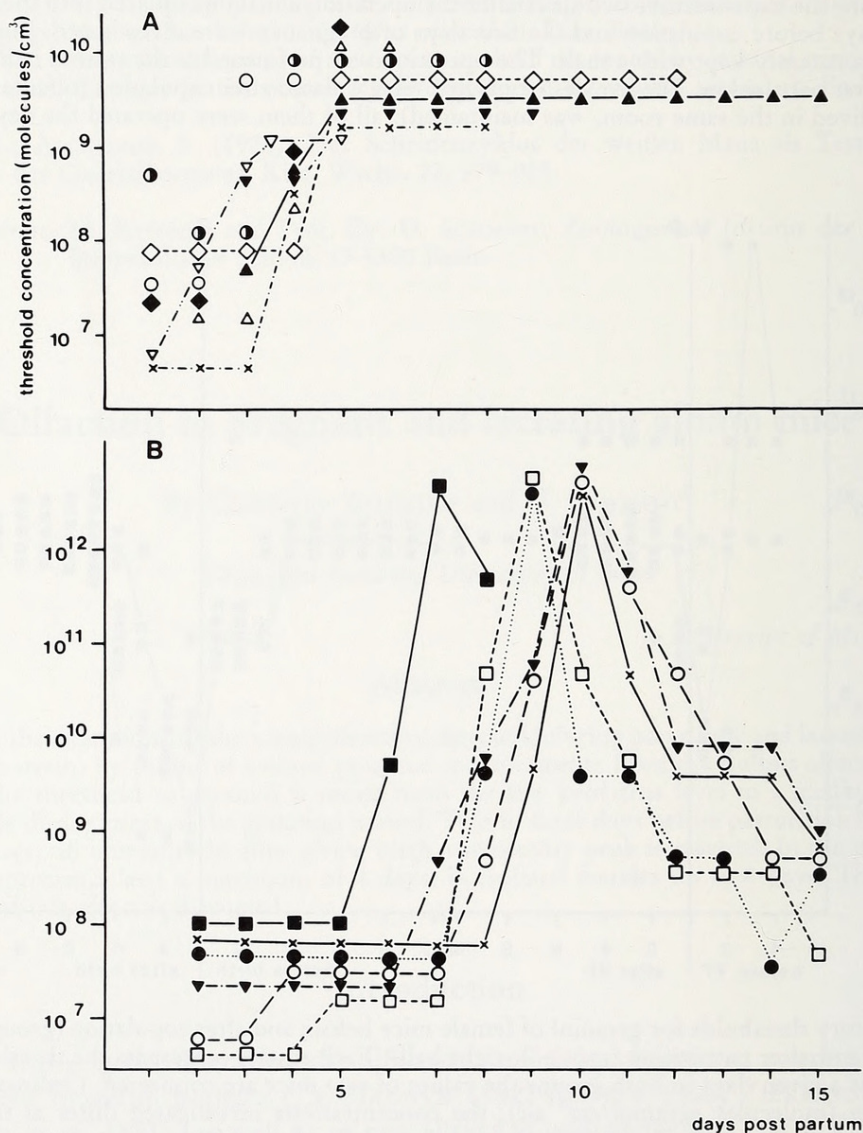


Fig. 2. Olfactory thresholds for geraniol during the post-partum-period. A: lactating females which were kept together with a male (group 2); B: isolated lactating females (group 3)



the same pattern of sensitivity changes as the other ones. It was not possible to determine when the first estrus occurred, as after parturition the vaginal smears do not show the typical composition (GREENWALD 1958).

### Olfactory sensitivity during the post-partum-period of isolated females

As the females of group 3 were operated the day after giving birth, the post-partum-day 2 was the first one investigated. The minimal threshold values reached after birth were the same as in group 2, but the sensitivity peak remained for about double the time as in females kept together with males (fig. 2). In group 2 the decrease of sensitivity started between post-partum-day 3 to 5, in the isolated females the olfactory sensitivity was diminished in most of the cases not until day 7 or 8. The animal in which a decline occurred already at day 6 (fig. 2, squares), had a very small litter of only 5 pups, whereas the other females had 8 to 12 juveniles.

Latest at day 10 extremely high threshold values were found in all animals. The geraniol concentration needed to register an olfactory evoked potential was  $10^5$  to  $10^6$  times higher than after birth. The vaginal smears showed that at this time the females reached the metestrus phase. In the following days sensitivity increased again, consistent with normal cycling.

### Discussion

In the course of the different sexual phases, female house mice experience a tremendous change of their olfactory ability. Whereas in males the olfactory thresholds differ maximal at the factor  $10^2$  (C. SCHMIDT 1979), in the freely cycling females the difference between the

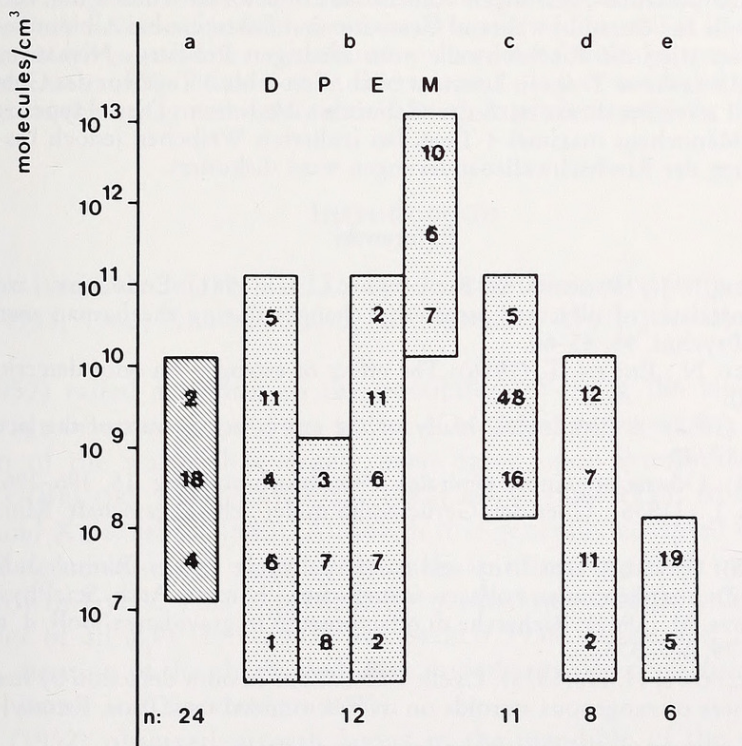


Fig. 3. Comparison of threshold values for geraniol in male mice (hatched column, a) and females at different reproductive stages (punctuated columns). b: freely cycling females (D diestrus, P proestrus, E estrus, M metestrus); c: gravid animals; d: post-partum-day 2 to 5 in lactating females kept with males; e: post-partum-day 2 to 5 in isolated lactating females. The figures in the columns show the number of days a given threshold value was obtained; n gives the number of animals investigated in each group



lowest threshold values in proestrus and the highest in metestrus amounts up to the factor  $10^6$ . During gestation olfactory sensitivity is most of the time slightly less than in the males (fig. 3, columns a and c); only shortly before parturition takes place male and female threshold values match. Irrespective of the presence of a male, the females reach very low thresholds after giving birth. At this time the olfactory acuity in females is on the average 10 times better than in males. In the isolated females this keen sense of smell remains for several days, the presence of a male reduces this sensitivity peak to 4 days at the maximum.

What are the biological implications of these changes in olfactory acuity? Regarding the extremes in the cycling female, only the sensitivity peak during proestrus seems to be advantageous. During this time the female has to find a suitable partner which may be aided by olfactory stimuli. The extremely low sensitivity during metestrus, whereby the animal must be nearly anosmatic, should be of disadvantage to the mouse.

Of course these results were obtained with females artificially retained from males. Under natural conditions males should always be available to the female. This situation is imitated in group 1 and 2 of the present study. Here it becomes evident that in the presence of a male the female does not reach the low metestrus level. The period of hyperosmia on the other hand falls in a time where olfactory guided behaviour seems to be most important. After parturition the female has to recognize her own pups and, as receptivity commences quickly, is engaged in sexual behaviour. If a male is not available at once, as in group 3, the hyperosmia is considerably prolonged. The improvement of olfaction during a time, when the sense of smell is especially needed, should be of great value to the female mouse.

### Zusammenfassung

#### *Untersuchungen zur Riechfähigkeit trächtiger und laktierender Albinomäuse*

Mit Hilfe von evoked-potential-Messungen vom Bulbus olfactorius wurden die Veränderungen der neuralen Riechschwelle für Geraniol während Gestation und Laktation bei Albinomäusen untersucht. Nach der Kopulation stieg die Riechschwelle vom niedrigen Proöstrus-Niveau auf ein mittleres Niveau an, das fast die gesamte Tragzeit konstant blieb. Erst 2 bis 3 Tage vor der Geburt erhöhte sich die Riechschärfe und erreichte direkt nach der Geburt ein Maximum. Diese Hyperosmie dauerte bei Anwesenheit eines Männchens maximal 4 Tage, bei isolierten Weibchen jedoch bis zu 8 Tage. Die biologische Bedeutung der Riechschwellenänderungen wird diskutiert.

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## Age determination of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus), by means of mandibular growth layers

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### Abstract

Examined the growth layers in 112 walrus mandibles (*Odobenus rosmarus* Linnaeus) to determine their applicability in age determination. Growth layers are formed in the lateral portion of the ramus mandibularis in both males and females, from the first year of life until at least the 27th year. The number of mandibular growth layers was found to correspond with the number of annual growth layers in the cementum of the cheek teeth in the ratio of 1 : 1. It is concluded that readings of both mandibular and cheek teeth growth layers should be made when determining the age in the walrus.

### Introduction

Dental growth layers are widely used in age determination of seals (e. g. SCHEFFER 1950; LAWS 1952, 1953, 1962; KLEVEZAL and KLEINENBERG 1967; JONSGÅRD, 1969; MORRIS 1972).

MOHR (1952) called attention to the possibility of using the layering in the tooth cementum in age determination of the walrus (*Odobenus rosmarus* L.). Subsequently, age determination of the walrus has largely been based upon interpretation of cementum growth layers (BROOKS 1954; FAY 1955, 1982; MANSFIELD 1958; BURNS 1965; KRYLOV 1965; BORN and KRISTENSEN 1980). Although it is generally accepted that this method is usable, age determination in some individuals is often impeded by indistinctness of cementum growth layers. This is particularly marked in subadult walruses of both sexes and in females of all ages (FAY 1955; MANSFIELD 1958; BORN and KRISTENSEN 1980). Furthermore, attrition of the cheek teeth may impede age determination in older walruses (BURNS 1965; BORN and KRISTENSEN 1980).

CHAPSKII (1952) observed growth layers in the mandible of the walrus (*Odobenus rosmarus*) and the harp seal (*Pagophilus groenlandicus*). He demonstrated that in the harp seal the number of mandibular growth layers is correlated with estimates of age based on other criteria and suggested that the mandibular growth layers are formed annually. However, CHAPSKII (1952) neither gave a detailed description of the layering in the walrus mandible, nor did he use the layering in age determination of the walrus. Therefore we



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