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Mammary pheromone-induced odour learning influences sucking behaviour and milk intake in the newborn rabbit

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Newborn rabbits, *Oryctolagus cuniculus*, locate their mother's nipples through typical orocephalic movements elicited by odour stimuli, in particular by the mammary pheromone (MP). The MP also promotes neonatal odour learning: after single pairing with the MP, an initially neutral odorant becomes able to elicit sucking-related head-searching/oral-grasping movements. However, the behavioural significance of the MP-induced odour learning remains poorly understood. We carried out three experiments to explore its influence on milk intake and compare its consequences with those resulting from nursing-induced conditioning. First, pups conditioned to an odorant by pairing with the MP on postnatal days 2–3 were shown to gain more milk on day 4 during nursing by a female carrying the conditioned odorant along the nipple lines. Second, surprisingly, nursing-induced odour learning failed to induce this effect. We therefore determined whether the location of the conditioned odorant on or around the nipples modified the pups' milk intake: it appeared that after nursing-induced conditioning, the pups gained more milk when the conditioned odorant was applied directly on the nipples. Moreover, several results showed that pups could learn different odorants during successive days of conditioning, and that the more recently acquired cue was the most influential on milk intake. This study suggests that the MP plays a critical role to ensure sucking performance in newborn rabbits, not only through its releasing effect, but also through its ability to promote the acquisition of novel odours carried by the mother.
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The days following birth are decisive for the survival of newborn mammals. They need to rapidly contact the mother and reach her nipples to get nutrients and antibodies carried in colostrum and milk (Blum & Hammon, 2000; Goursaud & Nowak, 1999; Xu, 1996). In species bearing altricial newborns, suckling is initiated by the mother but neonates have to locate and orally grasp the nipples by themselves. To that goal, they respond to thermal, tactile and odour stimuli provided by the mother (e.g. Al Aïn, Belin, Schaal, & Patris, 2013; Larson & Stein, 1984; Raihani, Gonzalez, Arteaga, & Hudson, 2009; Schaal, 2010; Teicher & Blass, 1977; Varendi, Porter, & Winberg, 1994). In the European rabbit, *Oryctolagus cuniculus*, lactating females produce two kinds of olfactory stimuli that alter the pups' behaviour: individual-specific cues depending on the physiological state and diet of the female (Bilkó, Altbäcker, & Hudson, 1994; Coureaud & Schaal, 2000; Coureaud, Schaal, Hudson, Orgeur, & Coudert, 2002; Hudson & Distel, 1982) and species-specific signals emitted by all lactating females of the species (Hudson & Distel, 1983). Among the latter, a volatile compound isolated from milk, 2-methylbut-2-enal, releases the typical head-searching/oral-grasping movements usually displayed by pups during nursing. This compound, showing pheromonal properties (as defined by Beauchamp, Doty, Moulton, & Mugford, 1976), has been called the mammary pheromone (MP; Coureaud, 2001; Coureaud, Langlois, Perrier, & Schaal, 2003; Moncomble et al., 2005; Schaal et al., 2003). Its efficacy in releasing searching–grasping responses in pups is general to *O. cuniculus*, although it changes during the lactation period. Indeed, both domestic and wild rabbit pups respond to the MP, with the response rates highest during the first 10 postnatal days, progressively decreasing thereafter and completely vanishing at weaning (Coureaud, Rödel, Kurz, & Schaal, 2008). Some pups (<10%), however, are unresponsive on postnatal day 1, which leads to deficient milk intake and high mortality before weaning (especially in low birth weight individuals; Coureaud, Fortun-Lamothe, Langlois, & Schaal, 2007). In addition to variations in pup responsiveness, the emission of MP in milk is variable during the postpartum period. Indeed, rabbit milk

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contains a higher concentration of MP in early than late lactation (Coureaud, Langlois, Perrier, & Schaal, 2006). Collectively, these results indicate that the MP is a key releasing signal that controls the interaction of rabbit neonates with the doe.

Nursing provides much more than food to neonates. It also provides the opportunity to learn about the surroundings during reinforcing contacts with the mother and her body, especially during the intake of milk (Brake, 1981; Delaunay-El Allam, Marlier, & Schaal, 2006; Hepper & Wells, 2006; Johanson & Hall, 1979). Conditioning that occurs during nursing has consequences for the next sucking episodes (Cheslock, Varlinskaya, Petrov, & Spear, 2000; Miller & Spear, 2008; Pedersen, Williams, & Blass, 1982) and also for food or sexual preferences later during development (Fillion & Blass, 1986; Galef & Henderson, 1972). Newborn rabbits are able to learn novel odour cues during the first nursing episodes (Allingham, Brennan, Distel, & Hudson, 1999; Bilkó et al., 1994; Coureaud, Moncomble, et al., 2006; Hudson, 1985; Hudson, Labra-Cardero, & Mendoza-Soylovna, 2002; Ivanitskii, 1958; Kindermann, Gervais, & Hudson, 1991; Serra, Ferreira, Mirabito, Levy, & Nowak, 2009). They need only a single exposure to an artificial odorant painted on the mother's abdomen just before nursing; when the same odorant is presented again 24 h later, it triggers the head-searching movements that are typically usually released by the female's abdomen or her milk. Among the reinforcing events that occur during nursing, tactile or thermal properties of the maternal fur, expression of searching or sucking actions, milk intake, gastric filling or postabsorptive events linked to satiation have been considered (Hudson et al., 2002; Serra et al., 2009). An additional reinforcing factor is the MP itself, which functions as an extremely efficient promoter of odour learning. Thus, after single and simultaneous exposure to an initially neutral odorant paired with the MP (in the absence of the mother), rabbit pups exhibit a strong searching - grasping response when later exposed to the odorant alone (Charra, Datiche, Gigot, Schaal, & Coureaud, 2013; Coureaud, Languille, Schaal, & Hars, 2009; Coureaud, Moncomble, et al., 2006; Patris, Perrier, Schaal, & Coureaud, 2008). The response induced after conditioning with the MP is maximal 24 h after the pairing (i.e. when the next nursing happens) and is similar to that resulting from nursing-induced conditioning (Coureaud, Moncomble, et al., 2006). Moreover, the MP allows pups to learn a mixture of several odorants during a single conditioning session, or distinct odorants encountered during successive conditionings (e.g. Coureaud, Hamdani, Schaal, & Thomas-Danguin, 2009; Coureaud, Thomas-Danguin, Le Berre, & Schaal, 2008; Coureaud, Thomas-Danguin, Wilson, & Ferreira, 2014; Romagny, Thomas-Danguin, & Coureaud, 2015; Sinding et al., 2013; Sinding, Thomas-Danguin, Crepeaux, Schaal, & Coureaud, 2011). In other words, the MP is not only a releaser of nipple-search behaviour but also a potent reinforcing agent for neonatal odour learning.

To date, the influence of MP-induced odour learning on neonatal behaviour has not been studied in the natural context of interaction with the mother. One may suggest that it facilitates the acquisition of odour cues carried on the maternal abdomen on one day, which could improve the responsiveness of pups to the mother on the next day, ending in better nipple location and sucking performance. Such a mechanism would be particularly adaptive in the rabbit since nursing occurs only once per day for less than 5 min (Zarrow, Denenberg, & Anderson, 1965) and neonatal survival directly depends on sucking success during the very first nursing episodes (Coureaud et al., 2000). Here, we investigated the influence of MP-induced learning of an odorant on neonates in terms of ability to obtain milk (Experiment 1) and compared this influence with that created by nursing-induced learning (Experiment 2). We also evaluated whether the site where the conditioned odorant is applied on the maternal abdomen (nipple versus non-nipple areas) influenced nipple location by rabbit pups and milk intake (Experiment 3). We hypothesized that both MP-induced and nursing-induced odour learning will positively influence the neonatal ability to find the nipples and suck, and that this effect would be maximal when the conditioned odorant is restricted to the nipples themselves.

GENERAL METHODS

Animals, Breeding and Housing Conditions

New Zealand rabbits (Charles River Strain, France) were housed in the breeding unit of the Centre de Zootechnie (Université de Bourgogne, Dijon). Females and males were kept in individual cages (74×72 cm and 42 cm high and 64×60 cm and 35 cm high, respectively for females and males). For pregnant does, a nestbox (39×25 cm and 32 cm high) was added to the outside of the cages 2 days before the day of birth (day 0). To equalize the nursing experience of the pups, the females were allowed to enter the nest once per day for 15 min to nurse (at 1130 hours; see Ethical Note). Animals were kept under a constant 12:12 h light:dark cycle (light on at 0700 hours) and ambient air temperature was maintained at 19–21 °C. Water and pellet food (Lapin Elevage 110, Safe, France) were provided ad libitum.

A total of 242 pups born from 42 females were used. On postnatal day 1, 3 h after nursing, the pups were individually weighed (Sartorius, Palaiseau, France; accuracy: 0.1 g) and marked on their back. In each litter, the six pups presenting the most homogeneous weight and for which milk intake was confirmed (by screening of gastric content through the transparent abdominal skin; e.g. Coureaud et al., 2000) were selected as experimental animals. The remaining pups were left in the litter (if <8) or adopted (if >8) in other litters which were not used for the present study.

Stimuli

The MP (2-methylbut-2-enal) was used as the unconditioned stimulus. Ethyl acetoacetate (E) and limonene (L) constituted the conditioned and/or control stimuli. These odorants were chosen because they spontaneously elicit only sniffing in newborn rabbits (Coureaud, Languille, et al., 2009; Coureaud, Moncomble, et al., 2006). The odorants and the E+MP or L+MP mixtures (50/50 v/v ratio) were prepared in distilled water at a final concentration of 10^{-5} g/ml (an efficient level for MP-induced conditioning; Coureaud, Moncomble, et al., 2006). All the odorants were purchased from Aldrich (Saint-Quentin-Fallavier, France).

Odour-learning Procedures

Two methods were used to induce odour learning in pups, one using the reinforcing properties of the MP (experiment 1) and the other based on the multimodal reinforcing context formed by the nursing situation (including the MP naturally emitted in milk) (Experiments 2 and 3). Both were repeated on postnatal days 2 and 3 to optimize the acquisition of the learned odorant.

The MP-induced odour learning procedure was carried out following a procedure described in previous studies (e.g. Charra et al., 2013; Coureaud, Moncomble, et al., 2006; Coureaud et al., 2014; Sinding et al., 2013): 1–2 h before the scheduled nursing time (i.e. between 0930 and 1030 hours), the pups were transferred from the nest to another room of the breeding unit, in a box maintained at ambient temperature. They were then exposed to a cotton pad (19×14 cm; Fig. 1) scented with 6 ml of either the E+MP mixture (group E_{MP}; $N = 43$ pups), the L+MP mixture (group L_{MP}; $N = 38$) or water (control group W; $N = 18$). This odour pad was held

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