



# Configural processing of odor mixture: Does the learning of elements prevent the perception of configuration in the newborn rabbit?



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## HIGHLIGHTS

- Repeated conditioning to configural mixture decreases pups' response to components.
- Pre-exposure to components promotes specific responsiveness to these odorants.
- Pre-exposure to components does not alter the perception of configuration.
- Behavioral response to configural mixture depends on familiar/unfamiliar odor cues.
- Neonates would perceive the maximum of information carried by complex odors.

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## ABSTRACT

Although elemental perception of odor mixtures allows us to perceive the component odor qualities, configural perception leads to the emergence of a new odor percept. The 6-odorant Red Cordial (RC) mixture is weak configurally perceived in newborn rabbits, meaning that pups respond to the odorants after conditioning to the mixture but cannot generalize to the mixture after conditioning to a single odorant. They need to know more than 50% of the elements to respond to the mixture. This suggests that their responsiveness to RC depends on the familiar vs. unfamiliar bits of information that they perceive in it. To go further, we tested the complementary hypothesis that after learning 4 or 5 odorants, the configural perception disappears, allowing pure elemental perception of the whole mixture. In Exp. 1, repeated conditionings to RC decreased the pups' responsiveness to the odorants, i.e., facilitated RC configural perception. In Exp. 2, pups were first conditioned to a sub-mixture of 4 or 5 RC elements and then repeatedly conditioned to RC to determine whether early elemental learning reduced the facilitation of RC configural perception. As pups weakly responded to the RC mixture components, the early conditioning did not prevent this facilitation. In Exp. 3, after daily conditioning to the sub-mixture and then to the whole mixture, the configural perception of RC remained unaffected. The present results confirm that rabbit pups respond to the configural RC mixture according to the perceived ratio of familiar/unfamiliar cues and highlight that the perception of the RC configuration resists the previous acquisition of elements that compose the mixture.

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## 1. Introduction

The olfactory system processes odor mixtures in the alternative, but not systematically exclusive, elemental and configural ways. Elemental perception consists of perceiving the odor quality of the mixture as similar to the odor quality of its elements [e.g., 1–4]. Conversely, perception is robust configural when a specific percept, the configuration, emerges from the mixture and carries an odor quality distinct from the quality of each odorant [e.g., 5–9]. For instance, in human adults, the strawberry

odor of ethyl isobutyrate (odorant A) and the caramel odor of ethyl maltol (odorant B) elicit the configural perception of a pineapple odor in the AB mixture [10,11].

The configural perception can be “weak” when organisms perceive, in addition to the configuration, the component odor qualities [12]. Thus, the AB mixture configurally perceived in human adults is “weak configurally perceived” in newborn rabbits. Indeed, when 1-day-old pups are conditioned once to the AB mixture, they behaviorally respond later to both AB and odorants A and B; however, they do not respond to the AB mixture after a single conditioning trial to odorant A or B. They would thus perceive specifically in the AB mixture a particular AB odor quality in addition to those of elements A and B [13,14]. This is confirmed, after conditioning to the mixture, by the creation of a configural memory of AB distinct from the elemental memory of A and B [15,16].

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Interestingly, if a single conditioning trial to one element is not sufficient for pups to generalize their conditioned response to the mixture, they do generalize after the successive acquisition of A and B. Thus, the fact to know more than 50% of the individual bits of information contained in a weak configurally perceived binary mixture is required to induce pups' responsiveness to that mixture [13].

Similar investigations have been made recently in the case of senary odor mixtures. Rabbit pups indeed perceive the 6-component Red Cordial (RC) odor mixture in the weak configural way. As for AB, the conditioning to the mixture induces responsiveness to the odorants, but conditioning to one element does not promote responsiveness to the mixture [17]. Moreover, pups do not respond to RC after conditioning to 2 or 3 RC odorants, but they do after conditioning to RC sub-mixtures of 4 or 5 elements [18]. Such responsiveness to the whole mixture after conditioning to a sufficient number of its elements raises the question of odor mixture processing in animals, a critical skill for the representation of their chemosensory world. Specifically, is the perception of a configuration permanent in a mixture, or is it modulated by experience and early exposure to the mixture components? The previous results did not allow us to draw definitive conclusions on this question; therefore, two concurrent hypotheses have been suggested [18]:

The first hypothesis stated that even after conditioning to 4 or 5 odorants, the RC mixture remains weak configural. Newborn rabbits would then still perceive the odor quality of the six components and of a seventh cue, the RC configuration. Therefore, they would respond to the mixture after learning more than 50% of the individual information, that is, 4 out of the 7 bits of information. Thus, their responsiveness would depend on the ratio of familiar (learned elements) to unfamiliar bits of information (non-learned elements + the configuration).

The second hypothesis stated that the processing of the RC mixture changes according to the number of odorants previously acquired by the pups: when more than 50% of the odorants are learned, the perception of the RC configuration would be prevented because the saliency of the learned odorants increases. Consequently, the mixture would become perceived in a pure elemental way, allowing perceptual access to the odorants. Conversely, conditioning to 50% or less of the elements ( $\leq 3$  odorants) would maintain the perception of the configuration; this singular odor quality would then prevent the generalization of the pups' behavioral response to the whole mixture. According to this second hypothesis, it would not be the familiar/unfamiliar ratio of a fixed number of bits of information that drives the mixture processing but the perception/absence of perception of the configuration.

The present study aimed to distinguish between these two hypotheses. To that goal, our experimental strategy required two steps. At first, the perception of the RC configuration was strengthened to optimize its perception in the mixture. Then, we attempted to break the perception of the configuration by pre-exposing the newborns to more than 50% of the mixture elements. In a preliminary experiment (Experiment 1), rabbit pups were repeatedly conditioned to RC (by coupling with the mammary pheromone [19]) for three days to control for their improved responsiveness to RC at the expense of its elements (a similar experience-dependent effect on configural perception was previously highlighted with the AB mixture; [20]). Then, we tested the hypothesis of the perceptual disappearance of the RC configuration through a single conditioning trial to sub-mixtures of 4 or 5 RC elements 24 h before the repeated conditionings to RC (Experiment 2). As conditioning to elemental sub-mixtures is equivalent to simultaneous conditioning to the distinct elements that compose the sub-mixture (i.e., the pups later respond to each element [18]), we suspected that after learning more than 50% of the RC elements, pups would not perceive the RC

configuration in the whole mixture anymore. Finally, to examine the same hypothesis while taking into account that the single early conditioning to an elemental sub-mixture could be altered by the subsequent repeated conditionings to the mixture, pups were daily conditioned to both the sub-mixture and whole RC mixture for three days (Experiment 3). If the hypothesis was verified, this procedure could be at least as efficient as that of Exp. 2 because the daily conditioning to the elements contained in the sub-mixture would sufficiently increase their saliency to prevent the perception of the RC configuration. In this last experiment, we also ran a control assay, using the elementally perceived RC<sup>mod</sup> mixture, to assess whether the effects observed in our experimental paradigms were specific to configural processing.

## 2. Materials and methods

### 2.1. Animals and housing conditions

Male and female New Zealand rabbits, *Oryctolagus cuniculus* (Linnaeus) (Charles River; L'Arbresle, France), were kept in individual cages at the Centre de Zootechnie de l'Université de Bourgogne. A nest box (0.39 × 0.25 × 0.32 m) was added on the outside of the pregnant females' cages 2 days before delivery (the day of delivery was considered postnatal day 0). To equalize the pups' nursing experience, all the females had access to their nest between 11:30 and 11:45 a.m. This procedure allowed following the brief (3–4 min) daily nursing of the species [21]. The animals were kept under a constant 12 h:12 h light:dark cycle (light on at 07:00 a.m.) with ambient air temperature maintained at 21–22 °C. Water and pelleted food (Lapin Elevage 110, Safe, France) were provided ad libitum. A total of 206 newborns from 44 females were used. We strictly followed the local, institutional and national rules (French Ministries of Agriculture and of Higher Education and Research) regarding the care and experimental use of the animals. Thus, all experiments were carried out in accordance with the ethical rules enforced by French law and were approved by the Ethical Committee of the University of Burgundy (Dijon, France; no. 5305).

### 2.2. Odorants and mixtures

The odorants were purchased from Sigma-Aldrich (Saint-Quentin Fallavier, France). Stock solutions were prepared at 1% w/w in ethanol (anhydrous, 99.9% Carlo Erba, France) and then diluted in purified water (MilliQ System, Millipore®, Molsheim, France) and mixed to reach the target concentration and ratio of odorants in mixtures. The mixtures, sub-mixtures or single odorants were finally diluted in a solvent made of purified water and a maximum of 0.1% of absolute ethanol. At this concentration, ethanol does not carry significant odor for rabbit pups: it is certainly not detectable and thus is not active on their behavior [13].

The RC mixture was composed of 6 odorants: vanillin (odorant V; CAS # 8014-42-4), frambinone (F; CAS # 5471-51-2), isoamyl acetate (IA; CAS # 123-92-2),  $\beta$ -ionone (B; CAS # 79-77-6), ethyl acetate (EA; CAS # 141-78-6) and damascenone (D, CAS # 23696-85-7). The component proportions were, respectively, 41.8/41.8/5.0/4.3/4.3/2.8% (final concentrations of 3.3/3.3/0.39/0.34/0.34/0.22 × 10<sup>-6</sup> g/ml) for V/F/IA/B/EA/D. At these proportions, the mixture elicits configural perception of Red Cordial odor (i.e., grenadine) in human adults and weak configural perception in rabbit neonates [17,18]. In Experiment 3, we also used the RC<sup>mod</sup> mixture, which was composed of the 6 odorants included in RC but in different proportions (5/4.3/2.8/41.8/4.3/41.8%, respectively for V/F/IA/B/EA/D). At these proportions, RC<sup>mod</sup> is elementally processed by newborn rabbits [17].

All the RC (or RC<sup>mod</sup>) components were also used as single stimuli. Then, the single odorant concentrations were the same as the concentrations of each odorant in the mixture. Previous analyses showed that the concentration of odorants or their respective vapor pressures are

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