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Report

Single Scale for Odor Intensity in Rat Olfaction

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Summary

Humans and laboratory animals are thought to discriminate sensory objects using elemental perceptual features computed by neural circuits in the brain [1, 2]. However, it is often difficult to identify the perceptual features that animals use to make specific comparisons. In olfaction, changes in the concentration of a given odor lead to discriminable changes in both its perceived quality [3, 4] and intensity [5, 6]. Humans use perceived intensity to compare quantities of different odors. Here we establish that laboratory rats also use perceived intensity to compare concentrations of different odors and reveal the perceptual organization of this elemental feature. We first trained rats to classify concentrations of single odors as high or low. When subsequently classifying concentrations of two odors presented on different trials of the same session, rats made errors consistent with using a single intensity criterion for both odors. This allowed us to investigate the relative perceived intensity of different odor pairs. Odor intensity was not only a function of concentration, but varied also with molecular weight and exposure time. These findings demonstrate the role of perceived intensity as an elemental perceptual feature of odors in rat olfaction.

Results and Discussion

Complex sensory objects are thought to be discriminated on the basis of differential responses of neurons tuned to specific perceptual properties. In vision, for example, knowing the main perceptual features used to compare faces was critical to identifying the neural circuitry underlying face perception in laboratory animals [7]. However, in olfaction, it is difficult to manipulate individual perceptual features, making it hard to specify which perceptual features laboratory animals use to compare different odors.

Even monomolecular odors can only be described using a large set of word descriptors yielding a complex perceptual space [8–10]. However, simply changing the concentration of an odor changes its associated descriptors [3, 4], indicating that concentration alters a variety of perceptual features, each in principle useful for discrimination. Though concentration can alter perceived odor quality, humans can compare concentrations of different odors using perceived intensity [6]. At equal concentrations, different odors can have different intensities as determined by physicochemical properties of the odor molecules [11, 12] and exposure time [5, 13, 14]. Critically, stronger odors can be intensity matched to weaker odors by dilution, making intensity a useful metric for comparing odor quantities [15, 16] along a common sensory scale [17].

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Rodents can discriminate odor concentrations [18–20], but the perceptual features they use to do so have not been specified. To investigate how animals perceive odor concentrations, we trained rats to classify different odor concentrations in a two-alternative choice task (Figure 1A). On different trials, we presented an odor at one of eight concentrations prepared by flowing different amounts of air from the headspace of an odor vial into a clean air stream. Rats were rewarded for going to the left reward port for the four higher ("high") and into the right reward port for the four lower ("low") concentrations within each presented range (Figure 1A). We ensured fast odor delivery (Figure S1A available online) and confirmed that only odor cues were used for task performance (Figure S1B).

Task performance was well described using standard psychometric functions [21] estimating three perceptual parameters: the perceived category boundary (μ), corresponding to rats' estimate of the boundary between high and low concentrations; noise (σ), measuring concentration discriminability; and guess rate (λ), estimating the proportion of trials on which the animal guessed the answer.

Rats Discriminate Odor Concentrations in Logarithmic Coordinates

Linear changes in stimulus quantity cause nonlinear increments in perceived intensity, often adequately described by a logarithm [22]. If intensity changes linearly with concentration, then rats' performance should be symmetric about the category bound with linear concentration difference $(|c - \mu|)$, where c is the odor concentration. However, if intensity changes logarithmically, then performance should be symmetric in log units $(|\log(c) - \log(\mu)|)$. Consistent with a logarithmic intensity representation, performance was significantly more symmetric in log units (Figures 1B–1D and S1C). We therefore used log-spaced concentration steps for further experiments.

Discrimination Performance Is Largely Invariant across Odors and Concentration Range

We next tested discrimination performance as a function of presented concentration range. To change the presented concentration range, we varied the liquid dilution (c_{liq}) of the odor in the vial (see the Supplemental Experimental Procedures). Figure 1E shows average results for the odor limonene presented at concentration ranges spanning three orders of magnitude. For each range, rats correctly discriminated high and low concentrations. Overlaying psychometric functions in common units of odor flow (Figure 1F) revealed only minor differences (Figure S1D). The concentration difference needed for 75% correct performance remained a fixed fraction (27% ± 6%) of the trained category boundary (Figure 1G). However, performance fell toward chance as the odors were diluted further (Figure S1E).

Rats Compare Concentrations of Different Odors Using a Shared Intensity Feature

To determine whether rats classify concentrations of different odors using a common intensity feature, we had rats independently classify high and low concentrations of two different

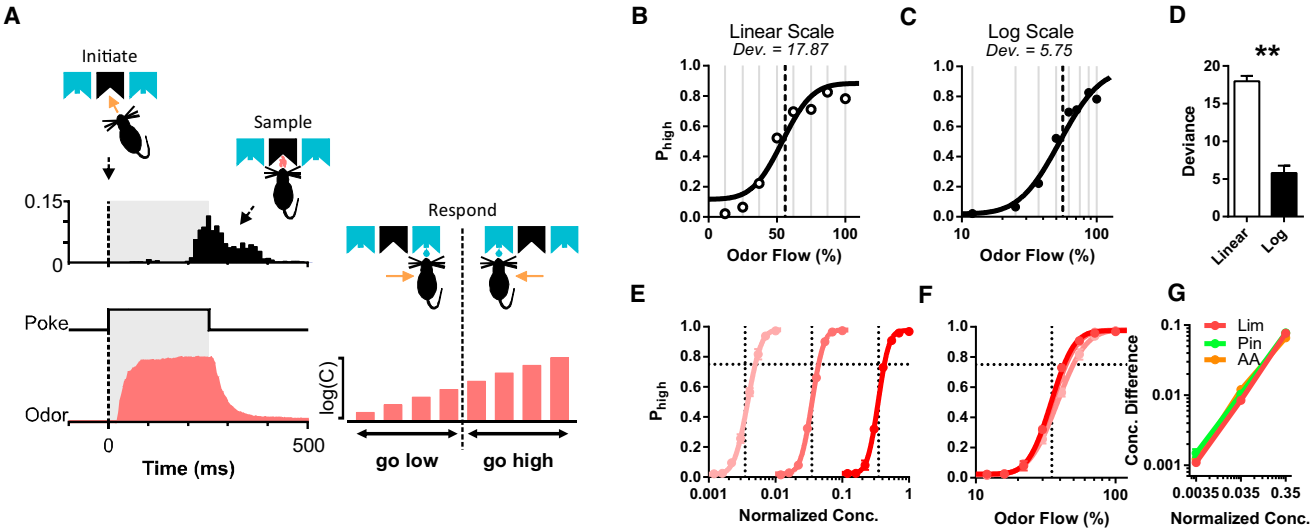

Figure 1. Individual Odor Concentration Classification Performance

(A) Behavioral paradigm. Top left: rats initiate trials by poking into an odor port (dashed line) and then sample the odor (top left). Histogram: sampling time distribution for one example session. Bottom left: kinetics of odor delivered for a typical sampling time measured using a photoionization detector (arbitrary units). Right: rats are rewarded for poking into either the left ("go high") or right ("go low") reward port depending on presented odor concentration. Bottom right: schematic of different presented odor concentrations (log scale).

(B and C) Example performance (single session; odor: pentyl acetate 10%) for a naive rat trained with linearly spaced odor concentrations. Each point denotes probability of going high (see A). Dashed lines denote trained category boundary. Smooth curves are the fitted psychometric functions fitted using linear (B) or log-transformed (C) concentrations.

(D) Deviance values (mean, SEM, n = 3 rats) summarized for linear and log transformed fits. Model deviance is lower in log versus linear units (paired t test: $t(2) = 7.17$, $p = 0.01$).

(E) Average concentration classification performance (n = 6 rats) for three ranges of odor concentration (limonene). Psychometric functions constructed using average of the parameters fitted for individual animals. Shading denotes odor level. Vertical dashed lines correspond to median log odor concentration presented in each range.

(F) Psychometric functions in (A) overlaid in units of flow from the headspace of the odor vial. At higher concentrations, psychometric functions had lower noise (ANOVA main effect of concentration, $F(2,49) = 15.32$, $p < 2 \times 10^{-5}$) and better estimate of the category bound ($F(2,49) = 13.32$, $p < 4 \times 10^{-5}$). Guess rates were low, 1.8% ± 0.9%, and constant across conditions ($F(2,49) = 0.08$, $p = 0.92$).

(G) Normalized concentration difference needed to obtain $P_{high} = 0.75$ (dashed horizontal line in E) as a function of trained category boundary (dashed vertical lines in E). Concentration on the x axis has been normalized such that the maximum presented concentration range is 1.

Error bars represent the SEM. Asterisks denote significance level (**$p < 0.01$). See also Figure S1.

odors presented on different trials of the same experimental session. If concentration ranges of the paired odors match in intensity, then performance for each odor in this two-odor task should be identical to that of the single odor task. This is because even a single intensity criterion can separate the high and low concentrations of intensity-matched odor concentration ranges. A single criterion, however, predicts systematic biases in perceived category bounds when intensities are mismatched. If one of the odors is more intense, then low concentrations of that odor would be misclassified as high, whereas if the odor was less intense, then high concentrations of that odor would be misclassified as low. This intensity mismatch would be reflected by systematic shifts of the perceived category boundaries for each odor. Alternately, if rats use independent intensity criteria for the two odors, then errors should not depend systematically on intensity mismatch.

On different sessions of our two-odor task, we presented each odor at one of the three concentration ranges (c_{liq} = 100%, 10%, and 1%) for a total of nine odor concentration range pairings. Prior to the two-odor task, we trained rats to classify each odor individually at the relevant concentration range. As before, rats were rewarded for discriminating the four high from the four low concentrations of each odor.

For the odor limonene paired with pinene, overall performance declined from 85% ± 0.1% correct for the one-odor task to 82% ± 0.1% correct for the two-odor task (Figure 2A, bars). For any two odors tested, we always found a liquid dilution pairing ($\Delta \log(c)_{liq} = \log 10(c_{liq}^{Odor1}) - \log 10(c_{liq}^{Odor2})$) at which performance with two odors was the same as for odors presented individually. For limonene paired with pinene, this point was at roughly equal dilutions ($\Delta \log(c)_{liq} = 0$; Figure 2A, color plots). From this point, performance declined as we changed the concentration range of either odor (Figure 2A, dots).

Decreased performance in the two-odor task was due to shifts in the perceived category boundaries (μ) for each odor (Figure 2B). At equal dilutions, psychometric functions for limonene and pinene were identical to those from the one-odor task (Figure 2B, center). This is expected only if concentration ranges of the paired odors match in intensity. When the concentration range of pinene was increased, rats went high more often for pinene and less often for limonene (Figure 2B, right). Decreasing pinene concentration had the reverse effect (Figure 2B, left). Such shifts in the perceived category boundaries for each odor are expected if rats use a single intensity criterion for performing the task.

To quantify this effect, we calculated an intensity mismatch index (ΔI) as the difference in category boundary values for the

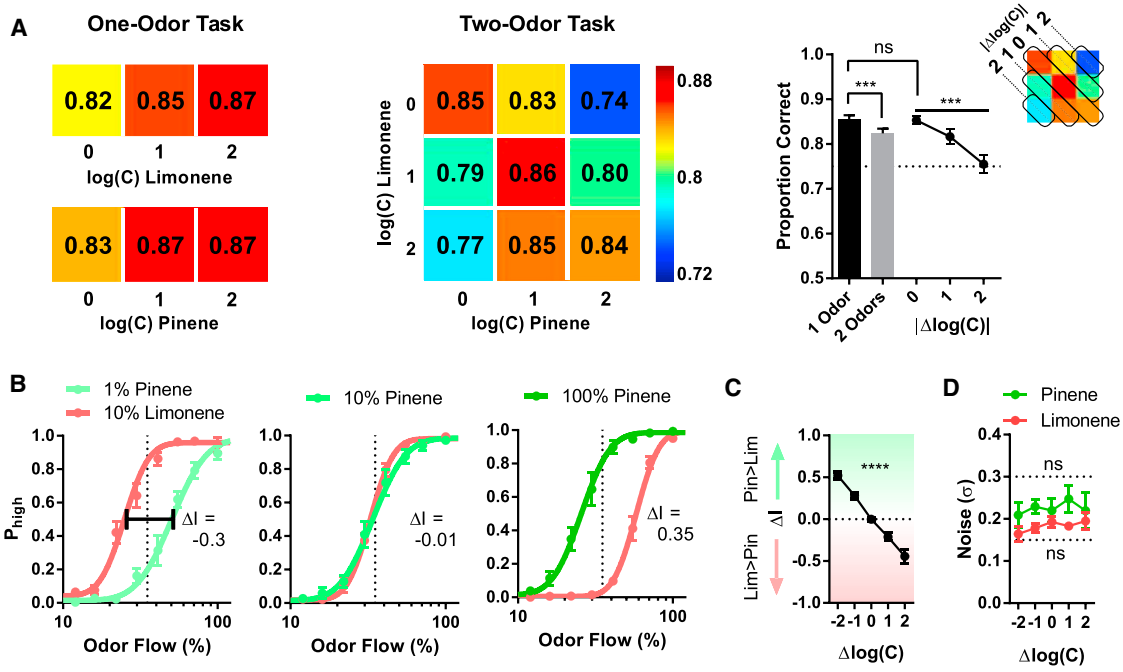

Figure 2. Mismatches in Odor Intensity Bias Concentration Classification

(A) Left: average one-odor task performance (n = 6 rats) as a function of presented odor concentration range for limonene (top) and pinene (bottom). Middle: average two-odor task performance as a function of limonene (ordinate) and pinene (abscissa) concentration. Right: bars show average task performance collapsed across concentration for the one-odor versus the two-odor task (paired t test: $t(5) = 7.86$, $p < 6 \times 10^{-4}$). Dots show two-odor task performance as a function of concentration range difference (see inset; ANOVA main effect of $\Delta \log(c)_{liq}$, $F(2,10) = 27.12$, $p < 1 \times 10^{-4}$).

(B) Two-odor task performance as a function of pinene concentration (limonene fixed at 10%; n = 6 rats). Left to right, pinene varied from 1% to 100%.

(C) Relative intensity mismatch index as a function of concentration range difference. Relative intensity varied with concentration (ANOVA main effect of $\Delta \log(c)_{liq}$, $F(4,20) = 75.64$, $p < 9 \times 10^{-12}$; linear trend $R^2 = 0.90$, $p < 1 \times 10^{-5}$).

(D) Discrimination noise for pinene and limonene plotted as a function of concentration range difference. ANOVA revealed no effect of concentration range for pinene ($p = 0.84$) or limonene ($p = 0.54$).

Error bars represent the SEM. Asterisks denote significance level (***$p < 0.001$, ****$p < 0.0001$). See also Figure S2.

two odors $(\log 10(\mu^{Odor1}) - \log 10(\mu^{Odor2}))$. ΔI grew linearly with odor concentration difference $(\Delta \log(c)_{liq})$ in accordance with a logarithmic intensity representation (Figures 2C and S2A). Intensity mismatch values were not related to training history (Figure S2B), were consistent over repeated tests (Figures S2C and S2D), and were observed even with novel odors (Figures S2E and S2F). In contrast to ΔI, there was no difference in discrimination noise (σ) for pinene or limonene with concentration range (Figure 2D), indicating that performance declined only because rats did not set independent intensity criteria for the two odors.

Adaptation to an Odor Reduces Its Relative Intensity

Perceived intensity of odors rapidly decreases with sensory adaptation [5, 23]. Adaptation to one of the odors in the two-odor task selectively reduced its intensity relative to another "reference" odor. We first measured intensity mismatch (ΔI) between 10% pinene and 1% pentyl acetate relative to the reference odor 10% limonene. As before, 10% pinene was intensity matched to 10% limonene ($\Delta I = 0$; Figures 2B and 3A); however, 1% pentyl acetate was stronger ($\Delta I > 0$; Figure 3D). To induce adaptation, we presented the adapting odor (10% pinene or 1% pentyl acetate) at 35% odor flow rate for 300 ms on each trial prior to the test concentration of either the same odor or the reference odor 10% limonene (Figure S3). Adaptation to pinene decreased its intensity relative to limonene ($\Delta I < 0$; Figures 3B and 3C). Similarly, adaptation decreased intensity of pentyl acetate, now making it match 10% limonene ($\Delta I = 0$; Figure 3E). Adaptation effects were comparable with 3- to 10-fold dilution of the adapted odor (Figures 3C and 3F).

Intensity of Odors Is Determined by Airborne Concentration and Molecular Weight

Perceived intensity of odors is related to their physicochemical properties [5, 11–14]. We measured ΔI as a function of airborne concentration (c_{air}) for 12 pairs of 11 different odors (see the Supplemental Experimental Procedures and [24]). In all 12 pairs, changing concentration of one of the odors resulted in a similar linear change in ΔI (Figures 4A and 4B). However, equal concentrations of some odor pairs yielded large ΔI values. Human psychophysics suggested that heavier odors are more intense [11, 12, 25]. Plotting the concentration offset needed to intensity match paired odors (c_{air}^{offset}) as a function of relative molecular weight revealed a robust ordered relationship (Figure 4C; see the Supplemental Experimental Procedures).

For example, pairing the smaller limonene (136 amu) with the larger decanal (156 amu; relative molecular weight = −0.07) yields $c_{air}^{offset} = 0.68 \pm 0.16$. Thus, decanal must be approximately five times less concentrated than limonene to match in intensity. Pairing limonene with ethyl acetate (88 amu; relative molecular weight = 0.22) yields $c_{air}^{offset} = -1.36 \pm 0.12$. Finally, pairing decanal with ethyl acetate (relative molecular

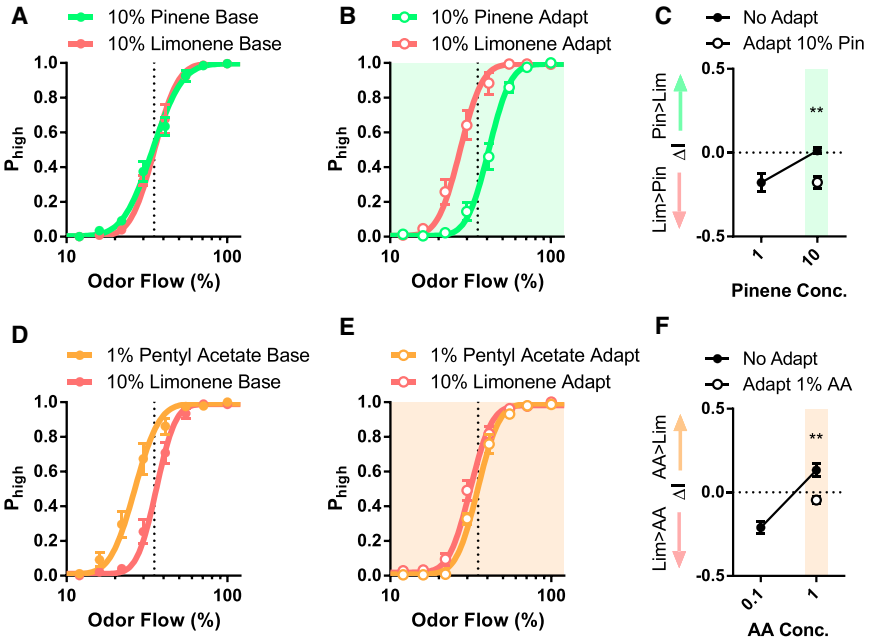

Figure 3. Adaptation to an Odor Reduces Its Relative Intensity

(A) Psychometric functions for 10% pinene (green) and 10% limonene (red) in the two-odor task.

(B) Same as (A), but with an adapting pinene concentration sampled for at least 300 ms prior to the test stimulus on each trial. The adapting pinene concentration was fixed at 35% odor flow.

(C) Intensity mismatch between pinene and 10% limonene as a function of pinene concentration (filled circles). Intensity mismatch with adaptation is greater than without (open circles; paired t test, $t(6) = 4.27$, $p = 5.2 \times 10^{-3}$).

(D–F) Same as (A)–(C), respectively, but for 1% pentyl acetate (AA; orange) paired with 10% limonene (red). Adaptation was induced with AA. Note leftward shift of 1% AA curve relative to 10% limonene (i.e., AA more intense) disappears after adaptation ($t(6) = 4.08$, $p = 6.5 \times 10^{-3}$). Data are from n = 7 rats.

Error bars represent the SEM. Asterisks denote statistical significance (**p < 0.01). See also Figure S3.

weight = 0.28) yields the expected increase in $c_{air}^{offset} = -2.37 \pm 0.08$. Thus, our perceptual measure of intensity mismatch reflects the physicochemical differences between paired odors.

Conclusions

Using a targeted perceptual assay, we show that rats discriminate concentrations of different odors using the common perceptual feature of odor intensity. We obtained a behavioral measure of intensity mismatch (ΔI) between any two paired odors. A zero value of intensity mismatch indicated when the two odors were perceived as equally intense. This point of equal intensity was determined through an interplay between odor concentration, molecular weight, and exposure time. We suggest that intensity is an elemental perceptual feature in rat olfaction.

Our measurements not only confirm the idea that rats have a single scale for odor intensity, but suggest that they use a single intensity criterion for classifying concentrations of different odors. Rats accurately classified odor concentrations as high or low relative to arbitrarily chosen category boundaries (Figures 1E–1G and 2A). However, when rats classified concentrations of two odors presented on different trials of a single behavioral session, performance was impaired (Figure 2). This could have occurred due to increased uncertainty regarding the position of the trained category boundary for each odor [26]. However, odor concentrations were equally discriminable independent of paired concentration ranges (Figure 2D). Instead, rats made errors due to shifts in perceived category bounds for each odor. This behavior is expected if rats use a single intensity criterion governing their response to both odors.

Interestingly, the linear slope between odor intensity mismatch (ΔI) and concentration difference $\Delta \log(c)$ was less than one. There are two ways to interpret this finding. One possibility is that rats form separate but somehow intensity-biased criteria for each odor. Alternately, rats may be using a single intensity criterion for classifying both odors, but with rapid adaptation to concentration range. Stronger adaptation to the more-intense odor could decrease the intensity difference in a manner similar to differential context effects in taste perception [27, 28].

Rat and human perception share many features. In human studies, intensity is often related to concentration as a power function with an exponent less than one [5, 29, 30]. Here we show that both odor concentration discriminability and the intensity mismatch index between odors appear to be consistent with a logarithmic organization of perceived intensity (but other forms cannot be discounted [31]). For suprathreshold odors, rats' discrimination performance was scale invariant as observed in human subjects [32, 33], and, in accord with human studies [5, 14, 34], perceived intensity decreased rapidly with adaptation in rats. Finally, the relationship between molecular weight and intensity in rats is similar to measurements in humans [11]. These data suggest possible links between human odor perception and neurophysiology in animal models.

Several sources may contribute to the neural representation of perceived intensity. Odors stimulate not only olfactory receptors, but also neurons in the trigeminal nerve [35, 36]. However, intensity mismatch behaved similarly across a 100-fold variation in odor concentration and with the odor phenyl ethyl alcohol, which is likely not perceived via trigeminal activation [37]. This argues that trigeminal activation is not necessary for intensity perception in rats [35].

The results of this study suggest a systematic link between the neural representations of different odors. Similar percepts are thought to be generated by similar patterns of neural activity. Our finding of a common percept of intensity across different odors implies the existence of a common neural representation for this perceptual feature. Previous studies investigating neural odor representations have suggested that odors are represented as arbitrary points within a multidimensional neural space [38, 39]. Nearby points within this neural space are thought to give rise to similar perceptual qualities [40–42]. However, in this framework, there is little to distinguish representations of different odors and different concentrations of the same odors. Indeed, different odors have been observed to lie closer than different concentrations of the same odor in neural space [39, 43]. We suggest that an

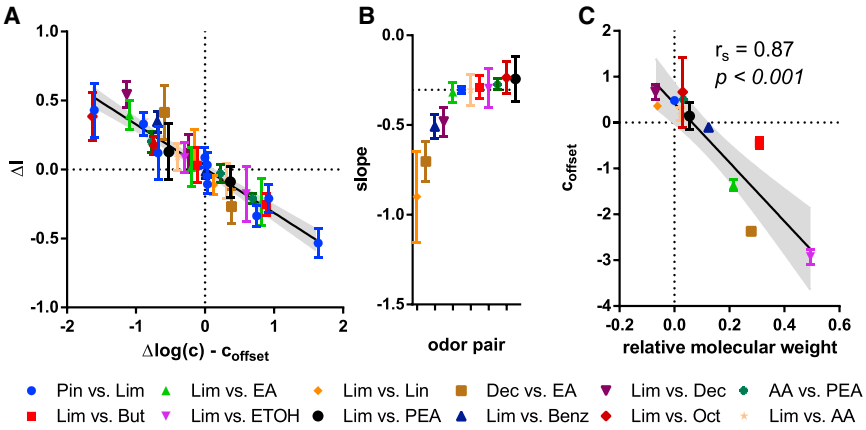

Figure 4. Intensity Mismatch Index between Odors Is a Function of Airborne Concentration and Molecular Weight

(A) Intensity mismatch index as a function of relative airborne concentration for 11 odor pairs ($n \geq 5$ rats per point). Relative concentrations yielding zero intensity mismatch (c_{offset}) have been subtracted to facilitate comparison. Line and shaded region show regression line fitted to all points and 95% confidence interval.

(B) Individual regression slopes for ΔI versus $\Delta \log(c)_{air}$ for each odor pair. The dotted horizontal line is the median slope value.

(C) Concentration offset at isointensity ($\Delta I = 0$) as a function of relative molecular weight between odor molecules (Spearman $r_s = 0.87$, $p < 0.001$). The line and shaded region show regression line fitted to all points and 95% confidence interval. Error bars represent the SD in (A) and 68% confidence intervals in (B) and (C).

arbitrary representation space is not consistent with perception of odor intensity. Instead, our results are consistent with an ordered representation of odor intensity along a single common dimension in neural space [44].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.01.059.

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