Humans Can Discriminate More than 1 Trillion Olfactory Stimuli

C. Bushdid,[1]* M. O. Magnasco,[2] L. B. Vosshall,[1,3] A. Keller[1]†

Humans can discriminate several million different colors and almost half a million different tones, but the number of discriminable olfactory stimuli remains unknown. The lay and scientific literature typically claims that humans can discriminate 10,000 odors, but this number has never been empirically validated. We determined the resolution of the human sense of smell by testing the capacity of humans to discriminate odor mixtures with varying numbers of shared components. On the basis of the results of psychophysical testing, we calculated that humans can discriminate at least 1 trillion olfactory stimuli. This is far more than previous estimates of distinguishable olfactory stimuli. It demonstrates that the human olfactory system, with its hundreds of different olfactory receptors, far outperforms the other senses in the number of physically different stimuli it can discriminate.

To determine how many stimuli can be discriminated, one must know the range and resolution of the sensory system. Color stimuli vary in wavelength and intensity. Tones vary in frequency and loudness. We can therefore determine the resolution of these modalities along those axes and then calculate the number of discriminable tones and colors from the range and resolution. Humans can detect light with a wavelength between 390 and 700 nm and tones in the frequency range between 20 and 20,000 Hz. Working within this range, researchers carried out psychophysical experiments with color or tone discrimination tasks in order to estimate the average resolution of the visual and auditory systems. From these experiments, they estimated that humans can distinguish between 2.3 million and 7.5 million colors (*1*, *2*) and ~340,000 tones (*3*). In the olfactory system, it is more difficult to estimate the range and resolution because the dimensions and physical boundaries of the olfactory stimulus space are not known. Further, olfactory stimuli are typically mixtures of odor molecules that differ in their components. Therefore, the strategies used for other sensory modalities cannot be applied to the human olfactory system. In the absence of a straightforward empirical approach, theoretical considerations have been used to estimate the number of discriminable olfactory stimuli. An influential study from 1927 posited four elementary odor sensations with sufficient resolution along those four dimensions to allow humans to rate each elementary sensation on a nine-point scale (*4*). The number of discriminable olfactory sensations was therefore estimated to be 9^4 or 6561 (*4*). This number was later rounded up to 10,000 and is widely cited in lay and scientific publications (*5*–*7*). Although this number was initially calculated to reflect how many olfactory stimuli humans can discriminate, it has also sometimes been used as the number of different odor molecules that exist, or the number of odor molecules that humans can detect. We carried out mixture discrimination testing to determine a lower limit of the number of olfactory stimuli that humans can discriminate.

Natural olfactory stimuli are almost always mixtures of large numbers of diverse components at different ratios. The characteristic scent of a rose, for example, is produced by a mixture of 275 components (*8*), although typically, only a small percentage of components contribute to the perceived smell. We reduced the complexity by investigating only mixtures of 10, 20, or 30 components drawn from a collection of 128 odorous molecules (table S1). These 128 molecules were previously intensity-matched by Sobel and co-workers, which enabled us to produce mixtures in which each component contributes equally to the overall smell of the mix-

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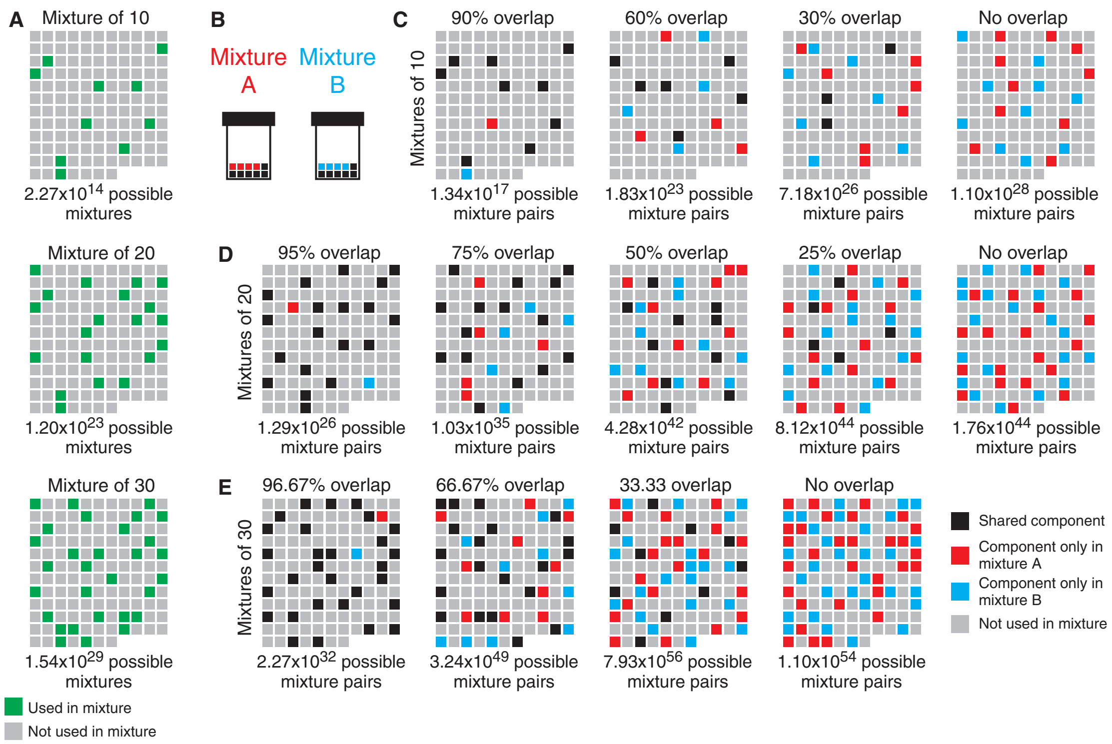

Fig. 1. Odor mixtures used to test the resolution of the human olfactory system. (**A**) Illustration of sample mixtures with exactly 10, 20, or 30 components (green squares) picked from a collection of 128 odorous molecules (gray squares) and the number of possible mixtures of each type. (**B**) Example of one mixture pair. (**C** to **E**) Schematics of each of the 13 types of odor pairs used for discrimination tests, along with the total number of possible mixture pairs of each type.

ture (9). The 128 molecules cover much of the perceptual and physicochemical diversity of odorous molecules (10–12) because the collection contains most of a collection of 86 odorous molecules that were selected to be well distributed in both perceptual and physicochemical stimulus space (9).

To generate each mixture, we combined these components together at equal ratios. The 128 components can be combined into 2.27×10^{14} different mixtures of exactly 10, 1.20×10^{23} different mixtures of exactly 20, and 1.54×10^{29} different mixtures of exactly 30 (Fig. 1A). The most salient difference between two mixtures with the same number of components is the percentage of components in which they differ. We therefore performed psychophysical testing to determine the resolution of the human olfactory system along this axis. We asked by what percentage two mixtures must differ on average so that they can be discriminated by the average human nose. This percentage difference in components is the resolution of the olfactory system.

Subjects performed forced-choice discrimination tests to determine the discriminability of pairs of mixtures (referred to here as "mixture A" and "mixture B") that varied in the percentage of shared components (Fig. 1B). In double-blind experiments, subjects were presented with three odor vials, two of which contained the same mixture, whereas the third contained a different mixture. The testing procedure was computerized by using a custom-written application in which subjects were instructed to identify the odd odor vial on the basis of odor quality. Each subject completed the same 264 discrimination tests. The order of the tests was randomized. For each of 13 types of stimulus pairs (Figs. 1, C to E, and 2A), 20 different stimuli pairs were tested, for a total of 260 mixture discrimination tests. In addition, four control discrimination tests comprising individual odor molecules were interleaved across the mixture discrimination tests so as to measure general olfactory acuity and subject compliance. Because we wished to ensure that discrimination was based on odor quality differences and not small intensity differences, one of the three stimuli in a test was diluted in propylene glycol at a 1:2 ratio, the other at a 1:4 ratio, and the third was not diluted. The dilutions were assigned to the stimuli at random. The components and dilutions of all stimuli used in this study are given in table S2.

Twenty-eight subjects completed the study, but two were excluded from the analysis because they failed to correctly identify the odd odor in at least three of the four control tests. Data from 26 subjects [17 female; median age 30 (range of 20 to 48); 14 Caucasian, 5 African-American, 5 Asian, 2 Other; 4 Hispanic] are included in the analysis presented here.

Pairs of mixtures are more difficult to distinguish the more they overlap. At least half of the tested subjects could discriminate mixture pairs that overlapped by less than 75% of their components. Some could also discriminate mixture pairs that overlapped by 75 and 90%, but none could discriminate mixture pairs with more than 90% overlap (Fig. 2B). In this evaluation, the results of 20 mixture pairs of a certain type (for example, mixtures of 20 components that overlap by 75%) are pooled. Specific mixture interactions that are known to occur in odor mixtures, such as synergy and masking, are averaged out. To assess whether this biased our results, we also analyzed the results for each individual mixture pair, averaged across the 26 subjects (Fig. 2C). The results of this analysis were very similar. Of the 260 pairs of mixtures that were tested for discriminability, subjects performed above chance level for 227. For 148 of those, 14 or more of the 26 subjects (54%) chose the correct vial, resulting in a statistically significant difference from chance (Fig. 2C).

The resolution (or difference limen) of the visual and auditory system is defined as the difference in frequency between two stimuli that is required for reliable discrimination. In the olfactory system, resolution can be defined as the highest percentage overlap in components between two mixtures at which those mixtures can be distinguished. The resolution of the olfactory system is not uniform across the olfactory stimulus space. For example, half of the mixtures of 20 components with 50% overlap could be discriminated, whereas the other half were indiscriminable (Fig. 2C, middle). Nonuniform resolution across stimulus spaces is also found in other sensory systems. In hearing, for example, frequency resolution is much better at low than at high frequencies (3). In vision, wavelength discrimination is best near 560 nm, at which a difference in wavelength of 0.2 nm can be discriminated under optimal conditions (13).

We extrapolated functions that relate the percentage mixture overlap to mixture discriminability from our data. The function that relates the percentage mixture overlap (x) with the percentage of subjects that can discriminate the mixtures (y) is $y = -0.81x + 91.45$ (Fig. 3A). The function that relates the percentage mixture overlap (x) with the percentage of discriminable pairs (y) is $y = -0.77x + 94.22$ (Fig. 3B). According to these formulae, most subjects can discriminate mixture pairs that overlap by less than 51.17%. Most pairs that overlap by less than 57.43% can be discriminated.

To calculate a lower limit of how many discriminable mixtures there are, the number of possible mixtures and the difference between two mixtures that renders them indistinguishable have to be known. There are 2.27×10^{14} possible mixtures of exactly 10 (out of 128), 1.20×10^{23} possible mixtures of exactly 20, and 1.54×10^{29} possible mixtures of exactly 30. Using the numbers from our data, a lower limit of how many discriminable mixtures there are can be calculated. Mathematically, this

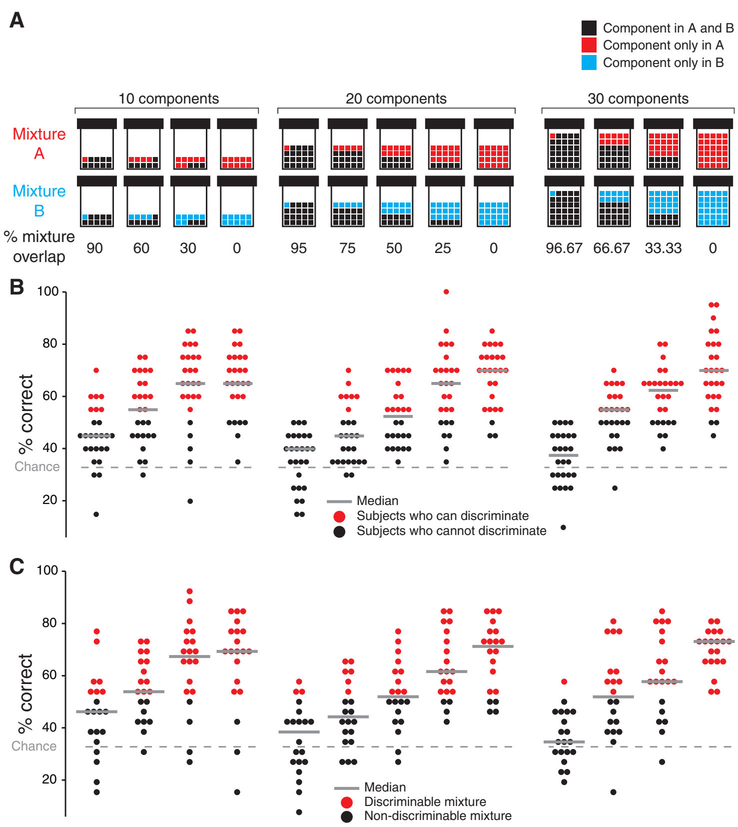

Fig. 2. An empirical investigation of the resolution of the human olfactory system. **(A)** Schematic of the discrimination tests carried out for mixtures of 10, 20, or 30 odorous molecules. **(B** and **C)** Results of discrimination tests with 26 subjects asked to discriminate mixtures of 10 (left), 20 (middle), or 30 (right) components with decreasing overlap from left to right. The dotted line represents the chance detection level (33.3%). For (B), dots represent performance of individual subjects across 20 mixture pairs. For (C), dots represent average performance of all 26 subjects for a given mixture pair. Statistically significant discriminability (red dots) was assessed with a χ^2 test; $P < 0.05$.

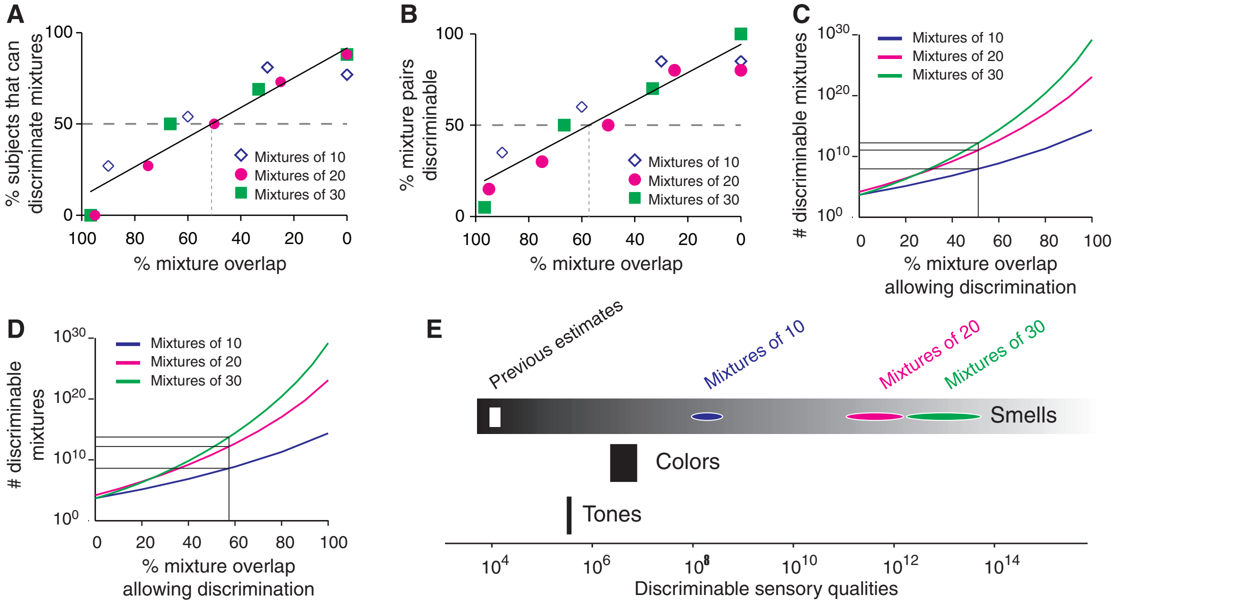

Fig. 3. The number of discriminable olfactory stimuli. (**A**) Discrimination capacity of subjects according to percentage of mixture overlap. (**B**) Discriminability of mixture pairs according to percentage of mixture overlap. (**C**) Extrapolation of the number of discriminable mixtures derived from (A). (**D**) Extrapolation of the number of discriminable mixtures derived from (B). (**E**) Summary of discriminable sensory stimuli across sensory modalities. Data are curated from the following sources: smells (previous estimates) (*5*–*7*), tones (*3*), and colors (*1*, *2*).

presents a coding problem that can be formulated in information theory as a problem of packing spheres in multidimensional space (*14*). The solution to this problem (details are available in the supplementary materials, materials and methods) shows that a resolution of 51.17% overlap results in 9.37×10^7 distinguishable mixtures of exactly 10, 1.12×10^{11} mixtures of exactly 20, and 1.72×10^{12} mixtures of exactly 30 (Fig. 3C). A resolution of 57.43% overlap results in 4.01×10^8, 1.55×10^{12}, and 5.58×10^{13} discriminable mixtures, respectively (Fig. 3D).

Mixtures that overlap by less than 51.17% can be discriminated by the majority of subjects, which means that humans can, on average, discriminate more than 1 trillion mixtures of 30 components. However, there are large differences between subjects. The number of discriminable mixtures with 30 components in one subject of this study is 1.03×10^{28}, whereas it is only 7.84×10^7 in another subject (fig. S1).

One can calculate the number of mixtures that can be discriminated by either using the discrimination capacity of subjects or by the discriminability of stimulus pairs. Depending on what criteria are used, our results show that humans can discriminate 1.72×10^{12} or 5.58×10^{13} mixtures of 30 components out of the collection of 128 odorous molecules. 1.72×10^{12} may seem like an astonishingly large number. However, there are 1.54×10^{29} possible mixtures of 30 from the 128 components used here. Therefore, if there are 1.72×10^{12} discriminable stimuli, this means that for each mixture tested there will be 8.95×10^{16} other mixtures that cannot be discriminated from it.

Our results show that there are several orders of magnitude more discriminable olfactory stimuli than colors (*1*, *2*) or tones (*3*) (Fig. 3E). Colors are spatially arranged to create a large number of visual objects that are the building blocks of visual experiences, and tones can be combined to form a large number of chords that form auditory objects. The number of visual and auditory objects is much larger than the number of colors and tones, but it is unknown how many of these objects humans can discriminate. However, the difference between the number of discriminable olfactory stimuli and colors or tones is even larger if one considers that the number of discernible tones and colors includes stimuli that differ in loudness or brightness. We focused here only on stimulus quality and ruled out intensity-based discrimination. Thus, our estimate of 1.72×10^{12} is a conservative one yet is still several orders of magnitude higher than previous estimates of the number of discriminable olfactory stimuli (*5*–*7*). The actual number of distinguishable olfactory stimuli is likely to be even higher than 1.72×10^{12} for three reasons. First, it is currently not known how many odorous molecules there are or how many of them can be discriminated from the others. However, there are considerably more possible odorous molecules than the 128 different components that we used. Second, components can be combined in mixtures of more than 30 components. Third, even mixtures with the same components can be distinguished if the components are mixed at different ratios (*15*). Our results therefore establish only a lower limit of the number of discriminable olfactory stimuli. Although this lower limit of greater than 1 trillion is several orders of magnitude more than distinguishable colors or tones, it is presumably dramatically lower than the actual number of discriminable olfactory stimuli.

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Supplementary Materials
www.sciencemag.org/content/343/6177/1370/suppl/DC1
Materials and Methods
Fig. S1
Tables S1 and S2

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Supplementary Material for

Humans Can Discriminate More Than 1 Trillion Olfactory Stimuli

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This PDF file includes:

Materials and Methods

Fig. S1

Other Supplementary Material for this manuscript includes the following:
(available at www.sciencemag.org/content/343/6177/1369/suppl/DC1)

Tables S1 and S2

Materials and Methods

Study Subjects

Each subject in the study completed the same 264 discrimination tests over three visits to the Rockefeller University Hospital Outpatient Unit. Each subject completed the three visits over a period of three to nine days. The median duration of the visits was 1 h and 6 min (range: 38 min to 2 h 54 min). Only English-speaking subjects aged 18 to 50 with no allergies to fragrances or smells were enrolled in this study. Further exclusion criteria were active head cold, upper respiratory infection, or seasonal nasal allergies as well as a history of nasal health problems, and any other pre-existing medical conditions that may cause reduced olfactory acuity, such as: head injury, cancer therapy, radiation to head and neck, and alcoholism. All subjects gave their informed consent to participate and all procedures were approved by the Rockefeller University Institutional Review Board. Subjects were compensated for their participation in the study.

Psychophysics

Subjects performed olfactory three-alternative forced-choice discrimination tests that are also known as triangle tests. For these tests, subjects were presented with three odor vials, two of which contained the same mixture, whereas the third contained a different mixture. The testing procedure was computerized using a custom-written Microsoft Access application in which subjects were instructed to identify the odd odor vial based on odor quality and scan the bar code affixed to the side of that vial. The application was written so that the order of the visits as well as the order of the tests during a visit was randomized. A tray containing all the vials was presented to the subjects. Subjects were instructed to open the vials, sniff the contents, and follow instructions on the computer screen. Subjects are numbered in Table S2 according to their overall performance in discriminating the 260 mixture pairs, such that Subject 1 had the worst performance and Subject 26 the best. Although Subject 1 successfully discriminated 3 of 4 control discrimination tests, this individual performed close to chance for the 260 mixture pairs (34.6% correct). In showing extremes of inter-individual discrimination ability in Fig. S1, we therefore show data from Subject 2 and not Subject 1.

Calculation of the Number of Mixtures and Mixture Pairs

There are C = 128 odorous molecules in the collection from which the components of the mixtures were picked. The 13 types of mixture pairs differ in the number of components (N = 10, 20, or 30) in the mixtures and in the number of components in which the two mixtures overlap (O, where $0 \leq O < N$). The formula to calculate the number of possible mixtures is:

$$\binom{C}{N} = \left(\frac{C!}{(C-N)!\,(N!)}\right)$$

The procedure to calculate the number of possible pairs of mixtures of N components that overlap by O components is to choose one of the two members of the pair, which is chosen arbitrarily as N out of C. Then we have to choose O elements. The formula to calculate the number of possible pairs is:

$$\binom{C}{N}\binom{N}{O}\binom{C-N}{N-O}/2$$

Numbers are rounded for display but were computed with arbitrary precision using Mathematica.

<u>Calculation of the Number of Discriminable Mixtures From the Empirically Determined Resolution</u>

When calculating the number of discriminable stimuli that differ along a single dimension, such as the wavelength of monochromatic light, we parcel the range of stimuli into segments whose size equals the difference limen (or resolution). For a hypothetical example, if we could perceive light with wavelengths in the range between 400 and 700 nm and discriminate two lights when they differ by more than 10 nm, there would be 30 segments of size 10 nm:

400 nm ↔ 410 nm, 410 nm ↔ 420 nm, ..., 690 nm ↔ 700 nm.

An equivalent representation of these segments can be given by labeling them by their center:

405 nm +/- 5 nm, 415 nm +/- 5 nm, ..., 695 nm +/- 5 nm.

In this second representation we have chosen one particular stimulus from each segment, the center of the interval, as an explicit representative. There are 30 stimuli (405 nm, 415 nm, ..., 695 nm) each of which is separated from the others by at least one difference limen. The 30 stimuli form a set of stimuli that are mutually discriminable, so in this hypothetical example we can discriminate 30 different colors. Notice that in moving from the first to the second representation of these segments, we switched from describing segments as having a width (or diameter) equal to the limen (10 nm) to having a center and a radius around that center of half the limen (5 nm).

When the stimulus space is two-dimensional, instead of calculating the number of segments of a certain width, one would calculate how many circles of a certain diameter can be packed into the stimulus space. For a three-dimensional stimulus space, one would count spheres that can be packed into the three-dimensional space. This mathematical procedure can be generalized to stimulus spaces with more than three dimensions. Thus, the number of stimuli that can be discriminated in a multidimensional stimulus space can be determined through *sphere packing* (*14*). Regardless of the number of dimensions of the stimulus space, one can calculate how many spheres of a diameter equal to the difference limen can be packed into the stimulus space. The number of these spheres that can be packed into the stimulus space is the number of discriminable stimuli, just as in a one-dimensional stimulus space the number of segments with width equal to the difference limen that can be packed into the space is the number of discriminable stimuli.

We applied this strategy of sphere packing in a multi-dimensional stimulus space to calculate the number of discriminable mixtures from the difference limens that we empirically determined in the psychophysical experiments presented here. The question that we addressed by this calculation was how many mixtures of N components out of a collection of C components exist that all differ from one another by more than D components. If two mixtures of N that differ by more than D components can be discriminated, this is also the number of discriminable mixtures. D is the difference limen. For pairs of mixtures, D is the number of components in the mixtures (N) minus the number of components that are present in both (the overlap O) for pairs which still can be discriminated (D = N-O). In the geometric analogy, the question how many discriminable mixtures there are, is the problem of how many balls of diameter D (or radius R; D = 2*R) can be packed into a C-dimensional space.

Calculating the number of balls that can be packed into a multidimensional space is a two-step process. First, we had to calculate how many mixtures are contained in each ball of a diameter equal to the difference limen [formula (2) below]. These are mixtures that cannot be discriminated from one another. Then, the total number of all mixtures in the stimulus space has to be divided by the number of mixtures contained in each of these balls to arrive at the number of balls that can be packed into the stimulus space [formula (3) below]. This is the number of discriminable mixtures.

To calculate how many mixtures are contained in a ball of a certain diameter, we first calculated how many mixtures are contained in a *sphere* of a certain diameter [formula (1) below] and then, using the results of this calculation, the number of mixtures in a *ball* of that diameter [formula (2) below]. A *sphere* is a spherical surface or shell, so a sphere of radius R around its center X is the set of all points which is *precisely* at distance R from X. A *ball* is the spherical surface and everything within it, so a ball of radius R around its center X is the set of all points at distances *smaller than or equal to* R. Spheres are hollow while balls are solid. In our case, the points in stimulus space represent mixtures. The mixtures on the sphere around any give mixture X all differ by exactly R components from mixture X. The mixtures in the ball all differ by R or less components from X. More importantly, all mixtures in one ball differ from each other by less than the difference limen D (=N-O). Therefore, all the mixtures in a ball are indiscriminable, just as for all the light stimuli between 400 and 410 nm in the above example.

How many different mixtures of N components are contained in a sphere of radius R around a mixture X in a C-dimensional space? The sphere of radius 1 around mixture X consists of all the mixtures in which precisely one component has been changed. They all overlap with mixture X by N-1 components. There are N choices of the single component to be changed, and each one can be changed to any component not already in X, of which there are C-N. Thus the sphere of radius 1 contains N*(C-N) odor mixtures. Similarly, for the sphere of radius 2 we have to choose 2 components from X. There are N(N-1)/2=$\binom{N}{2}$ such choices, and these two components can be changed to any of the C-N components not in X, giving us $\binom{C-N}{2}$ such choices. Since these choices are independent, the formula to calculate how many different mixtures of N components are contained in the sphere of radius R in a C-dimensional space is:

$$sphe(R) = \binom{N}{R}\binom{C-N}{R} \qquad \text{Formula (1)}$$

Formula (1) allows us to calculate the number of mixtures that differ by *exactly R* components from a mixture X. To calculate how many mixtures differ by *R or less* components, it has to be calculated how many mixtures are contained in a ball (not a sphere) with a diameter equal to the difference limen. The number of stimuli contained in a ball is calculated by summing the numbers of stimuli contained in the spheres that make up the ball. Because we cannot change components fractionally, the number of stimuli contained in a ball with radius R it the sum of the numbers of mixtures in the spheres of radius R, R-1, R-2, ..., , and 0 (The sphere of radius 0 contains only mixture X itself). Thus, the formula to calculate how many different mixtures of N components are contained in the ball of radius R in a C-dimensional space is:

$$ball(R) = \sum_{r=0}^{R} sphe(r) \qquad \text{Formula (2)}$$

Formula (2) allows us to calculate the number of mixtures that differ by *R or fewer* components from a mixture X. If two mixtures can only be discriminated if they differ by more than D (=2*R) components, then *ball(R)* is the number of mixtures that cannot be discriminated from one another. In the geometric analogy, it is the size of the ball around a point X that contains all the mixtures that cannot be discriminated from the mixture at its center and from each other.

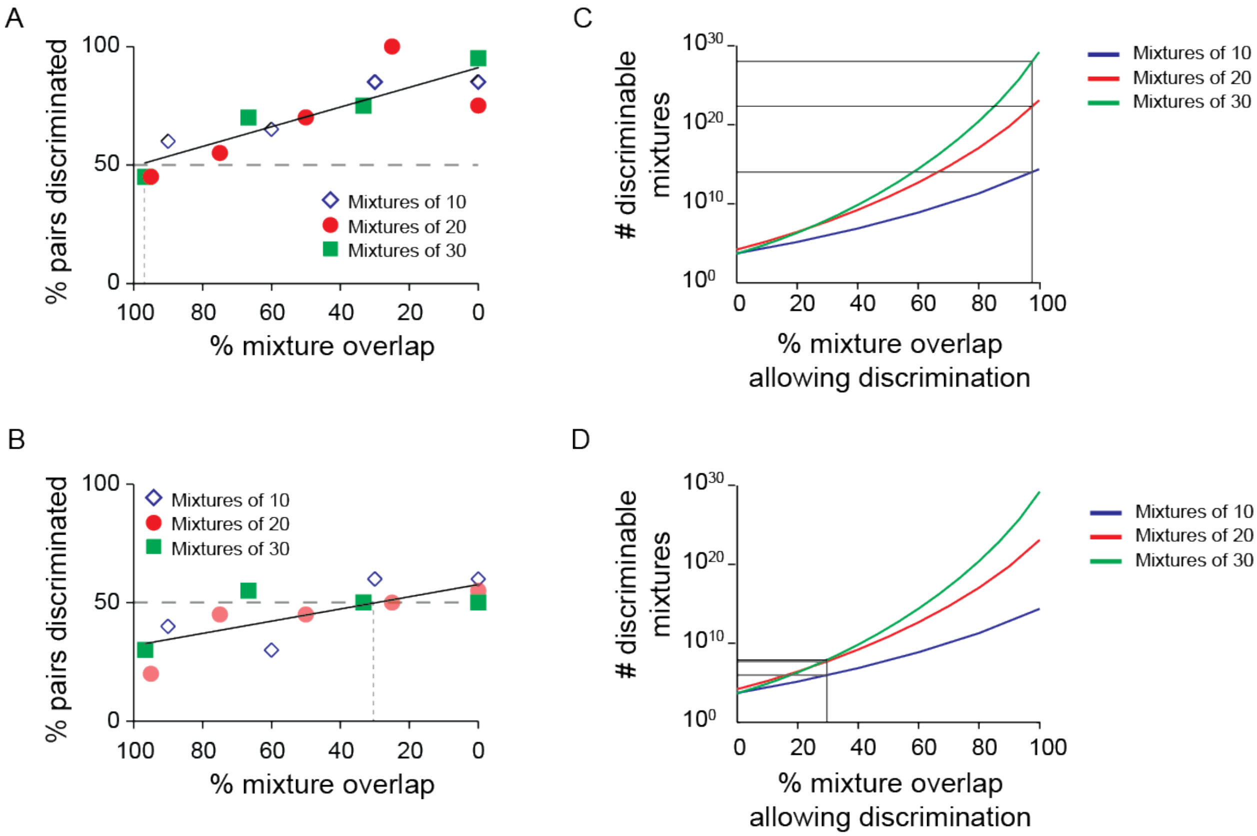
In a final step, to approximate the number of discriminable mixtures, it has to be calculated how many balls of size *ball(R)* can be packed into the stimulus space. This is done by dividing the total number of mixtures in the stimulus space by the number of mixtures contained in a ball of diameter D. The formula to calculate this is:

$$disc(D) = \frac{\binom{C}{N}}{\sum_{r=0}^{D/2}\binom{N}{R}\binom{C-N}{R}} \qquad \text{Formula (3)}$$

disc(D) is the number of discriminable mixtures of N out of a collection of C if only mixtures that differ by more than D components can be discriminated (D=2*R=N-O). This is an upper bound as it fails to count the “dead space” in the corners between spheres.

Formula (3) was used to generate the graphs in Fig. 3 C/D and Fig. S1 C/D. C is 128 in these cases and the value of O changes along the x-axis. The three lines are the results of formula (3) for three different values of N (10, 20, and 30). The numbers of discriminable mixtures reported in this paper were then extrapolated from the graphs using Mathematica by determining the number of discriminable mixtures that correspond to the values of O (in percentage) that were shown in the psychophysical testing to correspond to the difference limen.

Fig. S1.



Inter-individual variability in the discrimination capacity of subjects. (A) Discrimination capacity of subject 26 (Table S2) according to % mixture overlap. (B) Discrimination capacity of subject 2 (Table S2) according to % mixture overlap (C, D) Extrapolation of the number of discriminable mixtures derived from A and B, respectively.

Additional table S1 (separate file)
The 128 odorous molecules used in this study.

Additional table S2 (separate file)
The odor mixtures used in this study and the results of the discrimination tasks.