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Report

Hunter-Gatherer Olfaction Is Special

Highlights

- People struggle to name odors, but this limitation is not universal
- Is superior olfactory performance due to subsistence, ecology or language family?
- Hunter-gatherers and non-hunter-gatherers from the same environment were compared
- Only hunter-gatherers were proficient odor namers, showing subsistence is crucial

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In Brief

People struggle to name odors, but this limitation is not universal. Majid and Kruspe investigate whether superior olfactory performance is due to subsistence, ecology, or language family. By comparing closely related communities in the Malay Peninsula, they find that only hunter-gatherers are proficient odor namers, suggesting that subsistence is crucial.

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Hunter-Gatherer Olfaction Is Special

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SUMMARY

People struggle to name odors [1–4]. This has been attributed to a diminution of olfaction in trade-off to vision [5–10]. This presumption has been challenged recently by data from the hunter-gatherer Jahai who, unlike English speakers, find odors as easy to name as colors [4]. Is the superior olfactory performance among the Jahai because of their ecology (tropical rainforest), their language family (Aslian), or because of their subsistence (they are hunter-gatherers)? We provide novel evidence from the hunter-gatherer Semaq Beri and the non-hunter-gatherer (swidden-horticulturalist) Semelai that subsistence is the critical factor. Semaq Beri and Semelai speakers—who speak closely related languages and live in the tropical rainforest of the Malay Peninsula—took part in a controlled odor- and color-naming experiment. The swidden-horticulturalist Semelai found odors much more difficult to name than colors, replicating the typical Western finding. But for the hunter-gatherer Semaq Beri odor naming was as easy as color naming, suggesting that hunter-gatherer olfactory cognition is special.

RESULTS

Olfaction has long been considered the least significant of the human senses [11]. Biological anthropologists have suggested that vision supplanted olfaction as humans became upright [5]. The convergence of the orbits, associated with stereoscopic vision, forced a reduction of olfactory apparatus in our ancestors [6]: primates have a comparatively smaller olfactory bulb [7]; a proportionally smaller surface area of the nasal cavity is covered with the olfactory epithelium [8]; and there is a negative correlation between olfactory and visual brain structures [9]. Moreover, there is evidence of a genetic trade-off between vision and olfaction with the advent of trichromatic vision [10], with more than 60% of olfactory receptor genes functionally inactive in humans [12]. This asymmetry between vision and olfaction appears in language, too [1]. References to vision in everyday conversation far outstrip references to olfaction [2]. There are more lexical distinctions made for visual than for olfactory phenomena [1], so when forced to talk about specific smell qualities, people resort to analogies using source-based descriptions instead (e.g., *it smells like banana*, *chocolate*, etc.). Under experimental conditions, familiar odors encountered in daily life are rarely named correctly [3]. Taken together, the evidence suggests that odors may be ineffable [1].

This presumption has recently been challenged by findings from two hunter-gatherer communities in the Malay Peninsula—the Jahai and Maniq [4, 13, 14]. In one experiment where Jahai speakers were asked to name odors and colors, their naming was compared to age- and gender-matched English speakers from the US. While English speakers had higher codability for colors than odors, Jahai speakers found odors as easy to name as colors. In fact, they had higher codability for odors than English speakers did, even though the odors were typical Western smells [4]. Linguistic analysis shows that the Jahai language has a dozen dedicated words to describe different qualities of smells [13]; e.g., *pʔus* refers to moldy or musty odors of old dwellings, decaying vegetation, mushrooms, stale food, and some types of dried plants.

It is unclear what factors might underlie the evolution of dedicated olfactory vocabulary and the improved ability to name odors. Both Jahai and Maniq are related Aslian languages (a branch of the larger Austroasiatic family), spoken by hunter-gatherers living in tropical rainforest in the Malay Peninsula, are part of the same Semang culture group [15], and share phenotypic traits characterized by short stature, dark skin, and “peppercorn” hair [16]. Any of these factors—language-relatedness, environment, culture, biology—could be relevant [17]. We present new evidence that the inability to name odors is a culturally contingent fact related to subsistence mode. We compared speakers of two related Southern Aslian languages, who traditionally engaged in different subsistence modes: the mobile hunter-gatherer Semaq Beri and the more sedentary Semelai, who combined swidden rice cultivation and the collection of forest products for trade (Figure 1). If ease of olfactory naming is related to cultural practices, then we would expect the Semaq Beri to behave like the Jahai and name odors as easily as they do colors, whereas the Semelai should pattern differently. That is exactly what we found (Figure 2).

Semaq Beri and Semelai participants took part in an odor- and color-naming experiment (STAR Methods). Following previous work [4], we measured naming performance by calculating agreement between speakers in their descriptions using Simpson’s Diversity Index [18]. This measure captures the notion that the easier it is to linguistically express a perceptual experience—i.e., the more codable it is—the more likely speakers are

Figure 1. Semaq Beri and Semelai Going about Their Daily Lives

(A–D) (A) Semaq Beri woman foraging for yams, and (C) children making a new fire to avoid mixing cooking odors; (B) Semelai women harvesting rice, and (D) burning fragrant incense to quell a storm.

within a community to agree in their descriptions of that experience. While the hunter-gatherer Semaq Beri showed equal ease in naming odors and colors $F(1, 94) = 1.149$, $p = 0.287$, $\eta_p^2 = 0.012$, the swidden-horticulturalist Semelai showed an asymmetry with lower codability for smells than colors $F(1, 94) = 63.636$, $p < .0001$, $\eta_p^2 = 0.404$. More importantly, Semaq Beri had higher codability for odors than the Semelai $F(1, 94) = 15.094$, $p < .0001$, $\eta_p^2 = 0.138$ (Figure 2). The hunter-gatherer Semaq Beri predominantly used domain-specific abstract terms (e.g., *musty*, *blue*) for both odors (86%) and colors (80%), and there was no statistical difference between domains $\chi^2(1, N = 1{,}387) = 0.707$, $p = 0.400$. The swidden-horticulturalist Semelai, on the other hand, showed a different strategy. They used abstract descriptions for color (e.g., *blue*, *green*; 78%) like the Semaq Beri (see also Figure 3) but predominantly source-based descriptions for odors (e.g., *banana, chocolate*; 56%); $\chi^2(1, N = 1{,}595) = 959.03$, $p = 0.0001$.

DISCUSSION

Our results confirm previous speculation that hunter-gatherers might be particularly attuned to odors [19]. In our study, we compared odor naming to color naming following previous comparative studies [1, 4, 20, 21], which build on a long-line of cross-cultural investigation of perceptual qualities [22–26]. An alternative would have been to compare odor naming to picture naming. It has been suggested that the olfactory system strives for object recognition, just as the visual system does [27, 28]; although this position is not uncontroversial [29, 30]. Our data suggests that, at least at the linguistic level, odors and colors are treated as equivalent: similar strategies are used to express both (Figure 2). The parallel also suggests that there may be an evolutionary sequence to olfactory lexicons to be uncovered [31], just as has been proposed for color lexicons previously [22]. Hunter-gatherers have been found to have some of the simplest color lexicons, often only making a basic distinction between "black," "white," and possibly "red," with additional terms being added with increasing cultural complexity [22, 32, 33]. Could the inverse hold for smell?

Further data is required to know definitively one way or the other, but there is some tantalizing evidence already. Odor lexicons have been reported for hunter-gatherer communities in as far-flung places as Thailand, Gabon, and Mexico, where speakers occupy different environmental niches from tropical rainforest to desert [4, 13, 14, 19, 34–37]; although they have also been claimed in other cultural contexts without a hunter-gatherer lifestyle [13, 38–41]. In fact, both the Semaq Beri and Semelai languages have odor lexicons, but dedicated terminology does not guarantee codability in communication. Witness the differential codability of color in the two languages here. There are a comparable number of basic color categories in both languages (Figure 3), but the Semelai, nevertheless, demonstrated higher naming agreement for color. This shows that there is no necessary relationship between having "words for things" and psycholinguistic codability [1].

Does the critical difference between Semaq Beri and Semelai really boil down to subsistence mode? Matters are more complex and interesting. As stated previously, a trade-off between the senses with olfaction being suppressed at the advent of trichromatic vision [10] predicts that people should universally be better at naming colors than odors. This is not supported by our Semaq Beri results. In fact, the genetic trade-off account is problematic considering that there has been a gradual loss of olfactory receptor (OR) genes in primate evolution rather than the abrupt loss predicted [42]. Even if such a trade-off was supported, the fact that both color and olfaction are used for foraging in other species [43–46] suggests that both senses can play an important functional role for humans, too.

Within the human lineage, OR genes vary substantially both within [47–50] and between populations [51–54]. It has been shown that African populations have more functional OR genes than non-African populations [53], and African Pygmies have more than Bedouins, Yemenite Jews, and Ashkenazi Jews [52]. So it is not a big leap to suggest that there may be a genetic component to the group differences reported here. The Semang, Senoi, and Malayic culture-groups have genetically distinct profiles [55], although no relevant studies of OR genes exist for these communities. But it is worth pointing out that OR genes are

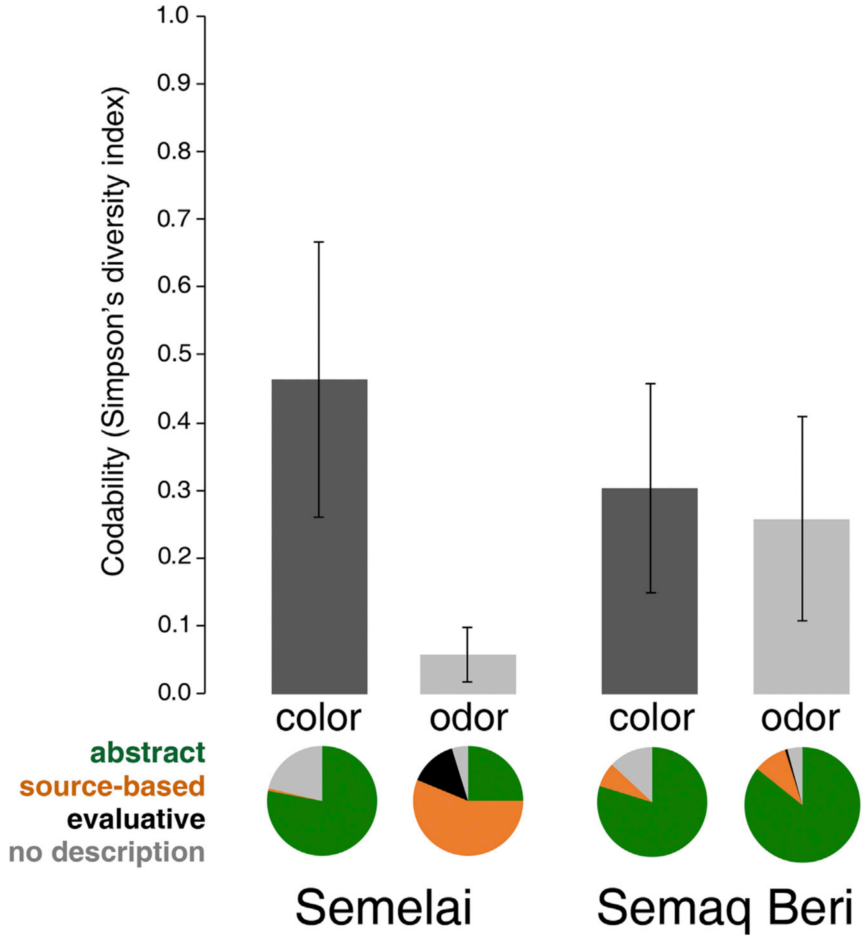

Figure 2. Codability of Odors and Colors

For Semaq Beri participants, odors are as codable as colors, while Semelai participants show poor codability for odors. Error bars depict standard deviation.

linked to perceiving odors, not naming them. Odor-naming difficulties have been attributed instead to brain connectivity: either olfactory and language areas of the brain are too weakly connected [56], too directly connected [28], or their neural signals interfere with each other [57]. This suggests that if we were to look for a genetic basis of odor-naming, the relevant genes would regulate neuroanatomical connectivity rather than odor perception, per se.

Our study compared two groups who both live in the humid tropical rainforest of the Malay Peninsula. Compared to the more temperate zones of Europe and Northern America, this part of the world contains far more biological diversity and thus arguably hosts more varied odor-emitting sources: there are more than 850 species of orchids, 83 species of bat, 1,200 species of termites, and 1,000 species of butterfly, for example [58]. High rainfall, humidity, and temperature in the rainforest increases molecular volatility [59], creating more odorous surroundings overall. Primary rainforest can be dense, with estimates suggesting that only 1%–3% of light reaches the forest floor [58]. Perhaps this visual gloominess downgrades vision, making olfaction more salient. These characteristics of the environment, shared by the Semaq Beri and Semelai, suggest that we should not be looking for explanatory factors in their environmental niche. However, their difference in subsistence modes means that the communities interact differently with the environment. The Semaq Beri traditionally lived inside the forest, but the Semelai lived in swiddens, produced by slashing-and-burning vegetation. So although surrounded by forest, there was a distinct physical demarcation between human-space and forest-space. The communities are thus creating different local environments as part of their cultural practices.

In sum, the hunter-gatherer Semaq Beri behave just like the hunter-gatherer Jahai: odors are as codable as colors for them. However, the non-hunter-gatherer Semelai behave more

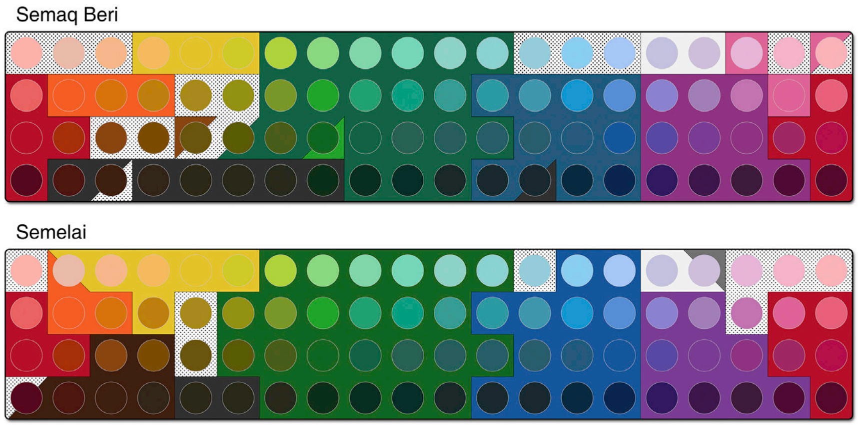

Figure 3. Color Maps for Semelai and Semaq Beri

Color areas reflect color-chips described with the same word. Dotted areas represent color-chips for which there was no dominant name.

like English speakers: odors are difficult to name. These broad cultural categories hide a wealth of relevant cultural practices. For example, the Semaq Beri and Semelai have different attitudes toward the forest, and their religious practices also diverge. Semaq Beri men readily move around alone in the forest, but the Semelai are reluctant to do so without company. The Semaq Beri use their odor lexicon whatever their business, while the Semelai have a taboo on using odor terms in the forest. The Semaq Beri believe that people have an inherent personal odor, and people manage their social spaces to avoid inappropriately mixing their odors (e.g., a brother and sister sitting too close together is considered incest). The Semelai do not share this belief. Ultimately, the differences between the groups are richer than a simple classification into "hunter-gatherer" versus "non-hunter-gatherer." Nevertheless, we show that lifestyle and subsistence are important determinants in the ineffability of odors, and explanations of human olfactory abilities must include a cultural dimension.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Subjects
  - Stimuli
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AUTHOR CONTRIBUTIONS

A.M. and N.K. contributed equally to the study conception and design. N.K. collected the data. N.K. and A.M. coded and processed the data. A.M. analyzed the data. A.M. and N.K. jointly wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests should be directed to and will be fulfilled by the Lead Contact Asifa Majid, asifa.majid@let.ru.nl.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Subjects

The data were collected and treated according to the ethical guidelines of American Psychological Association, as approved by the local Ethics Assessment Committee at Radboud University. Twenty Semaq Beri participants (18 females) were tested in total. However, due to practical restrictions, only 18 participants provided data for the odor-naming task, and 16 for the color-naming task. Older members of the group (35+ years) have no formal education. Most of the younger speakers have attended, but not completed primary school; one participant was attending secondary school at the time of testing. Recently some of the women have attended an adult literacy program. The language of instruction in school is Malay. Aside from schooling, there is also exposure to Malay through television and pop-culture. Older speakers have limited proficiency in the local variety of Malay; younger speakers are relatively more proficient, although Malay is only ever spoken with outsiders. Seven of the participants also speak Batek Deq, a neighboring language from the less-closely related Northern branch of Aslian. All participants still pursue aspects of traditional foraging, but their livelihood relies increasingly on collection and trade in forest produce.

Twenty-one Semelai participants were tested (17 females). Two participants had no formal education, while the others varied from incomplete primary education (n = 12) to secondary level education (n = 7). Proficiency in Malay varied over the sample, from passive knowledge in older participants to low-level bilingualism among the young. Malay is only ever used with non-Semelai, but again there is constant exposure through television and pop-culture. The Semelai participants are settled, and mostly small-holding rubber-tappers. Four of the male and two of the female participants had spent periods (from 2-20 years) working as laborers outside the community.

All sessions were conducted in the villages in which the participants reside. The sessions were conducted in either Semaq Beri or Semelai, as appropriate. Before collecting naming data, all participants were screened for color blindness using Ishihara plates [60]. Smoking, and chewing betel from the age of weaning are prevalent in both communities. Participants were asked to refrain from both before and during testing.

The precise age of many participants is difficult to ascertain, but ranged from the teens to seventies. Based on our best information, there was no significant difference in age between Semaq Beri ($M = 34$) and Semelai ($M = 38$) speakers $t(38) = 1.01$, $p = 0.32$.

Stimuli

For the odor task, we used “Sniffin’ Sticks” [61]. These are marker pens containing an odorant (instead of ink) which the participant can smell by removing the marker cap and smelling the tip. Sixteen odors were used: orange, leather, cinnamon, peppermint, banana, lemon, licorice, turpentine, garlic, coffee, apple, clove, pineapple, rose, anise, and fish. For the color task, participants saw 80 Munsell color chips, sampling 20 equally spaced hues at 4 degrees of brightness [60]. Odors and colors were presented in a randomized fixed order. After the free naming task, participants were shown a sheet with all 80 color chips laid out according to hue and brightness, plus 4 additional achromatic colors, and asked to identify the best example of the most frequent colors elicited from the naming task [62].

Procedure

Participants were tested in their native language, and asked “*What smell is this?*” or “*What color is this?*” Both languages share an indigenous abstract term *kʰləm* for odor, and a borrowed term *kalə* for color. Where possible, sessions were video- and audio-recorded, and later transcribed, as well as noted on site. In addition to the experimental data collection, ethnographic-based interviews were conducted on the cultural significance of the two perceptual domains.

QUANTIFICATION AND STATISTICAL ANALYSIS

Following [4], we coded agreement between speakers in their main responses using Simpson’s Diversity Index [18], calculated using $D = \sum n(n-1)/N(N-1)$, where n = the total number of responses using that particular name and N = the total number of responses across all names. Simpson’s Diversity Index provides a summary statistic that takes into account the number of different words produced, as well as how often each word appeared: zero indicates each participant gave a unique response for a stimulus, while 1 indicates all participants agreed and the same word was used by all. In calculating agreement, we ignored modification and hedging in the full responses: e.g., *quite red, very red, pinkish red*, etc were all coded as *red*.

Codability scores across items [63] were analyzed using a 2-by-2 ANOVA, treating language as a within-items factor and sensory domain as a between-items factor. We began by analyzing agreement on first responses, as these can be taken to be the most salient linguistic responses. There was no main effect of language $F(1, 94) = 0.482$, $p = 0.49$, $\eta_p^2 = 0.005$; i.e., the two groups showed comparable agreement patterns. There was an effect of sensory domain $F(1, 94) = 36.709$, $p < .0001$, $\eta_p^2 = 0.281$, but critically there was an interaction between language and domain $F(1, 94) = 40.950$, $p < .0001$, $\eta_p^2 = 0.303$ (see Figure 1). In Semaq Beri odors were as codable as colors $F(1, 94) = 1.149$, $p = 0.287$, $\eta_p^2 = 0.012$, but in Semelai they were significantly less codable $F(1, 94) = 63.636$, $p < .0001$, $\eta_p^2 = 0.404$ (see Figure 1). Semaq Beri speakers agreed more in how they described odors than Semelai speakers did $F(1, 94) = 15.094$, $p < .0001$, $\eta_p^2 = 0.138$; but the Semelai agreed more with each other in how to describe colors $F(1, 94) = 48.823$, $p < .0001$, $\eta_p^2 = 0.342$.

We also calculated Simpson's Diversity Index taking all responses into consideration, to test whether agreement in naming increased (especially for odors) when alternate names were considered. The pattern of results was the same. There remained an interaction between language and domain $F(1, 94) = 31.29$, $p < .0001$, $\eta_p^2 = 0.25$. As before, odors were more codable in Semaq Beri than Semelai $F(1, 94) = 8.206$, $p = .005$, $\eta_p^2 = 0.080$; while colors were more codable in Semelai $F(1, 94) = 53.239$, $p < .0001$, $\eta_p^2 = 0.362$.

Finally, we examined the types of responses for each domain. Based on previous literature [4], the main linguistic strategy of interest was the use of abstract (e.g., *blue, musty*) versus source-based terminology (e.g., *leaf-colored, like a banana*). Semaq Beri speakers used domain-specific abstract terms for both odors (86%) and colors (80%), and there was no statistical difference between domains $\chi^2(1, N = 1{,}387) = 0.707$, $p = 0.400$. Semelai speakers, on the other hand, used predominantly abstract terms for colors (78%), but source-based terms for odors (56%). This difference was statistically reliable $\chi^2(1, N = 1{,}595) = 959.03$, $p = 0.0001$. Overall, participants were conservative when naming colors and smells; preferring to give no response when unsure. No description accounted for 13% of Semaq Beri data for color, and 21% for Semelai color; but only 4% of Semaq Beri odour data, and 5% of Semelai odor data. Evaluative descriptions (e.g., *nice, disgusting*) did not appear at all for color in either community. Less than 1% of Semaq Beri responses were evaluative for odor, whereas 14% of Semelai were evaluative for odor (see Figure 2). So, when Semelai speakers did not offer a source-based description for odors, they were most likely to offer an evaluative description instead.

DATA AND SOFTWARE AVAILABILITY

The data are archived at RWAAI https://corpora.humlab.lu.se/ds/imdi_browser/?openhandle=10050/00-0000-0000-0003-CFA7-6.