

$(1-\alpha)c_1:(1+\alpha)c_2$ blend of the two odorants. A complete switch in preference, however, might occur for a relatively small value of α . This, together with a possible greater salience for honey-bee workers of hexadecane over methyl docosanoate, could explain Breed and Julian's data under a proportion hypothesis.

A priority cue hypothesis requires that the components of a blend are individually perceived. In worker honeybees, however, olfactory receptors do not function under a "labelled-line" paradigm but rather respond to classes of compounds^{8,9} to generate "across-fibre" patterns in the antennal lobe of their brains^{4,10}. Thus it is unlikely, in general, that bees can identify individual components in a stable blend. This is not to say that they do not perceive a blend that has a dominant component (in terms of salience) as being similar to that component on its own, or that they cannot identify components in blends that vary across space or with time¹¹. On the other hand, interaction effects¹² may cause the quality of a blend to be perceived as different from, rather than intermediate to, its component odorants, in which case the quality of the component odorants may be completely masked.

In making the statement "... the choice of [kin discrimination] cue compounds may be driven by the prioritization system. . .", Breed and Julian cite a study¹³ which actually supports a proportion rather than a priority hypothesis. In that study, aggression increases in a graded though asymmetrical way as differences in the discrimination signature are increased from purely genetic differences to both genetic and environmental differences. Further, data in a companion to that study¹⁴ indicate that the level of an aggressive response among individuals in a species of ant, as in the honey-bee¹⁵, is modulated in a graded fashion by both individualistic and *Ges-*

talt components of the nestmate recognition signature. These ant and honey-bee data are contrary to a priority cue hypothesis, which predicts that either the individualistic or *Gestalt* component should dominate so that no graded response is observed.

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BREED REPLIES — Getz, of course, is quite wrong: his critique fails on both empirical and logical grounds. Empirically, he suggests that hexadecane might simply be overpowering methyl docosanoate at the concentrations used, and that had a series of ratios been tried we might have found a pair of concentrations giving the contrary result. There are three problems with this argument.

First, the two compounds are equally effective in changing the recognition status of individuals. If hexadecane were more overpowering than methyl docosanoate, we would expect it to have a stronger effect in the controls; it does not. Second, the effect of hexadecane remains the same over a broad range of concentrations; it operates as an off/on signal rather than a graded signal over an order of magnitude of concentration differences (M. D. B. and R. Bowden, unpublished observations). The experimentally imposed cues do not work in a vacuum but co-occur with the cues that the bees already possess: if ratios were important the ratios between existing and imposed cues would assert themselves. Third, I tested tetracosanoic acid (which is equivalent in this system to methyl docosanoate) and hexadecane in 1:3 and 3:1 ratios, and found that 27.5% ($n = 51$) of the bees receiving a 3:1 ratio of tetracosanoic acid to hexadecane were attacked by bees treated with a 1:3 ratio, while the attack rate was 18.2% ($n = 39$) in controls (in which bees all received a 1:3 ratio). This difference is not statistically significant ($\chi^2 = 1.86$, d.f. = 1). This result is consistent with the data presented in our original paper.

The logical problem with Getz's ratio model is that as a bee flies to and from floral resources its surface is heated due to both internal heat production (from muscular activity) and to solar radiation. The thorax of a flying bee is usually several degrees warmer than the ambient temperature. Compounds that are known to be active in honey-bee recognition vary considerably in their volatility. As a flying bee heats up, concentrations of individual compounds will change differentially. Thus, the ratios of a bee arriving back at the colony may differ substantially from the ratios of

departing bees. Getz's model cannot account for how bees accommodate these changes.

Getz favours the ratio model but has no empirical evidence in this behavioural context to support his argument. He attempts to undermine our position by suggesting an impossibly difficult experimental design, based on the idea that if one tries enough different ratios and enough concentrations, ultimately evidence for a ratio model will appear. I suggest that the data in our original paper, perhaps strengthened by the additional information mentioned here, establish the principle of cue prioritization firmly enough that it can only be dislodged by an empirical demonstration to the contrary.

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Inside information

SIR — Gonnet and Benner¹ claim that words obtained from the one-letter code for amino acids in protein sequences "are candidates for the most unusable pieces of information". On the contrary, such words in a sequence can give valuable information about the protein. I have come across two such cases without even searching. The end of the sequence of the insulin-responsive glucose transporter (IRGT, Glut 4) from rat, mouse and man reads . . .END (. . .Glu Asn Asp)²⁻⁶. The second case, which may not be obvious to non-Swedes, is in the sequence of the pig lactate dehydrogenase: . . .SVIN. . . (. . .Ser Val Ile Asn. . ., at positions 302-305)⁷, which in Swedish means 'pig', and which should leave no doubts about the protein origin. However, the chicken lactate dehydrogenase H-chain is also labelled SVIN (ref. 8), which calls into question the reliability of these built-in pieces of information.

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