

Orchid pollination by sexual swindle

The flowers of *Ophrys* orchids mimic receptive females of usually only one pollinator species. Males of this species are attracted primarily by the odour of a flower and transfer the pollinia during so-called 'pseudocopulations' with the flowers¹⁻³. We have found that flowers of *O. sphegodes* produce the same compounds and in similar relative proportions as are found in the sex pheromone of its pollinator species, the solitary bee *Andrena nigroaenea*. Common straight-chain saturated and unsaturated hydrocarbons are the key components in this chemical mimicry, which seems to be an economical means of pollinator attraction.

Naturalists have long wondered why the shape and colour of the flowers of *Ophrys* are similar to those of certain insects⁴. The odour of a flower was found to be the most important signal triggering pseudocopulation behaviour². Although many odour components were produced by the flowers as well as by their pollinators⁵⁻⁷, there has been no convincing identification of the compounds that trigger pseudocopulation. We have used gas chromatography-electroantennographic detection to identify physiologically active compounds, which were subsequently tested in the field for behavioural activity. The activity of synthetic mixtures was compared with that of the sex pheromone of female bees and the pollinator-attracting scent of *Ophrys* flowers.

We tested various odour samples of female bees and orchid flowers for their attractiveness to male bees (Fig. 1). Of all bee-odour samples tested, cuticle extracts elicited the most intense behavioural reactions from males, indicating that this is where the sex pheromone of *A. nigroaenea* is located. Extracts from the *Ophrys* flower labellum also elicited frequent copulation attempts by males (Fig. 1).

In the experiments using gas chromatography-electroantennographic detection, 15 components from the attractive odour samples of female bees triggered electroantennographic responses in male antennae (Table 1). The *Ophrys* flower extracts contained all except one of these compounds. The compounds were identified by gas chromatographic-mass spectrometric analyses as straight-chain saturated and unsaturated hydrocarbons with 21-29 carbon atoms. Both sample types contained these compounds in very similar relative proportions (Table 1). To investigate the behavioural activity of electrophysiologically active compounds, we performed behavioural tests with male bees. A blend of 14 synthetic hydrocarbons occurring in both the bee scent and the flower scent, mixed in accordance with the relative proportions

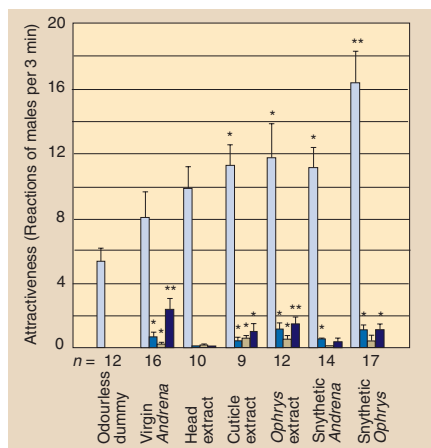


Figure 1 Reactions of *Andrena nigroaenea* males in behavioural tests in the field. Odourless dummies (Soxhlet-extracted, dried *A. nigroaenea* females) scented with different samples were offered to *A. nigroaenea* males in a patrolling area for 3 min. Means (\pm s.e.m.) of approaches to the dummy to less than 5 cm (pale blue bars), pouncing on the dummy (royal blue bars) and copulation attempts with the dummy (dark blue bars) are plotted. The Mann-Whitney *U*-test was used for statistical analysis. Asterisks indicate significant differences between the reaction types of the odourless-dummy group and each of the other six test groups at significance levels of * $P < 0.05$ and ** $P < 0.001$.

found in either sample type, elicited frequent copulation attempts in males when applied to a dummy (Fig. 1).

Our understanding of the mechanisms of chemical mimicry in *Ophrys* orchids has been constrained by a limited knowledge of the chemical composition of sex pheromones in the solitary bees and wasps that serve as pollinators. Earlier studies reported aliphatic 1- and 2-alcohols and terpenes in flowers and bee odours to be the key components for pollinator attraction in several *Ophrys* species^{5,7}. However, these compounds did not elicit definite copulation

attempts in male bees. This led to the hypothesis that *Ophrys* flowers produce only a set of "second-class attractivity compounds" that attract only the part of the pollinator population with a low threshold for sexual stimuli⁵.

Our results challenge this view. In *O. sphegodes*, we find that the behaviour-inducing odour bouquet is more or less identical to the sex pheromone of the female bees and therefore elicits nearly equally intense reactions. But the behaviourally active compounds are ubiquitous or occur in at least trace amounts in plant cuticular waxes⁸. The similarities in their relative amounts in orchid labella and attractive female bees supports the view that the specific pattern of otherwise common compounds is the key innovation of *O. sphegodes* for the attraction and deception of the pollinators.

These findings shed new light on the evolution of this fascinating insect-plant relationship. Cuticular hydrocarbons, as a part of the plant surface wax, primarily prevent the loss of water. During the evolution of chemical mimicry in *O. sphegodes*, these compounds obtained the additional function of attracting pollinators, which was achieved through alterations in their relative proportions. It seems feasible that, in an ancestor of *Ophrys*, the pattern in a mutant occasionally resembled that of the sex pheromone of a pollinator species. This could have led to pollination by sexually excited males of this species, and natural selection would have favoured further plant mutants with a hydrocarbon pattern with an even closer resemblance. Apart from advantages discussed elsewhere⁹, being pollinated by pseudocopulating males allowed the plant to decrease the costly emission¹⁰ of typical floral-odour compounds. Flowers of *O. sphegodes*, like those of many *Ophrys* species, emit only minute quantities of such volatiles^{5,11}. Chemical

Table 1 Electrophysiologically active compounds in cuticle extracts of virgin *Andrena nigroaenea* females and labellum extracts of *Ophrys sphegodes* flowers

Compound	Abundance (%)		Statistics <i>P</i>
	<i>Andrena</i>	<i>Ophrys</i>	
Henicosane	1.6 \pm 0.5	1.8 \pm 0.3	0.151
Docosane	0.6 \pm 0.1	0.5 \pm 0.1	0.909
Tricosane	28.7 \pm 2.4	30.6 \pm 1.8	0.705
Tetracosane	2.0 \pm 0.2	3.1 \pm 0.2	0.002
(<i>Z</i>)-9-pentacosene	3.4 \pm 1.8	0.6 \pm 0.1	0.406
Pentacosane	34.9 \pm 2.2	20.2 \pm 1.3	0.000
Hexacosane	1.6 \pm 0.1	2.1 \pm 0.2	0.016
(<i>Z</i>)-12 + (<i>Z</i>)-11-heptacosene	0.7 \pm 0.3	6.0 \pm 0.8	0.000
(<i>Z</i>)-9-heptacosene	5.1 \pm 1.6	7.6 \pm 1.0	0.112
Heptacosane	11.2 \pm 1.1	11.5 \pm 1.5	0.940
(<i>Z</i>)-12 + (<i>Z</i>)-11-nonacosene	3.7 \pm 1.4	6.7 \pm 1.0	0.010
(<i>Z</i>)-9-nonacosene	6.6 \pm 0.4	9.4 \pm 1.2	0.082

Abundances are given as mean \pm s.e.m. ($n = 10$); *P* values were calculated using the Mann-Whitney *U*-test.

mimicry in the sexually deceptive pollination system therefore also provided an economical way for the plant to ensure its transfer of gametes.

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Fractal analysis of Pollock's drip paintings

Scientific objectivity proves to be an essential tool for determining the fundamental content of the abstract paintings produced by Jackson Pollock in the late 1940s. Pollock dripped paint from a can onto vast canvases rolled out across the floor of his barn. Although this unorthodox technique has

been recognized as a crucial advancement in the evolution of modern art, the precise quality and significance of the patterns created are controversial. Here we describe an analysis of Pollock's patterns which shows, first, that they are fractal¹, reflecting the fingerprint of nature, and, second, that the fractal dimensions increased during Pollock's career.

To quantify the fractal content of Pollock's drip paintings, such as *Alchemy* (Fig. 1), we used the well-established 'box-counting' method² to calculate the fractal dimension D . We cover the scanned photograph of a Pollock painting with a computer-generated mesh of identical squares. The number of squares $N(L)$ that contain part of the painted pattern is then counted; this is repeated as the size, L , of the squares in the mesh is reduced. The largest size of square is chosen to match the canvas size ($L \approx 2.5$ m) and the smallest is chosen to match the finest paintwork ($L \approx 1$ mm). For fractal behaviour, $N(L)$ scales according to $N(L) \propto L^{-D}$, where $1 < D < 2$. The D values are extracted from the gradient of a graph of $\log N(L)$ plotted against $\log L$. This fractal analysis reveals two distinct D values occurring over the ranges $1 \text{ mm} < L < 5 \text{ cm}$ and $5 \text{ cm} < L < 2.5 \text{ m}$. Our analysis of a film of Pollock while painting shows that the fractal patterns occurring over the lower range are determined by the dripping process, whereas the fractal patterns across the higher range are shaped by his motions around the canvas.

Our analysis shows that Pollock refined his dripping technique: the fractal dimensions increased steadily through the years, from close to 1 in 1943 to 1.72 in 1952. Because D follows such a distinct evolution with time, the fractal analysis could be used as a quantitative, objective technique both to validate and date Pollock's drip paintings. The change in D reflects a dramatic evolution in visual character. His initial drip paintings of 1943 consisted of a single layer

of paint trajectories that occupied only 20% of the 0.35-m² canvas area; by 1952 he was painting multiple layers of trajectories that covered over 90% of his 9.96-m² canvas. It is important that Pollock introduced his fractals systematically: the initial fractal layer essentially determined D by acting as an anchor layer for the subsequent fractal layers, which then fine-tuned the value of D .

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Release from inhibition reveals the visual past

Prolonged viewing of a high-contrast repetitive pattern such as a grating leads to adaptation of the corresponding visual-processing channels¹. We have found that such viewing also leads to the short-term establishment of a subthreshold trace in the brain that can cause a visual illusion of the pattern during rebound from the cross-orientation inhibition^{2–4} that is induced by viewing moving patterns with an orthogonal orientation.

McKay⁵ reported that viewing a stationary pattern of radial lines causes the illusion of fine grains or wavy lines moving in circles. This has been explained as being due to antagonism between pattern and movement channels within an orientation column⁶. We have discovered a new visual after-effect by extending this model to explore antagonism between different orientation columns.

With the subject fixating at the centre, a windmill pattern is presented that slowly rotates at 0.2 Hz in one direction for 5 s, and then in the other direction (Fig. 1a). If this is followed by a pattern orthogonal to the windmill, namely concentric rings, diverging and converging for 5 s each at 2 Hz, viewing a blank screen after the concentric rings causes a vivid after-effect of a stationary windmill for a few seconds. This after-effect is quite different from that seen after viewing the concentric rings alone at 2 Hz, if indeed any after-effect is visible. With a cyclical presentation of the sequence shown in Fig. 1a, a striking windmill-like after-effect is always seen after the concentric rings (bottom left blank in Fig. 1a), but no comparable after-effect is visible immediately after the windmill (top right blank in Fig. 1a). We found that the after-effect could be produced if the rings were delayed by up to 30 s, but not after 60 s.



Figure 1 *Alchemy*, painted by Jackson Pollock in 1947. Drip paintings of this period are characterized by fractal dimensions close to 1.5. Reproduced by permission of ARS, NY and DACS, London, 1999.