Predator and prey views of spider camouflage

Both hunter and hunted fail to notice crab-spiders blending with coloured petals.

Crab-spiders (*Thomisus onustus*) positioned for hunting on flowers disguise themselves by assuming the same colour as the flower, a strategy that is assumed to fool both bird predators and insect prey. But although this mimicry is obvious to the human observer, it has never been examined with respect to different visual systems. Here we show that when female crab-spiders mimic different flower species, they are simultaneously cryptic in the colour-vision systems of both bird predators and hymenopteran prey.

In animal communication, colouring is a compromise between being conspicuous to conspecifics and being poorly visible to predators or prey[1]. Female crab-spiders adapt their entire body colour to that of the flowers on which they are trying to hide, a behaviour that is presumed to conceal them from predators and from the visiting pollinators that constitute their main prey[2].

To appear cryptic to both predators and prey, these spiders must precisely match the flower colour in their respective ranges of colour vision: four cone types, corresponding to ultraviolet (UV)–blue–green–red, for birds, and three (UV–blue–green) for insects[3,4]. However, these visual systems differ markedly in their range of sensitivity and number of photoreceptors, making a precise colour match for both unlikely.

We used spectroradiometry to measure the degree of matching (crypsis) of *T. onustus* collected on the corollae of two flower species (*Senecio jacobea* and *Mentha spicata*) growing around Tours, France. To analyse spider crypsis with respect to potential predators and prey on each flower, we computed and compared colour distances in the respective colour spaces of birds and Hymenoptera (see supplementary information).

For birds, spiders matched pink *Mentha* corollae when viewed through the four-cone colour-vision system (Fig. 1; $\chi^2 = 9$, d.f. $= 1$, $P < 0.01$). Likewise, on *Senecio*, each spider matched the individual yellow corolla on which it was waiting for prey ($\chi^2 = 7.5$, d.f. $= 1$, $P < 0.01$). But on the *Senecio* UV–yellow petal background, spiders produced a strong colour contrast that birds were likely to detect ($\chi^2 = 2.7$, d.f. $= 1$, $P > 0.05$). For Hymenoptera, spiders matched the blue-green colour of *Mentha* corollae in the three-cone colour-vision system ($\chi^2 = 4$, d.f. $= 1$, $P < 0.05$). They also effectively mimicked the individual blue-green colour of *Senecio* corollae ($\chi^2 = 7.5$, d.f. $= 1$, $P < 0.01$), but contrasted on UV–green petals when seen by Hymenoptera ($\chi^2 = 2.7$, d.f. $= 1$, $P > 0.05$).

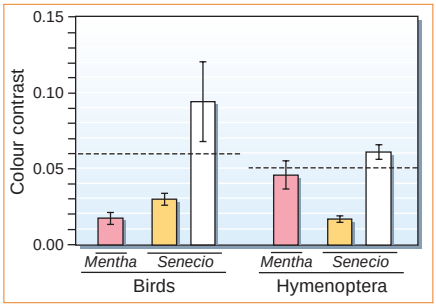

Figure 1 Colour contrast of spiders (mean euclidean distances ± s.e.m.) against *Mentha* corollae (pink bars), *Senecio* corollae (yellow bars) and *Senecio* petals (white bars) when viewed by birds and Hymenoptera. Dashed lines indicate thresholds for colour-contrast detection calculated for birds and Hymenoptera. For details of modelling calculations, see supplementary information.

To detect small targets, birds and bees can use achromatic vision instead of colour contrast[5,6]. Spiders were significantly brighter than corollae of *Mentha* (repeated-measures ANOVA, birds: $F_{1,17} = 8.5$, $P < 0.001$; Hymenoptera: $F_{1,17} = 8.6$, $P < 0.001$) and *Senecio* (birds: $F_{1,14} = 35.7$, $P < 0.001$; Hymenoptera: $F_{1,14} = 46.2$, $P < 0.001$), but were darker than *Senecio* petals (birds: $F_{1,14} = 133.7$, $P < 0.001$; Hymenoptera: $F_{1,14} = 157.3$, $P < 0.001$).

Our results indicate that crab-spiders' colour mimicry works successfully on the visual systems of both predator and prey, achromatic vision being potentially more efficient under particular viewing conditions. This aggressive mimicry may vary from species to species, as shown by *Misumena vatia*[7], a crab-spider that reduces its chromatic contrast to bees on white flowers (as in Fig. 2), as does *T. onustus*, but is also able to reduce its achromatic contrast on yellow flowers.

Figure 2 Master of disguise: a crab-spider (left), concealed against a flower's white petals, preys on an unsuspecting bee.

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COMMUNICATIONS ARISING

Brain evolution

Analysis of mammalian brain architecture

The mammalian brain is composed of several distinct parts which show different growth in evolution. Clark, Mitra and Wang[1] found that the two main cortices of the brain — the cerebral (neo-) cortex and the cerebellum — show very different growth, and that whereas the ratio of neocortex volume to total brain volume increases with evolution, the cerebellum occupies a constant proportion in different species. Here I compare the surface areas of the two cortices in different species and find that these show a simple proportionality. Contrary to the conclusion drawn by Clark *et al.*[1], this linear dependence of size implies that the two major cortices increase their computational capacity in parallel, suggesting a functional dependence of the one upon the other.

The results of Clark *et al.*[1] are unexpected, because it is known that the cerebellar parts that show the most pronounced growth in evolution are linked to the neocortex and that, congruently, the main input and output structures of the cerebellum (the pontine and dentate nuclei) are also closely linked to the neocortex in evolutionary growth[2]. Together with the

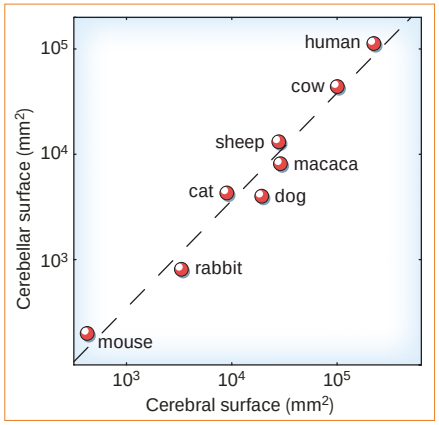

Figure 1 Logarithmic plot of cerebellar[11] versus cerebral cortex area[12]. The slope of the least-squares logarithmic regression line is 1.02 ($y = 1.02$, $x = -0.52$, Spearman's $r = 0.95$, $P < 0.0003$), indicating a linear dependence of cerebellar on cerebral cortex surface. (Brodmann's data provided by H. J. Jerison.)

neocortex, these two nuclei are among the brain structures that show the largest increase in primates[2]. This interconnectedness between the two cortices does not appear in the measurements of Clark and colleagues[1].

I have considered cortical surface areas, rather than volumes, as a potentially more appropriate measure of the computational capacity of sheet-like formations, and observe a linear relation between telencephalon and cerebellum over a wide range of different mammals (Fig. 1). As the cerebellum is a highly folded cortex of almost uniform thickness in all species, the increase in cerebellar size can also be measured in terms of cortical surface area.

However, the cerebral cortex increases in thickness by a factor of 7.6 across different mammalian species[3], making the increase in volume in larger species greater than proportional to the increase in area. This should be taken into account when considering the relative volumes of the two cortices. In the case of the cerebellum, its volume represents a constant fraction of the total brain volume, as shown by Clark *et al.*[1].

The discrepancy between the results of Clark *et al.*[1] and the constant ratio of cerebral and cerebellar surface areas may also be due to their inclusion of the white matter in the volumes of neocortex and cerebellum. The human neocortex consists of nearly 42% white matter, a peak value for primates, in which, as in other mammals, larger brains have a greater proportion of white matter[4]. In contrast, the cerebellum has a more-or-less constant proportion of white matter (30% in rats[5] and 26% in humans[6]).

The increase in neocortical white matter during evolution[7,8] probably reflects the need in larger brains to maintain the high connectivity required to operate associative networks[9]. The cerebellum, in contrast, lacks a system of intrinsic long-range connections and relies entirely on the operation of local short-range connections within the grey matter[10]. The cerebellar subcortical white matter is composed only of input and output fibres, the number of which is proportional to the surface area of the cortex.

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How did brains evolve?

Three reports on mammalian brain evolution[1–3] analyse the same comparative data on brain component volumes[4] but come to partially conflicting conclusions. Clark *et al.*[3] conclude from their analysis of volumetric brain proportions ("cerebrotypes") that cerebellum size is invariant across mammalian taxonomic groups, the neocortex and cerebellum do not co-vary in size (in contradiction to ref. 1), and cerebrotype-based measures identify directional changes in brain architecture. Here I provide evidence that calls each of these conclusions into question. The failure of the cerebrotype measure to identify species differences in brain architecture that are independent of gross brain size undermines the proposal by Clark *et al.* that it could be useful for detecting evolutionary patterns and phylogenetic relationships.

In attempting to establish uniformity of cerebellum size, Clark *et al.* do not use a multiple-comparisons procedure, instead carrying out *t*-tests for each taxon against all the other taxa, thereby pooling taxa with smaller- and larger-than-average cerebellum size. In contrast, analysis of variance (ANOVA) on cerebellar volume proportion in nine mammalian orders[5] (not including two echolocating taxa said to deviate from cerebellar constancy[3]) indicates significant variance ($F = 18.8$, d.f. = 7, 81, $P < 0.0001$, 15 of 28 pairwise comparisons significant). What Clark *et al.* have observed is that neocortex size varies more than cerebellum size, so that variation in the latter is small as a proportion of the whole. This does not, however, contradict an important evolutionary relationship between them.

The fact that, as the neocortical fraction of brain size increases, the cerebellum does not, like all the other structures, decrease as a proportion of total brain volume[3], suggests that the cerebellum and neocortex evolved together, but with the cerebellum evolving more slowly. When variation in the size of other brain structures is partialled out, there is a significant correlation between cerebellum and neocortex size (Fig. 2). This correlation is not dependent on using residuals from linear regression, as it is also found using simple ratios of cerebellum and neocortex size to the size of the rest of the brain (across taxa, $r^2 = 0.87$, d.f. = 1, 91, $P < 0.0001$). Neither is it an artefact of taxonomic effects such as 'grade shifts'[1], as it is apparent using the method of phylogenetically independent contrasts[6], which controls for such effects (primates, $r^2 = 0.33$, d.f. = 1,39, $P < 0.0001$; insectivores, $r^2 = 0.27$, d.f. = 1,32, $P = 0.002$). Data

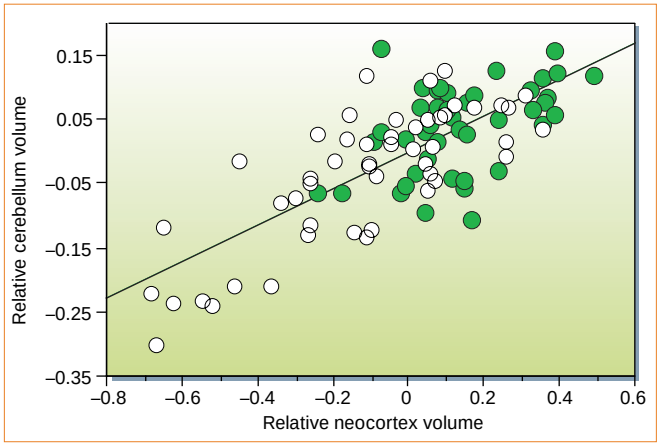

Figure 2 Correlated variation in the relative size of neocortex and cerebellum. Relative size was defined as the residual from the least-squares regression of structure volume on the volume of the rest of the brain. The correlation is significant across taxa ($r^2 = 0.57$ d.f. = 1,91, $P < 0.0001$, slope = 0.29), and also within each taxon (primates, filled circles, $r^2 = 0.22$, $P = 0.001$, slope = 0.20; insectivores, hollow circles, $r^2 = 0.62$, $P < 0.001$, slope = 0.24). The correlations are strengthened when the diencephalon, through which neocortex–cerebellum connections project, is excluded from the rest of the brain (for example, across taxa, $r^2 = 0.72$, $P < 0.0001$, slope = 0.35). In each case, slopes of substantially less than unity indicate that cerebellum size evolved more slowly than neocortex size.