

testing the two models came from constructing truncated *BLD10* alleles predicted to make shorter coiled coils. Expressing these truncated proteins in the *blid10* null mutant background led to production of structurally abnormal centrioles in which the number of triplet blades was reduced [8]. Centrioles with eight blades had a reduced diameter with the remaining eight blades arranged in an eightfold symmetric arrangement. The construct affected the blades along their entire length, and was due to mutation in a protein that does not localize to the central hub but rather to a structure associated with the blades themselves, thus the study satisfies both of our criteria defined above for a useful mutation. The result thus suggests that the normal ninefold symmetry of the centriole does not arise from an underlying symmetry in the cartwheel hub.

How then does *BLD10* determine centriole symmetry? Significantly, many of the abnormal centrioles show an abnormally short cartwheel spoke length and

a reduced diameter. Since the circumference of a circle is proportional to its diameter, a reduction in diameter by 1/9 would reduce the circumference by 1/9, corresponding to loss of one triplet. Thus it appears that the symmetry of the centriole is ultimately set by the diameter of the centriole, which is in turn set by the length of the cartwheel spokes [8]. The shorter spokes produced by truncated *BLD10* set the diameter to a smaller value, so that only eight triplets can now be accommodated. This study provides an interesting geometrical mechanism by which a length can control a number. Understanding centriole assembly is likely to reveal many more engineering-design principles that cells use to build complex structures.

References

1. Satir, P., and Satir, B. (1964). A model for ninefold symmetry in a keratin and cilia. *J. Theor. Biol.* 7, 123–128.
2. Albrecht-Buehler, G. (1990). The iris diaphragm model of centriole and basal body formation. *Cell Motil. Cytoskel.* 17, 197–213.
3. Rodrigues-Martins, A., Bettencourt-Dias, M., Riparbelli, M., Ferreira, C.,

- Ferreira, I., Callaini, G., and Glover, D.M. (2007). DSAS-6 organizes a tube-like centriole precursor, and its absence suggests modularity in centriole assembly. *Curr. Biol.* 17, 1465–1472.
4. O'Toole, E.T., Giddings, T.H., McIntosh, J.R., and Dutcher, S.K. (2003). Three-dimensional organization of basal bodies from wild-type and delta-tubulin deletion strains of *Chlamydomonas reinhardtii*. *Mol. Biol. Cell* 14, 2999–3012.
5. Preble, A.M., Giddings, T.H., and Dutcher, S.K. (2001). Extragenic bypass suppressors of mutations in the essential gene *BLD2* promote assembly of basal bodies with abnormal microtubules in *Chlamydomonas reinhardtii*. *Genetics* 157, 163–181.
6. Pelletier, L., O'Toole, E., ASchwager, A., Hyman, A.A., and Muller-Reichert, T. (2006). Centriole assembly in *Caenorhabditis elegans*. *Nature* 444, 619–623.
7. Matsuura, K., Lefebvre, P.A., Kamiya, R., and Hirono, M. (2004). *Bld10p*, a novel protein essential for basal body assembly in *Chlamydomonas*: localization to the cartwheel, the first ninefold symmetrical structure appearing during assembly. *J. Cell Biol.* 165, 663–671.
8. Hiraki, M., Nakazawa, Y., Kamiya, R., and Hirono, M. (2007). *Bld10p* constitutes the cartwheel-spoke tip and stabilizes the 9-fold symmetry of the centriole. *Curr. Biol.* 17, 1778–1783.

Department of Biochemistry and Biophysics, University of California-San Francisco, 600 16th St., San Francisco, California, USA.

E-mail: wmarshall@biochem.ucsf.edu

DOI: 10.1016/j.cub.2007.10.038

Animal Behaviour: Strategic Signalling by Cephalopods

Cuttlefish are masters of disguise, rapidly changing colour to blend with their backgrounds. A new study shows that they break camouflage to direct warning messages at certain predators, but only those likely to be dissuaded by visual signals.

Innes C. Cuthill

The study of anti-predator signals has proven to be a rich hunting ground for evolutionary biologists and cognitive psychologists. Empirical support for a number of classical evolutionary processes, such as kin-selected altruism, aposematism and mimicry, has come from studies of the signals made by prey to potential predators [1]. Perhaps even more striking, the use of different signals for different threats, and their apparently deceptive use for social manipulation, provide tantalising glimpses of the origins of language

and of a 'Theory of Mind' (where one individual interprets the behaviour of another in terms of some model of the latter's intentions or knowledge) [2]. The classic example of strategic anti-predator signalling comes from vervet monkeys' use of different alarm calls for different predators [3], but instances of the use of different signals for different threats have now been substantiated in a number of vertebrates (see references in [4]). A new experimental study by Keri Langridge and colleagues [4], reported in this issue of *Current Biology*, adds a new and important

twist to the field of anti-predator signalling. Not only does it concern a cephalopod mollusc, adding weight to the view that these invertebrates can match many vertebrates in their cognitive and behavioural complexity, but it provides the first clear example of strategic choice with respect to the likely effectiveness of different signals against specific predators.

Cuttlefish, like their relatives squid and octopus, have excellent vision and skin pigmentation (and texture) that is under direct and rapid neural control [5]. These attributes allow them unparalleled dynamic camouflage [6], combining general background resemblance, disruptive patterns and posture to achieve near-invisibility in a couple of seconds. But in the face of predators using tactile, olfactory or electromagnetic cues, visual deception may fail and here,



Figure 1. Juvenile cuttlefish displaying an 'eye-spot', part of the diematic display (photo courtesy of D. Osorio and K. Langridge).

jet-powered escape, perhaps accompanied by the familiar jet of ink, may be the best course of action. Another response to an imminent threat, long known to close observers of cephalopod behaviour [5], is the 'diematic display' (Figure 1), combining one or more high contrast spots with distinctive tentacle postures and a spreading of the body that increases apparent size. Langridge *et al.* [4], by staging encounters between naïve juvenile European cuttlefish and a range of natural predators (without allowing actual predation), have now shown that the molluscs can discriminate between classes of predator and switch defence tactics appropriately.

Camouflage is the cuttlefish's default strategy but, when disturbed by the potentially fatal risks posed by crabs or dogfish, cuttlefish opt for immediate escape or a rapid (startling?) darkening of the skin followed by jet-assisted withdrawal. The diematic display is instead used with small teleost fish and is often sufficient to cause the fish to move away. The inference is that small teleosts represent an intermediate danger — they are unlikely to eat the cuttlefish but may draw attention to it or disturb it — so a warning rather than flight is required. Furthermore, teleosts being visual predators, unlike dogfish, a striking visual signal is appropriate. Video footage of the cuttlefish is striking: a young sea bass comes too close and suddenly, from near invisibility, the cuttlefish 'winks' a large dark spot on its flank closest to the threat. Continued disturbance may evoke twin eye-spots and a vertical spread posture.

Apart from the (unwarranted) anthropocentric surprise that a mollusc is capable of such complex behaviour, this study raises several questions. First, what is it about the diematic display that is aversive to small fish? It is not a true warning (aposematic) signal, as the cuttlefish poses no danger to the predator. Is it the eye-like quality of the dark circular spots, their high contrast, or their rapid appearance and disappearance? These, not necessarily mutually exclusive, explanations echo questions about the function of eye-spot patterns in many taxa, most notably butterflies and fish [7,8]. Second, although it is reasonable to assume that the diematic display would be ineffective against crabs or dogfish, and flight is a costly and unnecessary response to small teleosts, these costs and benefits have not been quantified. It would seem that the display is potentially risky because camouflage is broken and it may attract the attention of more dangerous

predators. Finally, how do young cuttlefish discriminate between teleost fish and elasmobranchs such as dogfish? To a human observer these predators are superficially very similar, but clearly naïve cuttlefish have access to robust cues that allow rapid discrimination and appropriate action. The 'alien intelligence' of cephalopods continues to surprise, and develop as a remarkable model system for the study of animal coloration and perception.

References

1. Ruxton, G.D., Sherratt, T.N., and Speed, M.P. (2004). *Avoiding Attack* (Oxford: Oxford University Press).
2. Frith, C., and Frith, U. (2005). Theory of mind. *Curr. Biol.* 15, R644–R646.
3. Seyfarth, R.M., Cheney, D.L., and Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science* 210, 801–803.
4. Langridge, K., Broom, M., and Osorio, D. (2007). Selective signalling by cuttlefish to predators. *Curr. Biol.* 17, R1044–R1045.
5. Hanlon, R.T., and Messenger, J.B. (1996). *Cephalopod Behaviour* (Cambridge: Cambridge University Press).
6. Hanlon, R. (2007). Cephalopod dynamic camouflage. *Curr. Biol.* 17, R400–R404.
7. Stevens, M. (2005). The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biol. Rev.* 80, 1–16.
8. Stevens, M., Hopkins, E., Hinde, W., Adcock, A., Connolly, Y., Troscianko, T., and Cuthill, I.C. (2007). Field experiments on the effectiveness of 'eyespot' as predator deterrents. *Anim. Behav.*, online doi: 10.1016/j.anbehav.2007.01.031.

Centre for Behavioural Biology, School of Biological Sciences, Woodland Road, Bristol BS8 1UG, UK.
E-mail: i.cuthill@bristol.ac.uk

DOI: 10.1016/j.cub.2007.10.052

Neglect: Remembering the Space Left Behind

Our brain continuously creates various representations of the space around us as a function of our on-going behaviour. A recent study on how back space is represented in patients suffering from spatial neglect underscores the distinction between motor and non-motor space.

Arnaud Saj and Patrik Vuilleumier

How the brain represents space remains a debated issue. The

Euclidian model of space used in geometry extends seamlessly to infinity in three dimensions, but we can divide the space in which