

4. Wu, X., Bowers, B., Rao, K., Wei, Q., and Hammer, J.A., III. (1998). Visualization of melanosome dynamics within wild-type and dilute melanocytes suggests a paradigm for myosin V function in vivo. *J. Cell Biol.* **143**, 1899–1918.
5. Wu, X.S., Rao, K., Zhang, H., Wang, F., Sellers, J.R., Matesic, L.E., Copeland, N.G., Jenkins, N.A., and Hammer, J.A., III. (2002). Identification of an organelle receptor for myosin-Va. *Nat. Cell Biol.* **4**, 271–278.
6. Strom, M., Hume, A.N., Tarafder, A.K., Barkagianni, E., and Seabra, M.C. (2002). A family of Rab27a-binding proteins. Melanophilin links Rab27a and myosin Va function in melanosome transport. *J. Biol. Chem.* **277**, 25423–25430.
7. Fukuda, M., Kuroda, T.S., and Mikoshiba, K. (2002). Slac2-a/melanophilin, the missing link between Rab27a and myosin Va: implications of a tripartite protein complex for melanosome transport. *J. Biol. Chem.* **277**, 12432–12436.
8. Nagashima, K., Torii, S., Yi, Z., Igarashi, M., Okamoto, K., Takeuchi, T., and Izumi, T. (2002). Melanophilin directly links Rab27a and myosin Va through its distinct coiled-coil regions. *FEBS Lett.* **517**, 233–238.
9. Provance, D.W., Wei, M., Ipe, V., and Mercer, J.A. (2002). Melanophilin, the product of the leaden locus, is required for targeting of myosin-Va to melanosomes. *Traffic* **3**, 124–132.
10. Sheets, L., Ranson, D.G., Mellgren, E.M., Johnson, S.L., and Schnapp, B.J. (2007). Zebrafish melanophilin (Mlpha) facilitates melanosome dispersion by regulating dynein. *Curr. Biol.* **17**, 1721–1734.
11. Rodionov, V.I., Hope, A.J., Svitkina, T.M., and Borisy, G.G. (1998). Functional coordination of microtubule-based and actin-based motility in melanophores. *Curr. Biol.* **8**, 165–168.
12. Rodionov, V., Yi, J., Kashina, A., Oladipo, A., and Gross, S.P. (2003). Switching between microtubule- and actin-based transport systems in melanophores in controlled by cAMP levels. *Curr. Biol.* **13**, 1837–1847.

Laboratory of Cell Biology, Building 50, Room 2523, National Heart, Lung and Blood Institute, National Institutes of Health, Bethesda, Maryland 20892, USA.

*E-mail: hammerj@nhlbi.nih.gov

DOI: 10.1016/j.cub.2007.10.010

Sensory Ecology: See Me, Hear Me

The animal world is replete with vibrant colours: these are often used as display signals and selection has solved a fundamental problem in information transfer by enhancing the detectability of these signals against the backgrounds on which they are perceived by the particular sensory systems of their receivers.

Michael J. Ryan

In his landmark publication that launched Information Theory, Claude Shannon [1] stated that “the fundamental problem of communication is that of reproducing at one point either exactly or approximately a message selected at another point”. Although in its simplest version communication is a dyadic interaction between a signaler and a receiver, there is always the intervening transmission channel, and this channel is often noisy and it causes information to be lost. The fundamental problem in signal evolution is to enhance efficacy in a noisy world.

Noisy channels can vary with habitat, location, and time. Studies of various adaptations of animals to increase the efficacy of signal transmission have long been somewhat of a cottage industry in acoustic communication [2–4]. Sounds do not always transmit the same in all habitats. High frequency sounds usually attenuate (lose energy) more with distance than do low frequencies, and rapidly pulsed sounds usually degrade (lose quality) more than tones. The situation is often more severe in

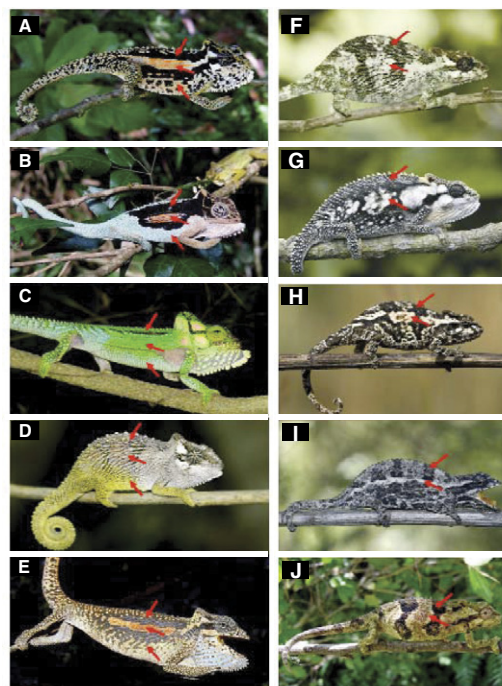
forest than in field. Many animals have evolved calls or songs that enhance signal transmission in their particular environment. Furthermore, the background sounds from wind, waves and other species can mask signals. Another adaptive strategy is to produce

signals that are less likely to be masked by other sounds in the environment. Recently, for example, it was shown that great tits in urban environments use higher frequencies to avoid the industrial din of cities [5].

Our understanding of parallel issues in visual communication have lagged behind. There were earlier and insightful studies [6–9], but the visual ecology of communication got a jump start from two sources, one conceptual and one technical. In Endler’s [10] presentation of sensory drive, he described the myriad constraints

Figure 1. Display coloration in male and female African dwarf chameleons.

On the left are shown examples of male display coloration, with each individual in the display posture (laterally compressed, casque raised, gular pouch expanded). Red arrows show where reflectance spectra were taken. (A) *B. transvaalense*, Woodbush; (B) *B. sp. Ngome*; (C) *B. damaranum*; (D) *B. caffrum*; (E) *B. setaroi*. On the right are shown examples of female display coloration, with each individual showing display coloration. Red arrows show where reflectance spectra were taken. (F) *B. caffrum*; (G) *B. ventrale*; (H) *B. transvaalense*, Graskop; (I) *B. taeniabronchum*; (J) *B. transvaalense*. (Photos reproduced with permission from [12].)



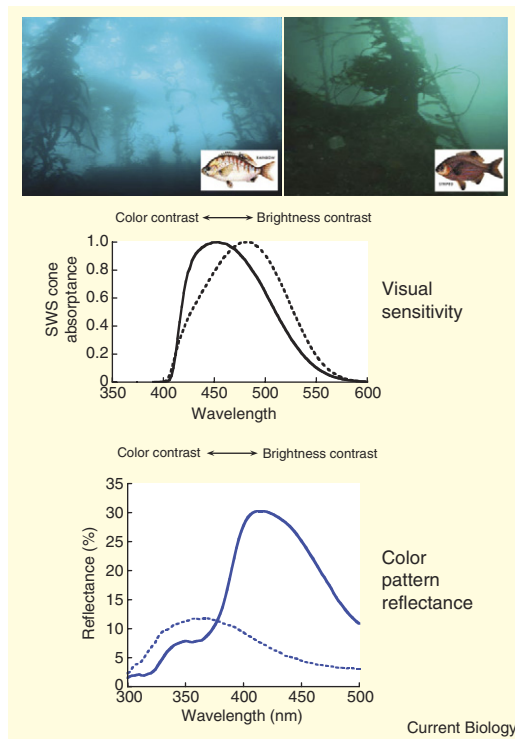


Figure 2. Coevolution of habitat, vision and color in surfperch.

Hypsurus caryi (rainbow surfperch) and *Embiotoca lateralis* (striped surfperch) occupy distinct optical habitats in the nearshore kelp forest environment: one that favors detection by color contrast (*H. caryi*) and one that favors detection by brightness contrast (*E. lateralis*). Each species has visual pigment and color pattern reflectance properties (from a blue patch) that have diverged towards the habitat-specific bias (*H. caryi* solid lines; *E. lateralis* dashed lines). (Figure courtesy of M.E. Cummings.)

perceived. They combined these data with a model that accounts for various properties of ‘the chameleon’ visual system and estimated the detectability of the signal as its contrast against the background and against other body parts. Both male and female coloration contrasts predictably with habitat to enhance signal detectability, and some of the time habitat shifts are accompanied by shifts in display coloration. There is also an interesting sexual dimorphism. Males achieve signal efficacy through the evolution of a diversity of colours, while females do so in black and white (Figure 1).

The chameleon study [12] argues strongly that habitat influences the evolution of the signal end of the communication dyad, but what about the receiver? The critical aspect of the visual model used by the authors is photopigment sensitivity. According to the authors, there is little variation in this visual parameter among the small handful of chameleons investigated (only one being a dwarf chameleon). They thus assume no evolution at the receiver end of the dyad. In other cases, however, the evolution of visual signals is a more complicated dance between both signals and receivers. This is exemplified wonderfully by a recent series of studies of surfperch by Cummings [13–15]. These fishes occupy one of the most diverse optical habitats on earth, the kelp forests off the coast of California (Figure 2). As with the dwarf chameleons, the optical habitat varies among species, as does the color spectrum of the fishes’ signals, but so does the visual pigment sensitivity. The visual sensitivity among species varies predictably to enhance target detection (for example, foraging items against background). But this can be achieved in two ways, either by enhancing chromatic (‘color’) contrast or luminance (‘brightness’) contrast. In terms of visual pigment tuning, the solutions are mutually exclusive, and different species rely on one or the other strategy and have visual systems adapted for prey detection in the visual world they inhabit. The next step in this evolutionary dance is the evolution

and selection forces under which visual communication evolves. His paper coincided with a wave of interest in the mechanisms underlying sexual selection by female choice, and made it clear that signal evolution results from a compromise of various selection forces and the contingencies imposed by the environment and the sensory biology of the receiver.

A more pragmatic motivator for visual ecology studies was technical. It is far easier to quantify and synthesize acoustic signals than it is to measure optical properties of signals and their environments, let alone synthesize them. Critical technical advances in studies of sound occurred with the advent of the sonograph and portable tape recorders in the middle of the last century [11]. These advances have recently been matched in the visual realm with field portable spectrophotometers that have become affordable for many field researchers in the last two decades or so. Although video playbacks and robotics still do not match the simplicity and robustness of acoustic playbacks of synthetic sounds, they are beginning to close this gap as well.

A recent paper by Stuart-Fox *et al.* [12] is an example of what has been birthed by the conceptual and technical advances in visual ecology. We all know that the world is a biologically diverse place even as we are stunned by how quickly that diversity is being lost. Given our own sensory biases, that diversity astounds us most when perceived through our eyes. The myriad of colours of butterflies in a field, fishes on a coral reef, or birds in a tropical forest can impress even the most obtuse observer. Another group that exhibits astounding visual diversity is the African dwarf chameleons (Figure 1). These animals are stunning in many ways; their adornment crests are spectacular and the unsynchronized movements of their eyes somewhat creepy. Foremost, however, is the striking variation in the colors and patterns of the 21 taxa in this group. These animals vary in their microhabitats, and thus the background against which they display. Stuart-Fox *et al.* [12] measured the spectrum of the light available to be reflected by signals, the reflectance of the signals themselves, and the background against which the signals are

of the male's display colors. Their signals have evolved to match the females' visual sensitivity, but they too can choose among strategies. If that species relies on chromatic contrast to find food, then males evolve signals that exploit the contrast channel, but if the species uses brightness contrast then male signals exploit that channel. Cummings presents strong phylogenetic data to support this coevolutionary process, with Occam's razor supporting a specific chain of events: changes in habitat leading to changes in vision and subsequent changes in color patterns.

These studies are just two of a burgeoning field of animal behavior. They integrate analyses of sensory systems and communication behavior and interpret their results in a phylogenetic context. Such studies are becoming

paradigmatic of integrative biology. And they are giving us some important insights into how the splendour of colours all around us have come into being.

References

1. Shannon, C.E. (1948). A mathematical theory of communication. *Bell Syst. Tech. J.* 27, 379–423, 623–656.
2. Morton, E.S. (1975). Ecological sources of selection on avian sounds. *Am. Nat.* 109, 17–34.
3. Marler, P. (1955). Characteristics of some animal calls. *Nature* 176, 6–8.
4. Wiley, R.H., and Richards, D.G. (1978). Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3, 69–94.
5. Slabbekoorn, H., and Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature* 424, 267.
6. Lythgoe, J.N. (1979). *The Ecology of Vision* (Oxford: Clarendon Press).
7. McFarland, W.N., and Munz, F.W. (1975). Part III: The evolution of photopic visual pigments in fishes. *Vis. Res.* 15, 1071–1080.
8. Lall, A.B., Selilger, H.H., Biggler, W.H., and Lloyd, J.E. (1980). Ecology of colors of firefly bioluminescence. *Science* 210, 560–562.

9. Hailman, J.P. (1977). *Optical Signals: Animal Communication and Light* (Bloomington: Indiana University Press).
10. Endler, J.A. (1992). Signals, signal conditions and the direction of evolution. *Am. Nat.* 139, S125–S153.
11. Rand, A.S. (2001). A history of frog calls studies: 405 B.C. to 1980. In *Anuran Communication*, M.J. Ryan, ed. (Washington: Smithsonian Institution Press), pp. 8–19.
12. Stuart-Fox, D., Moussalli, A., and Whiting, M.J. (2007). Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *Am. Nat.*, in press.
13. Cummings, M.E., and Partridge, J.C. (2001). Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. *J. Comp. Phys. A* 187, 875–889.
14. Cummings, M.E. (2004). Modelling divergence in luminance and chromatic detection performance across measured divergence in surfperch (Embiotocidae) habitats. *Vis. Res.* 44, 1127–1145.
15. Cummings, M.E. (2007). Sensory tradeoffs predict signal divergence in surfperch. *Evolution* 61, 530–545.

Department of Integrative Biology,
University of Texas, Austin,
Texas 78712, USA.
E-mail: Mryan@mail.utexas.edu

DOI: 10.1016/j.cub.2007.09.004

Signal Transduction: Networks and Integrated Circuits in Bacterial Cognition

Signal transduction systems that mediate adaptive changes in gene expression to specific sensory inputs have been well characterized. Recent studies have focused on mechanisms that allow crosstalk between different information-processing modalities.

Melinda D. Baker²
and Jeffry B. Stock^{1,2}

What are the decision-making mechanisms by which a bacterium controls the activities of its genes and proteins to adapt to changing environmental conditions? How do cells regulate the expression and activities of thousands of different genes and proteins to efficiently control motility, metabolism, growth and differentiation? The structures and functions of most regulatory components are well understood. Transcription factors and RNA polymerases interact with DNA to regulate gene expression. In some cases, small molecule second

messengers bind to transcription factors to control their activities; in others, kinases activate transcription or repression by adding phosphoryl groups to target proteins. Signals from outside the cell interact with membrane receptors that regulate the activities of sensor kinases as well as enzymes that control the production of second messengers. We understand how these activities can come together to form signal transduction pathways that function as specific regulatory modules dedicated to the generation of specific responses to distinct classes of sensory inputs.

But how do disparate regulatory modules interact to function as a cell? How are bacterial information processing networks organized?

The classic paradigm for a regulatory module is the system that controls lactose utilization in *Escherichia coli* [1]. The genes for lactose uptake and metabolism are regulated by a transcription factor that binds lactose so that *E. coli* in the gut tend to turn on lactose metabolism when they sense the presence of lactose (for example, after the mammalian host drinks milk). The structures of the genes and proteins that constitute this molecular switch have been resolved at atomic resolution and their functional interactions have been exhaustively investigated. *E. coli* exhibit a preference for glucose over lactose. When they sense the availability of glucose, the lactose genes are repressed. This mechanism involves additional transcription factors that are controlled by a regulatory module that is