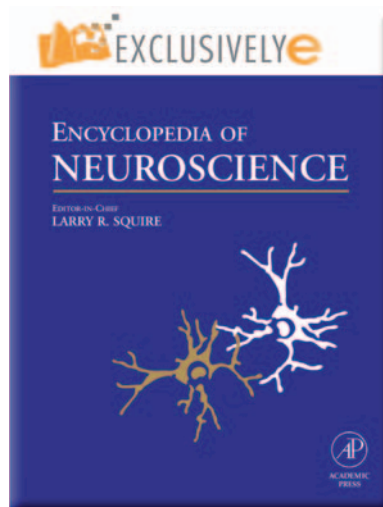


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Visual Signaling in Animals

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Introduction

The human visual sense is the most accessible and the most often studied of our five senses. It is perhaps no surprise, then, that, as scientists, humans have been especially attracted to the diversity of forms and functions of visual traits in other animals. Visual features include overt behaviors that animals exhibit, as well as their body sizes, shapes, colors, patterns, and structures. It has been argued by biologists as far back as Darwin that animals use prominent, often exaggerated movements by or features on the body in a form of 'visual communication.' Much more than 'body language,' which might be the first thing that comes to mind when asked about examples of behavioral communication, many varieties and intricacies of behaviors and morphologies, including facial expressions, colors, courtship displays, and protruding tissues like horns or feathers, constitute the repertoire of animals aiming to communicate information without vocalizing, odorizing, tasting, or touching.

Animals use signals in a variety of behavioral contexts, including breeding, predator avoidance, social grouping, and foraging. Moreover, animals exchange information about numerous attributes of individuals, including sex, individual identity, location, mate quality, breeding strategy, and genetic make-up. A major thrust in research on animal communication today is to understand the mechanisms via which animals control their signals. In addition to nutritional and immunological factors, the neural and endocrine bases of signal production have received much attention. A great deal of this work has been done in relation to vocal communication, but the emphasis on the neuroendocrinology of visual signals nearly rivals that on acoustic signals.

The aim of this article is to highlight some of the uses of behavioral and morphological visuals in animals and to pay special attention to those examples that have clear neural or endocrinological bases or that have apparent value for future investigations at these levels. As the ability to characterize and quantify animal signals and neuroendocrine pathways continues to improve, there is no doubt that numerous neuroendocrinological underpinnings of animal signals will be uncovered.

Behavioral Visual Signals

Courtship Displays

Perhaps the most exaggerated and thoroughly studied of the behavioral visual signals in animals, especially from the proximate perspective, are the courtship displays. These are predominantly performed by males and include precopulatory food offerings, dances, or other movements in the presence of a prospective or secured mate. Those behaviors exhibited most frequently by females include receptivity postures just prior to mating, except in mutually mate-selecting or sex role-reversed animals, in which case, females actively pursue and display for males.

Clearly the species for which we have the most detailed neurological information about a male courtship display is *Drosophila melanogaster*. Prior to mating, male fruit flies orient toward females and vibrate an extended wing, in addition to performing other behaviors (e.g., tapping, licking). Specific genes, *dissatisfaction* and *fruitless*, are linked to the sex-determination pathway and govern neurally based courtship behavior. Mutations to *dissatisfaction* alter male recognition of females as mates, such that males actively court other males. This is believed to have a neural basis, but controlling brain regions have not yet been identified. The *fruitless* gene, in contrast, has been tied more closely to abnormal courtship, and male-specific protein products of this gene have been identified in the superior protocerebrum of the brain, which has been implicated in courtship initiation. The central nervous system circuitry encoded by *fruitless* also includes olfactory neurons that appear to be required for the behavioral response of males to female sex pheromones. The interactive nature of male–female courtship interactions has been elucidated recently for other animal signals, especially in bowerbirds, but for no other visual signal has such a detailed, complex neural and genetic basis been uncovered.

Proximate studies of courtship displays in vertebrates have traditionally centered on gonadal sex steroid mediation, and a diversity of hormonal control mechanisms exist. Courtship dances and displays are testosterone-mediated in a number of bird species. However, strutting in male Japanese quail (*Coturnix japonica*) is sensitive to estrogens, and this differs from the way hormones control their courtship vocalization (crowing), which is more androgen-sensitive (e.g., testosterone and 5 α -dihydrotestosterone). Perhaps the two best-studied of the vertebrate courtship displays from a neuroscientific perspective are the

throat-fan (dewlap) extension of male anoles (*Anolis carolinensis*) and the bowing and nest soliciting of male ring doves (*Streptopelia risoria*). Male anoles evert a brightly colored flap of gular skin using (ceratohyoideus) muscles that bow out a piece of cartilage (retrobasal process) in the throat. This process is androgen-dependent, and the throat muscles are innervated by seasonally and sexually dimorphic motor neurons located in two regions of the brain stem. In male ring doves, bowing is testosterone-dependent, but nest-soliciting wing flapping (by both sexes) is estradiol-dependent, and both hormonally governed behaviors appear to be controlled in the anterior hypothalamus preoptic area (HPOA), as determined by carefully designed studies using hormone implants and enzyme blockers.

The flight displays of male dark-eyed juncos (*Junco hyemalis*) are an example of a courtship behavior that is testosterone-dependent and preferred by female mates. There are also a few excellent cases in which vertebrate courtship behaviors have been traced down to the neuromuscular and neuroendocrine paths. For example, loud, rapid courtship wingsnaps are produced by male, but not female, golden-collared manakins (*Manacus vitellinus*) resulting from a sexual dimorphism in wing musculature and sex steroid accumulation in regions of the spinal cord that innervate such musculature. Identifying such specific neuroendocrine paths for the musculature that controls other elaborate courtship behaviors, as has been done on the avian song system, should yield exciting avenues for future work.

Finally, despite these numerous examples, gonadal steroids are not always required for adult animals (e.g., certain cichlids, toads, sparrows, and primates) to maintain their courtship signals. In many cases, adrenal or brain-derived steroids are thought to be the sources of hormones that sustain the behavior. There can also be early-life effects of hormone that organize courtship later in life. Alternate hormones (e.g., peptide, protein) should also be considered as chemical signals for courtship behavior maintenance, much like the role of vasotocin in male rough-skinned newts (*Taricha granulosa*).

Parental Behavior and Aggression

Parental effort and aggression are two additional behaviors that often function as conspecific signals, in many cases increasing the attractiveness of potential male partners. There is an extensive literature on the endocrine basis for such behaviors in a wide variety of animals. Historically, prolactin has been viewed as 'the' parental hormone, but this is by no means universal. Prolactin stimulates milk letdown and subsequent delivery to young in mammal mothers

and facilitates offspring rearing in male and female birds. However, prolactin has no influence on lamb recognition and acceptance by mother sheep and generally is thought to play more of a role in the maintenance of parental behavior rather than its onset. Steroids and peptides, in contrast, strongly induce parental instincts toward offspring. In sheep, it is oxytocin release during birth that stimulates maternal interest in young. Estrogen, aromatized in the brain from testosterone, is a key sex steroid that drives paternal behavior in male California mice (*Peromyscus californicus*); testosterone, along with progesterone, traditionally inhibits parental tendencies and can even facilitate paternal aggression toward offspring (e.g., in rodents; see more on aggression in the next paragraph). The neural centers that mediate paternal behavior have been described in a few instances, particularly for prolactin action and crop milk production and regurgitation in ring doves and for oxytocin action in the paraventricular nucleus of the hypothalamus that promotes lamb acceptance in sheep. Brain sites for parental behavior are typically the same as those for sexual behavior in general (e.g., preoptic area, bed nucleus of the stria terminalis).

Testosterone, often interfering with parental behavior, is widely viewed as the 'aggression' hormone. Threatening, competitive, and fighting behaviors fluctuate in response to changing levels of testosterone, or derivatives such as 11-keto-testosterone (in fish), in male animals from all major vertebrate groups. A good example of a sexually valued, hormone-dependent aggressive signal involves the gray partridge (*Perdix perdix*), whose vigilance behavior, a form of aggression aimed at deterring predators, is testosterone-dependent in males and is sexually attractive to females. Brain-derived (from testosterone) estrogens can also influence male aggression (e.g., in mice). Though the proximate underpinnings of female aggression have been comparatively neglected, gonad-derived sex steroids control aggression in some females as well (e.g., mountain spiny lizards, *Sceloporus jarrovi*).

Nonsteroid hormonal mechanisms can underlie aggressive behavior, and to date these provide some of the best neural links to animal aggression. The role of neuropeptides has received increased attention in recent years, as vasopressin in mice, vasotocin in songbirds, and adrenal catecholamines in lizards all play pivotal roles in modulating competitiveness, but with different relative outcomes, sometimes even in closely related species. For example, septal infusions of vasotocin inhibited aggression in territorially breeding male violet-eared waxbills (*Uraeginthus granatina*) and field sparrows (*Spizella pusilla*) but promoted aggression in a colonial songbird, the zebra finch (*Taeniopygia guttata*). Work on

the green anole has also yielded insights into the turnover of serotonin, dopamine, adrenalin, and nor-adrenaline in brain stem nuclei as a function of aggressive signaling. Finally, yawning in humans and other animals is often viewed as a threatening social signal and can come under diverse neural and endocrine controls. Dopamine, acetylcholine, serotonin, nitric oxide, and oxytocin are among the neurochemicals that facilitate yawning, while opioid peptides can inhibit this behavior. Functional magnetic resonance imaging has recently been used in humans to show that brain regions involved with self-(bilateral precuneus and posterior cingulate) and facial-information processing (bilateral thalamus and parahippocampal gyrus) are active during yawning, suggesting an important neural basis for the communication value of yawning. Beyond these examples, however, the neuroendocrine basis for an aggressive or parental behavior that serves directly as a signal has rarely been determined.

In many instances, aggressive behavior itself is signaled by a different trait, a morphological 'badge of status' (e.g., color patch; body, horn, or antler size), that can come under neuroendocrine control. Examples are discussed in the next section.

Morphological Visual Signals

Colors and Patterns

Animals use colors and patterns to signal in mating or competitive contexts within their species as well as in cryptic, aposematic, or species isolation contexts among species. In the latter case, with the exception of rapid background matching in ectotherms, signals are highly pattern-(as opposed to intensity-) dependent, generally invariant among individuals, and come under genetic control, which for some may involve hormonal pathways (e.g., the role of α -melanocyte-stimulating hormone (α -MSH) and the melanocortin-1 receptor (MC1R) for melanic color patterns). The majority of the emphasis here will be on intraspecifically variable mating or competitive color signals.

Physiological color changes in fishes, amphibians, and reptiles have served as model examples for studying the neuroendocrinology of visual color signaling in animals. This is because light-absorbing pigments (e.g., melanin, carotenoid, pterin, purine) are harbored in living cells (chromatophores) that can actively aggregate or disperse molecules, in response to physiological triggers (and ultimately environmental cues), on a minute-to-minute basis. Here, hormones like α -MSH and melanin-concentrating hormone have profound regulatory functions for melanosome accumulation

(hence, skin darkening) in numerous ectotherms, although other hormones (e.g., epinephrine, serotonin, thyroxine, pro-opiomelanocortin, and somatolactin) have been implicated. An excellent example of such work on a color known to function as a signal is work on skin darkening in Arctic charr (*Salvelinus alpinus*) and the green anole. In charr, stressful social conditions induce serotonin and norepinephrine in the central nervous system to modulate pituitary release of adrenocorticotrophic hormone and α -MSH, which together drive skin darkening. Detailed neural and cellular work, in the context of rapid cryptic (background-matching) color acquisition, has also been performed in the African clawed frog (*Xenopus laevis*), where melanotrope cells from the pars intermedia of the pituitary release pro-opiomelanocortin-derived α -MSH to redistribute melanosomes and change color, and superchiasmatic neurons, which produce the neurotransmitters γ -aminobutyric acid, dopamine, and neuropeptide Y, transport these factors to axons contacting the melanotrope cells and ultimately inhibit α -MSH secretion. A paracrine factor (macrophage migration inhibitory factor) and autocrine factors (e.g., brain-derived neurotrophic factor) can also influence amphibian melanophore action.

Most colors of endotherms differ from those of ectotherms in that they are contained in dead tissue like feathers or hair and thus cannot be as dynamically linked to neuroendocrine processes. A classic case of such a signal is the bright red plumage of house finches (*Carpodacus mexicanus*), which is dependent on adequate nutrition (intake of proper carotenoid pigments from plant foods) and health. Still, hormonal regulation of bird coloration has received considerable attention (more than mammal color regulation), mostly from the perspective of sexual plumage dichromatism. The carotenoid-based red beak of male zebra finches and the melanin-based badge of the male house sparrow (*Passer domesticus*) are classic examples of bird colors that are exaggerated (made richer or larger in size) by androgens. It is important to point out that the sexual variation (dichromatism) observed in these cases cannot be overcome by hormones (e.g., inducing a male-like condition in females by administering testosterone); instead, the sex difference has a genetic basis. In the majority of work in this area, however, no proper procedures have been followed to rule out estrogenic (via aromatization from testosterone) control of color, and no neural link to such coloration has been established. Melanic colors in songbirds, especially Old World ploceids (e.g., bishops and widowbirds), are also sensitive to luteinizing hormone (LH).

Coat colors of mammals typically vary among species in melanin pattern and are genetically

determined. Many of these melanic features can be sensitive to hormones like α -MSH and are governed by the MC1R locus, and evidence from this is extensive in domesticated mammals (e.g., cattle, rodents, dogs). Some species also exhibit fleshy red and blue colors on the face or rump that dynamically respond to social (competitive) conditions and androgen levels (e.g., in mandrills, *Mandrillus sphinx*). Fast-acting neuroendocrine paths are also implicated in the social signal known as facial blushing in humans (e.g., sympathetic arousal of beta-adrenergic receptors, resulting in vasodilation).

Enlarged Integumentary Features

Body structures that are exaggerated beyond the basic head-to-toe morphology of an animal (structures such as horns or antlers; manes; feather crests; or fleshy tissues such as wattles, combs, or sexual swellings) often play valuable roles as attractive or competitive signals. For each of these categories of traits, an endocrine basis for their formation has been established. High testosterone levels promote seasonal mane growth and antler pedicle initiation in red deer (*Cervus elaphus*) stags, and low levels induce antler casting when breeding has ceased, but high levels do not necessarily promote antler growth. It has recently been shown at the cellular level that androgen receptors seasonally upregulate in hair follicles and allow for testosterone-dependent formation of the enlarged mane in this species. The seasonal cycle for female reindeer (*Rangifer tarandus*) antlers, which are smaller than males' antlers, is similarly sensitive to sex steroids, although the relative roles of testosterone and estrogen have not been clarified.

Classic work on the ornamental feather plumes in males (e.g., neck fringes, hackles) from certain strains of domestic chickens (*Gallus gallus*) shows that the male plumage is the default (genetically programmed) pattern and that only in the presence of estrogen does the female plumage develop. This can even be extended to strains (e.g., Sebright) whose males display female feathering, and this plumage is maintained by the aromatization of estrogen from testosterone in skin. Such estrogen dependence (and androgen independence) of ornamental plumage dichromatism is very common in large, ancestral birds (e.g., ostrich, gamebirds, waterfowl).

In contrast, the size of exaggerated fleshy integumentary structures, beyond their color appearance, can come under androgenic control. The size of combs on the heads of male roosters, red grouse (*Lagopus lagopus*), and black grouse (*Tetrao tetrix*) is testosterone-dependent. Sexual swellings on the hind end of some female Old World primates (e.g., olive baboons, *Papio cynocephalus anubis*) advertise

the timing of their fertility as well as their lifetime reproductive potential and thus are closely tied to ovarian hormone cycles.

Body Size and Symmetry

Generalized features of the body, including its overall size and the bilateral symmetry of certain attributes, have also received considerable attention as signals with which individuals can send and receive important information about a rival or prospective mate. In many species, for example, large males are dominant, and as indicated earlier, dominance is controlled by sex steroids. However, while hormones such as testosterone can increase muscle mass and other growth parameters in wild animals, as well as in humans, it appears that no study of a free-ranging animal has yet shown that testosterone or any other hormone modulates both body size and its role as a competitive signal.

Fluctuating asymmetries (FAs) in bilateral traits have been proposed to contain useful signaling information regarding the developmental (e.g., nutritional, health, genetic) history of individuals. Hormones may also play key roles in the development of features that later in life do not exhibit perfect symmetry and thus may be used as a signal. There was an outburst of studies on the signal content of FA in animals throughout the 1990s, and while interest has waned, some scientists studying humans have shown recent interest in the endocrine basis for FA signals. Sexually attractive odors are linked to the facial symmetry (and hence sexual attractiveness) of men, and these can be pheromonal, but regarding visual signals, soft-tissue symmetry itself is argued to have a hormonal basis, even on a dynamic scale. In a sample of ten men, researchers found that fingers, wrists, and ears were more asymmetric when circulating levels of LH and thyroxine were high and when levels of follicle-stimulating hormone were low. It has been argued that highly asymmetrical men tend to be more aggressive and that an endocrine mechanism underlies FA-linked behavior (e.g., LH through its effects on testosterone). However, experimental work is needed to better understand whether and how hormones and neural pathways may influence FA.

Extended Phenotypes: Where Morphology and Behavior Meet

Some organisms develop signals, not on their own bodies, but on or as structures in the environment ('extended phenotypes'). Nests and their construction, for example, can serve as signals of effort on which males or females base mating decisions (i.e., in sand gobies, *Pomatoschistus minutus*). Bowerbirds from Australia are also a classic example of a species that

builds a signal in the environment. Male bowerbirds build dummy nest structures not used to hold eggs but as a display trait and an arena in which to display themselves. Among bowerbird species, bowers can range from simple piles of sticks to elaborate, tall towers of sticks glued together and decorated with a black-painted moss rug and colorful objects like flower petals, snail shells, and butterfly wings (i.e., in *Amblyornis inornatus*). Species that have little plumage or body ornament tend to have more exaggerated bowers. Also, species with more complex bowers have a larger cerebellum, which is perhaps associated with greater motor skills and learning. In the satin bowerbird (*Ptilonorhynchus violaceus*), males with higher testosterone levels have more exaggerated displays, are more likely to build and hold a bower, and have high mating success.

Signal Perception

While the majority of work on animal visual signals has centered on the production and characteristics of the signal itself (e.g., signal ‘potential’), in reality this information is not technically what the signal receiver perceives and responds to as attractive or unattractive, dominant or submissive. Signal reception and perception require appropriate eye detection and tuning as well as neural information processing that decodes behavioral or morphological signal variation. A color, for example, is perceived by photoreceptors that are maximally sensitive to particular light wavelengths, and this light can be altered by both the ambient environment in which the animal is found and the light-filtering properties of the ocular media. Though vision researchers have now described the optical characteristics of some animal eyes and identified the true abilities and limits of signal reception, this is a field in its infancy and one that should prove fruitful for those keen on understanding variability in, control of, and interactions between signal perception and production. It is said that we cannot truly appreciate the ‘color sensation’ (or really any other visual sensation) of other animals until we map neuro-optical circuitry on top of visual acuity, and this should become more of a goal, collaborative or otherwise, of researchers studying signaling systems where truly ‘beauty is in the eyes – and brain – of the beholder’.

See also: Animal Communication: Honesty and Deception; Game Theory and the Economics of Animal Communication; Multimodal Signaling in Animals; Referentiality and Concepts in Animal Cognition; Sexual Selection and the Evolution of Animal Signals; Signal Transmission in Natural Environments; Signal Design Rules in Animal Communication.

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