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"Neurobiology and Communication in Parrots with an Emphasis on Eye Signaling"

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Abstract

This review serves as an interdisciplinary framework for understanding the adaptive value and mechanism of eye pinning. Eye pinning (pupillary constriction and dilation) in Psittacoidea is a conspicuous behavior that has yet to be studied in a scientifically controlled setting. After reviewing over 100 years of behavioral observations in literature and interviewing breeders and veterinarians, pinning appears to occur during both positive and negative states of arousal in the following contexts: territory defense, excitement and exploration of novel objects, tactile stimulation/ preening of a relaxed bird, courtship displays and copulation, and during vocal learning as well as a synchronous display to sounds during production. Birds are said to have voluntary control over the muscles of the iris. If this is true, eye pinning has the potential to be an intentional communicative signal.

Parrots are unique in their class in that they and only two other orders, songbirds and hummingbirds, possess song learning ability. Parrots' complex mimicking ability is thus far unrivaled by any other group in the animal kingdom apart from humans, as is their ability to synchronize muscles of the iris to sounds they are producing. Because eye pinning is observed in social contexts and during both courtship and song learning, it may have evolved out of pre-existing motor pathways for ancestral behaviors. To date there has been no research investigating the evolution and function of eye pinning. Social ecology, brain morphology, neuroanatomy, ocular anatomy, and somatosensory and auditory systems of the parrot were reviewed in this paper. Unique environments and complex social dynamics such as fission-fusion dynamics, social foraging, and long-term monogamous pair bonds may have contributed to shaping motor pathways, brain morphology, and anatomy to facilitate adaptations, including eye pinning, that increase an individual's success at communicating.

Diese Übersicht dient als fachübergreifendes Modell, um den adaptiven Wert und Mechanismus des sogenannten Augenfeuerwerks zu verstehen. Augenfeuerwerk (Erweiterung oder Verengung der Pupille) in Psittacoidea ist ein auffallendes Verhalten, was bisher nicht in einem wissentschaftlichen Rahmen untersucht wurde. Nachdem die Literatur von über 100 Jahren Verhaltensbeobachtungen untersucht wurde und Züchter und Tierärzte befragt wurden, scheint das Augenfeuerwerk Zeichen der positiven sowie negativen Erregung in den folgenden Zusammenhängen zu sein: Revierverteidigung, Aufregung, Erforschung neuer Objekte, taktile Stimulation/ Gefiederpflege eines entspannten Vogels, Paarungspiele/ Kopulation, während das Erlernen von Vokalisationen sowie als Synchronspiel zu den Vokalisationen. Es wird gesagt, dass die Vögel bewusste Kontrolle über die Muskulatur der Iris besitzen. Wenn dies der Fall sein sollte, wäre das Augenfeuerwerk eventuell ein absichtliches Kommunikationssignal.

Papageien sind einzigartig in ihrer Klasse, in dem sie und nur zwei andere Arten aus der Ordnung der Gesangvögel und Kolibris, die Fähigkeit besitzen, Lieder zu erlernen. Das komplexe Nachahmen sowie die Fähigkeit die Muskulatur der Regenbogenhaut mit den produzierten Lauten zu synchronisieren sind bisher ohne Konkurrenz in der Tierwelt. Da das Augenfeuerwerk in sozialem Kontext, während der Kopulation und beim Erlernen von Liedern beobachtet wurde, ist es durchaus möglich, dass es aus bereits vorhandenen motorischen Leitungsbahnen der Verhaltensweisen der Vorfahren stammt. Bis heute gibt es keine Forschung zum Thema der Evolution und Funktion des Augenfeuerwerks. Sozialökologie, Gehirnmorphologie, Neuroanatomie, Okularanatomie, somatosensorisches und akustisches System des Papageis wurden in dieser Magisterarbeit überprüft. Einzigartige Umgebungen und eine komplexe Sozialdynamik wie zum Beispiel die Spaltungsfusion, soziale Futtersuche, und die langfristige monogame Paarbildung führten eventuell dazu, motorische Leitungsbahnen, Gehirnmorphologie und Anatomie zu gestalten um Adaptionen, inklusive das Augenfeuerwerk, was zu zunehmenden Kommunikationserfolgen führt, zu fördern.

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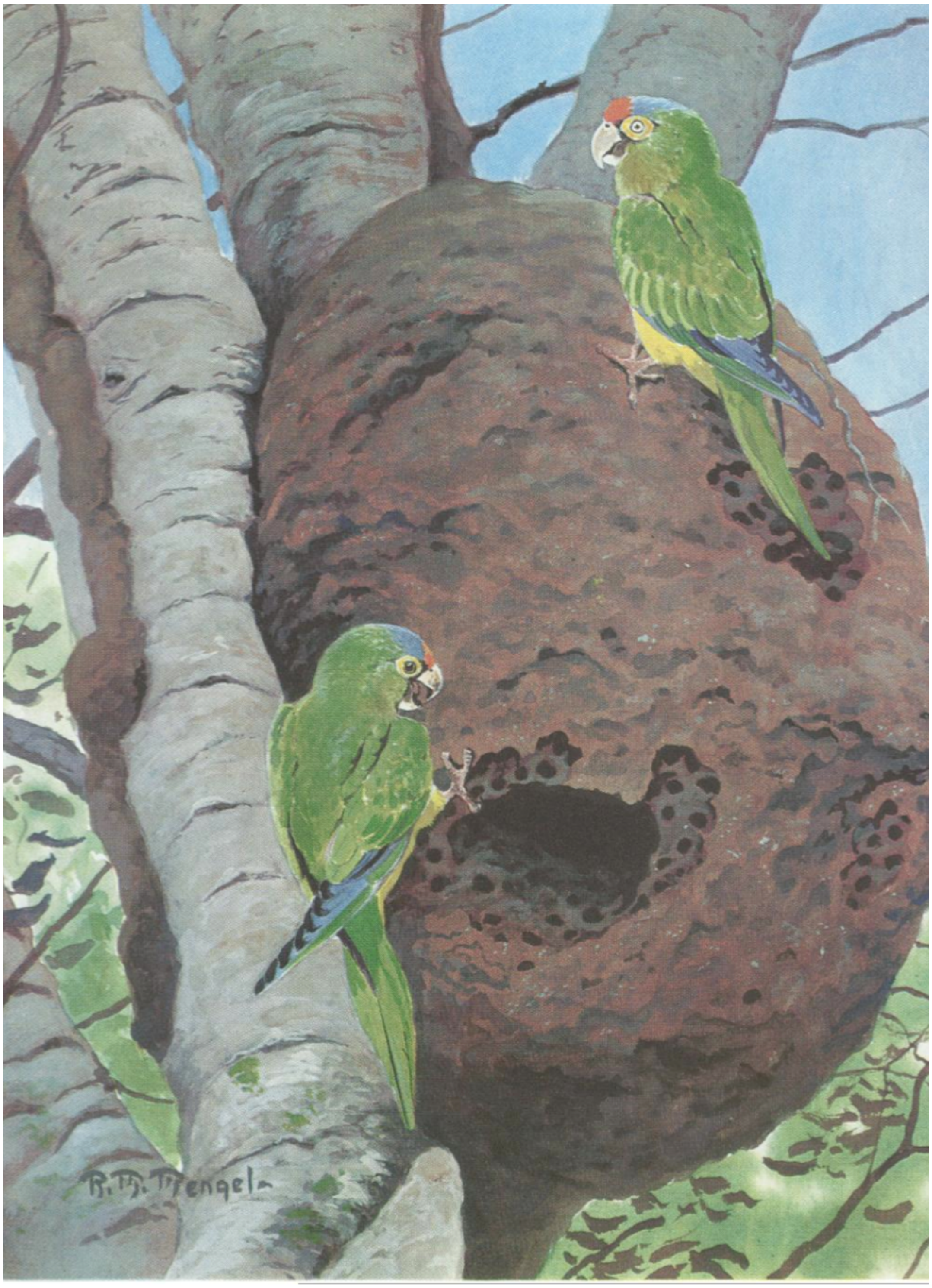


ORANGE-FRONTED PARAKEET
ARATINGA CANICULARIS

Pair at termitarium containing nest excavation

From a painting by Robert. M. Mengel
Reproduced from Hardy, 1963.

1

Introduction

1.1 Communication and signaling

There are approximately 9,000 recognized species of birds, about 370 of which belong to the parrot order, Psittaciformes. Psittaciformes splits into the superfamilies Strigopoidea (New Zealand parrots), Cacatuoidea (cockatoos), and Psittacoidea (true parrots) (Joseph et al 2012). All species within the parrot order are vocal learners, have a high telencephalic volume fraction, and with the exception of a few species who are more solitary, highly social (Burish et al 2004). Wild and captive parrot research indicates that a majority of species exhibit complex social structures and communication systems. Such systems have been established for predator detection and avoidance, feeding, breeding and pair-bond maintenance, staying in contact, defending the nest, and engaging in affiliative or aggressive social interactions. Although the mating structure is dominated by solitary nesting and monogamous pairs (of 352 species of parrots, 91% of species are solitary monogamous pairs, 6% are colonial nesters, 2% cooperative breeders, .8% polygynandrous, and .2% are characterized by lek mating (Bradbury and Balsby 2016)), most species of parrots forage in groups exhibiting high rates of fission-fusion dynamics in which groups repeatedly split into subgroups that merge again later on. Social structure and fission-fusion dynamics of each species are dependent on evolutionary and developmental history, availability of resources, mates, ecological pressures, and predators.

The multitude of factors influencing social interaction and structure in populations exhibiting fission-fusion dynamics as well as long-term monogamous pair bonds increases the amount of information a parrot has to learn, remember, and react to. Life in a complex social system, defined “in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time” (Freeberg et al. 2012, p. 1787), requires a higher degree of communicative ability and adaptability. Communication refers to the variety of tactics used to transfer knowledge and information in various environmental and social settings. Communication signals can be acoustic, visual, chemical, seismic, tactile, or electrical.

In humans, tactics for sending information range from intentional vocalizations, gestures, and facial expressions to less obvious and sometimes unintentional communication signals such as subconscious shifts in posture or facial expressions. While communication can effectively serve to bridge the gap between two individuals' mental states, the efficacy of sending a signal containing information about one's mental state via vocalizations, gestures, or facial expressions is only as strong as the ability of the receiver to perceive and process the information coming from the sender. Signaling complex mental states or emotions generally requires a more complex method of conveyance. Consequently, understanding those signals requires complex processing abilities in the receiver.

Emotion is critical in facilitating accurate and reliable responses to various stimuli in an organism's environment. From an evolutionary perspective, emotion facilitates intra- and inter-specific interactions including reproduction, aggression, pleasure-seeking, and fear. Humans have a relatively high level of emotional intelligence evident in our ability to communicate the subjective nature of our emotional processes effectively. Our "emotional processes are central for understanding adaptive and maladaptive functioning in a wide range of cross-disciplinary areas (e.g., prosocial behavior, close relationships, stereotyping and prejudice, moral judgments, economic decisions, biological responses to stress, and physical and mental health)" (Pietromonaco 2018, p. 1). The ability to experience strong and varying emotions likely co-evolved with our ability to communicate them as well as perceive them in others.

While strong emotional states can sometimes be intuited by observation (e.g. observing someone shaking while fearful or smiling and laughing when happy), the subjective nature in which an individual experiences events can make it difficult for a receiver to assess the specific strength, limitations, and direction of an emotion. Signals serve as a communicative tool that can be useful in aligning the intention and understanding of a sender and receiver. Any signal, including those produced in emotional contexts, is most efficient when it is perceived and learned quickly and able to be remembered. Signal evolution is therefore subject to pressures that facilitate receiver efficacy.

An effective signal should be easy to recognize and salient from other noise in the environment to preserve information content and predictive value (Parr et al 2005). Signal strength can be improved when the signal evolves to incorporate more than one component in at least one sensory modality. Such is a “multicomponent” signal. Signals that contain multiple components in more than one sensory modality are “multimodal” (Rowe 2013). A multicomponent signal may “enhance the detectability, discriminability or memorability of another signal component that provides information and to which the receiver predominantly responds” (Rowe 2013).

Parrots have been observed to generate various directed behaviors while experiencing emotional states:

- Beak clicking: greeting or warning
- Beak grinding: contentment
- Eye pinning: excitement, either good or bad
- Facial feather twitching: startled or intrigued
- Fluffing: prelude to preening or tension releaser
- Foot tapping: territorial defense
- Tail fanning: courtship or aggressive display (Welle 2006)

In general, as the types of interactions in a group increase, so does the information a group member has to remember about individual relationships and how to communicate accordingly based on new or prior interactions. Group living, including social foraging, can provide safety and fitness benefits to individuals; however, the benefits come at the cost of increased energetic demand devoted to learning about and communicating with multiple individuals. Learning increases survival, maturation, and stimulus response of adult born neurons. In parallel, adult neurogenesis facilitates learning in new conditions, including changes in the environment or new members of a social group (Mazengenya 2018). For example, juvenile budgerigars' (*Melopsittacus undulatus*) vocalizations and contact calls evolve as they mature through different levels of the social structure from "family group to juvenile crèche, to juvenile flock, to local nomadic flock, to resident breeding flock" (Farabaugh & Dooling 1996). Parrots have a life-long learning ability to acquire new vocalizations, which may have evolved in part due to a critical need to learn new flock members and maintain relationship and hierarchical knowledge associated with fission-fusion dynamics. The processing abilities required to manage social and environmental complexity coevolves with changes in brain architecture that facilitate successful patterns of behavior in various contexts.

1.2 Neurobiology of sociality: how social complexity leads to changes in brain morphology

Effective emotion-based signals should at the very least reflect a motivation and/or tendency of the signaler to engage in a series of actions given a set of social and environmental conditions. In primates, facial expressions and vocalizations are the primary means for communicating emotional states (Parr et al 2005). Brodmann's area 4 in primates is a cortical region implicated in execution of motor activities such as voluntary facial expression and human speech. The orofacial region of area 4 in humans and great apes has increased thickness in layer III with lower cell volume densities that likely provide more space for interconnections. Differences in cytoarchitectural patterns of this area may represent anatomical substrate for fine motor control of facial expressions and/or speech (Sherwood et al 2004) that likely contribute to the ability to communicate emotion. This serves as just one comparative example of how brain regions take on unique cytoarchitectural and morphological patterns that are shaped by and reflect communicative abilities.

The social intelligence hypothesis (SIH) suggests that, in complex social systems, heightened cognitive and communicative abilities increase an individual's chance of success. Moreover, it asserts that higher-level cognition and enlarged forebrains evolved due to challenges associated with a complex social environment (Barton 1996). Indeed, there is evidence that increased sociality is linked to increased relative brain size (Perez-Barberia et al. 2007). Research reveals associations not only between overall brain size and sociality, but associations between the volume of specific brain components and sociality. Normalizing volumes of specific brain components to whole brain volume gives a set of volume fractions referred to as a "cerebrotype". When derived from specific sensory or motor regions with clear function, cerebrotypes identify associations between brain regions and behavioral specializations, giving insight into how and where selection influences neural architecture.

In primates, cerebrotypes are linked to the enlargement of the cerebral cortex and are associated with increases in social structure (Clark et al. 2001). Bird brains are smaller in absolute size and therefore originally were expected to have a lower information-processing ability (hence the term "bird-brain"); however, some corvids and parrots exhibit the higher-level cognitive skills that primates do (Emery and Clayton 2004). The telencephalic volume fraction in birds is also strongly correlated with social complexity, which suggests that a high telencephalic volume fraction may be an anatomical substrate for social complexity and cognitive ability (Burish et al. 2004). The telencephalon's total brain volume is high in all Psittaciformes and approaches 80% in several parrot species (Iwaniuk et al 2005).

Work using an isotropic fractionator to determine the numbers of neurons in specific brain regions has shown that corvids and parrots have higher proportions of neurons in the pallial telencephalon than primates and other birds. Forebrains of corvids and parrots, considered some of the most intelligent birds, contain more neurons than the forebrains of primates with larger brains. Large-brained parrots also have a unique cerebrotype compared to large-brained songbirds: parrots have a relatively larger subpallium within the telencephalon that accommodates more telencephalic neurons (Olkowicz et al. 2016). The subpallium is responsible for neural regulation of feeding, reproduction, voluntary movement, and agonistic and stress behaviors. It is also associated with reward, memory, and learning (Kuenzel 2014).

Rather than basing intelligence on brain size deviation from brain-body allometry, these findings suggest heightened cognitive abilities depend on the number of neurons and their types of connections; more specifically, a "combination of a high number of cortical neurons, their packing density, interneuronal distance, and axonal conduction velocity" (Dicke and Roth, 2016, p. 1). Recruitment of new neurons occurs in the telencephalon of adult birds and has been observed in budgerigars and Congo and Timneh African grey parrots (Nottebohm 2011, Mazengenya 2018). Neurogenesis can be affected by age, environmental complexity, seasonal variation, hormones, stress and social complexity (Mazengenya 2018). In Mazengenya's study on African Grey parrots, the caudal nidopallium (NC) and the caudolateral nidopallium (NCL) showed the densest DCX immunoreactivity indicating neuronal recruitment. NC is associated with reproductive behaviors and NCL is thought to be analogous to the mammalian prefrontal cortex and involved in decision making and planning as well as speech (Mazengenya 2018, Gunturkun 2005).

Parrots, songbirds, and hummingbirds represent an interesting case of unique brain morphology. They have a highly specialized brain structure and anatomy of the forebrain: each of the three orders has seven interconnected cerebral nuclei that function as part of a song learning and sound production system. The morphology of these structures undergoes dramatic changes each breeding season. Volumes of the nuclei increase by up to 200% in open-ended and closed-ended song learners (Brenowitz 2004). Increased singing in canaries recruits neurons in the HVC (Nottebohm et al 1986), a cerebral song nucleus described in Chapter 1. In wild-caught song sparrows (Melospiza melody), HVC neuron numbers increase from 150,000 in the fall to 250,000 in the breeding season (Smith et al 1997). Seasonal changes in the environment and steroid sex hormones play a major role in song learning and production as well as juvenile development and adult plasticity of song circuits (Schlinger and Brenowitz 2009).

The song system receives input from regions of the brain responsible for coding novel or repeated stimuli, draws on learning and memory templates to produce context-dependent responses, further shapes the accuracy of those responses by incorporating neural feedback into engrams, and is subject to plasticity due to developmental and seasonal steroids and hormones. The processes that shape social and sexual preference and context-dependent responses associated with reproductive behaviors and song learning are shaped by overlapping developmental periods marked by extreme plasticity in brain morphology. Perhaps these pathways differentiate during development out of a shared rudimentary pathway. The differentiation may be driven by the interaction between genes, delayed telencephalic maturation and neurogenesis, early environmental (including social) experience, gene-expression, and steroid and hormonal influences. A shared rudimentary pathway or overlapping pathways activated by gene expression would account for similarity among the courtship and song systems, as well as similarity and variation in components and modalities of behaviors used as communication signals applied in complex environments.

1.3 Eye pinning as a candidate for complex signaling

The neurological changes associated with learning in complex environments can over generations effect change in overall brain shape and morphology. As mind and body interact with the environment, neurological and morphological changes in the brain that occur through adaptation further influence aspects of body anatomy and structure and vice versa. Psittacoidea are unique in the parrot order and other aves in that they exhibit rapid pupillary dilation and constriction (referred to as eye pinning from here on) during various interactions with their environment usually during heightened states of arousal. Constriction is highly visible because of stark contrast between the black pupil and a bright, colorful surrounding iris.

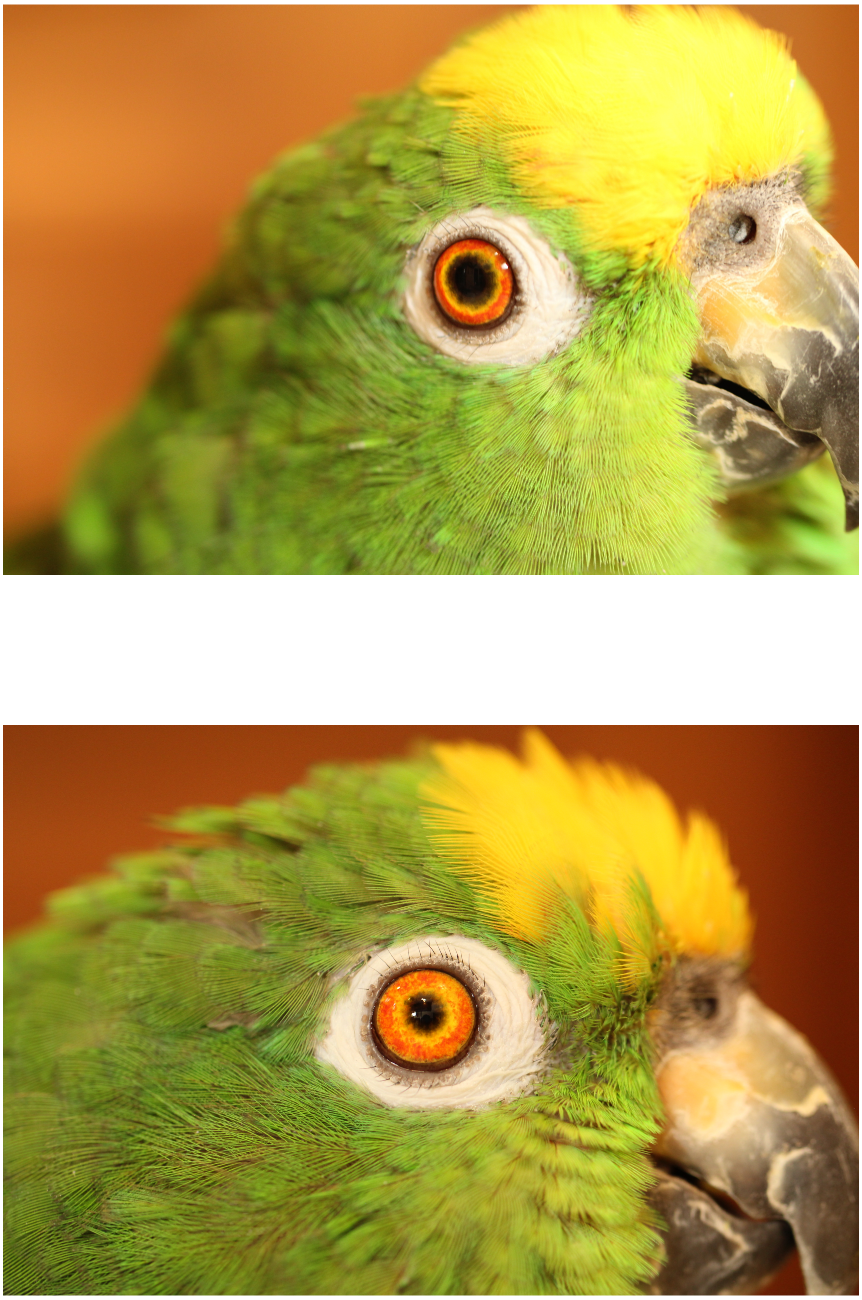


Figure 1 Yellow-front amazon pinning. © Andrew Kirby, 2017

Eye pinning is observable in Psittacoidea in both non-social and social contexts. In non-social contexts it can be observed while a parrot is approaching or inspecting a novel object of high interest (Gregory and Hopkins 1974, Aks and Werra 2001). Bird owners have indicated that eye pinning during feeding occurs when a parrot is feeding on something it is especially fond of. As a social function, eye pinning occurs 1) during territorial defense as a pre-bite warning to those who are invading the personal space of a parrot (Hardy 1963), 2) when parrots are calm and relaxed during tactile stimulation/ preening or after bathing (Taylor and Perrin 2005), 3) during courtship displays and copulation (Hardy 1963, Brockway 1964, Hardy 1966) and, perhaps most interestingly, 4) during auditory perception of sounds that will later be imitated, as well as in synchrony with those imitations as they are produced (Gregory and Hopkins 1974). Whether or not it occurs in contexts beyond these has yet to be determined.

The following chapters review systems used during complex methods of communication in parrots with an emphasis on addressing the evolution and function of eye pinning as a communication signal. Insight is based on literature review, personal experience, communication with behavioral researchers, and anecdotal observations of breeders, parrot owners, and veterinarians.

Parrots are unique in their class in that they and only two other orders, songbirds and hummingbirds, possess song learning ability. Parrots' complex mimicking ability is thus far unrivaled by any other group in the animal kingdom apart from humans. Here, the song learning system in songbirds is described in detail with comparison to parrots where possible. Current behavioral and neurological research regarding song learning is dominated by songbirds. There are noteworthy differences between the songbird and parrot song learning systems where parrot data is available, and I hope that in the years to come we see a shift into more comparative perspectives between the orders. This comparative perspective should ultimately direct empirical research that will shed light on the evolution of the song learning system and its ties to social cognition in parrots. The overlap of sensitive periods in the development of song learning and memory and social preference for sexual imprinting is discussed as it represents a pivotal time in development in which social behavior and communicative strategies towards other individuals is shaped.

There is also a chapter overviewing the connectivity of auditory and somatosensory systems in parrots as both play a role in communication involving vocalizations, gestures, and complex displays. The final chapter offers a review of ocular anatomy as the eye and its musculature may have unique structures associated with the ability to signal mental states.

Taking all this into account, this paper ultimately aims to integrate existing knowledge of parrot communication and the underlying pathways associated with it, theoretical, and empirical observations to inspire well-directed research geared towards understanding eye pinning as an emergent cognitive behavior. Further research would focus on how genetics and development, shaped by environmental and social experience and complexity, result in structural and morphological specializations that interact to create emergent cognitive traits in parrots.

2

Song Learning System

2.1 A unique trait

Song learning refers to learning to produce vocalizations by imitating a model. Parrots, songbirds, and hummingbirds are the only orders of birds capable of imitating non-innate sounds. Humans, pinnipeds, bats, cetaceans, and elephants are the only other animals known to be capable of vocal learning. “Vocal learning species share the presence of babbling, deafness-induced deterioration of learned vocalizations, dialects, and forebrain circuits that control production and learning of vocalizations” (Pfenning et al 2014, p. 1). The trait is thought to have evolved convergently. Song learning birds in particular have a unique, highly specialized brain structure and anatomy of the forebrain: each of the three orders has seven interconnected cerebral nuclei that function as part of a song learning and sound production system.

There are two theories regarding when the seven nuclei are thought to have evolved. The first is that each group evolved the song learning nuclei independently, resulting in three instances of convergent evolution. The second is that the common ancestor of songbirds and parrots evolved song learning nuclei, with a subsequent loss in suboscines and wrens, resulting in two instances of convergent evolution (Jarvis et al 2014). While the connectivity, shape, and location of nuclei varies, the functions of the nuclei are relatively consistent across parrots, songbirds, and hummingbirds. In each order, the seven cerebral nuclei are distributed in two pathways: an anterior pathway that forms a pallial-basal-ganglia-thalmic loop and influences vocal learning, imitation, syntax, and social context functions, and a posterior pathway that is connected with the vocal motor neurons of the brainstem and influences production of learned song (Chakraborty et al 2015).

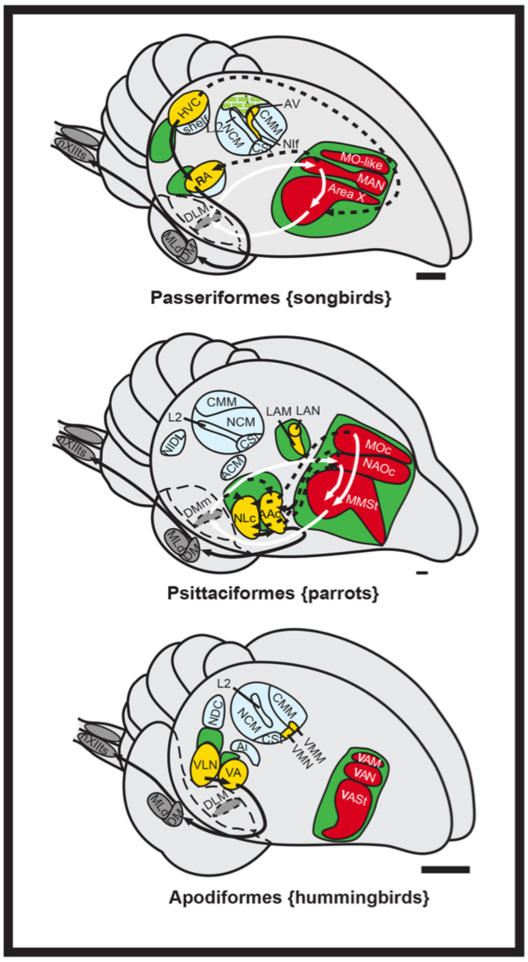


Figure 2a Song learning system in three orders. Reproduced from Chakraborty et al 2015

	Parrots	**Songbirds**
Anterior pathway		
anterior striatum	MMSt, magnocellular nucleus of the anterior striatum	Area X
anterior nidopallium	NAO, oval nucleus of the anterior nidopallium	MAN, magnocellular nucleus of the anterior nidopallium
anterior mesopallium	MO, oval nucleus of the anterior mesopallium	MO-like
Posterior pathway		
nidopallium	NLC, central nucleus of the lateral nidopallium	HVC
arcopallium	AAC, central nucleus of the anterior arcopallium	RA, robust nucleus of the arcopallium
nidopallium	IAN, lateral nucleus of the anterior nidopallium	NIf, interfacial nucleus of the nidopallium
mesopallium	IAM, lateral nucleus of the anterior mesopallium	Av, avalanche

Figure 2b Song nuclei of the anterior and posterior pathways in parrots and songbirds.

Although similarities exist in the song learning pathways of all three bird orders, there are noticeable differences. Parrot posterior nuclei are distributed in a different location compared to the more similarly located nuclei in songbirds and hummingbirds (Feenders et al 2008). The connectivity within each respective pathway for songbirds and parrots is similar, but there are major differences in the connectivity between the anterior and posterior pathways. In songbirds and parrots, the posterior vocal pathway receives projections from the anterior pathway via the analogous nuclei magnocellular nucleus of the anterior nidopallium (MAN) and oval nucleus of the anterior nidopallium (NAO). However, input to MAN and NAO comes from different nuclei in the posterior pathway: MAN receives input from the nidopallial HVC in songbirds (central nucleus of the lateral nidopallium, NLC in parrots) and NAO receives input from the central nucleus of the anterior arcopallium (AAC) in parrots (robust nucleus of the arcopallium, RA in songbirds) (Feenders et al 2008). Determining the factors that drive variation in location and connectivity of the nuclei in the orders can help determine which of the vocal learning theories is more accurate (convergent evolution in all three, or evolution and then a loss in sub oscines and wrens). Variations in morphology, gene-expression, song pathway connectivity, and connectivity to auditory and motor structures may account for major behavioral differences in parrots, such as abilities to imitate, entrain, and continue learning and producing new vocalizations throughout life.

Analyses of brain gene expression profiles suggest that similarities in the vocal learning pathways arise because the song-learning system evolved as a duplicate of a pre-existing motor control system shared by all vertebrates. The theory asserts that "cerebral systems that control vocal learning in distantly related animals evolved as specializations of a pre-existing motor system inherited from their common ancestor that controls movement, and perhaps motor learning" (Feenders et al 2008, p. 19). This concept was inspired by the fact that the seven cerebral nuclei in each vocal learning group lie within or next to non-vocal movement activated areas of the brain.

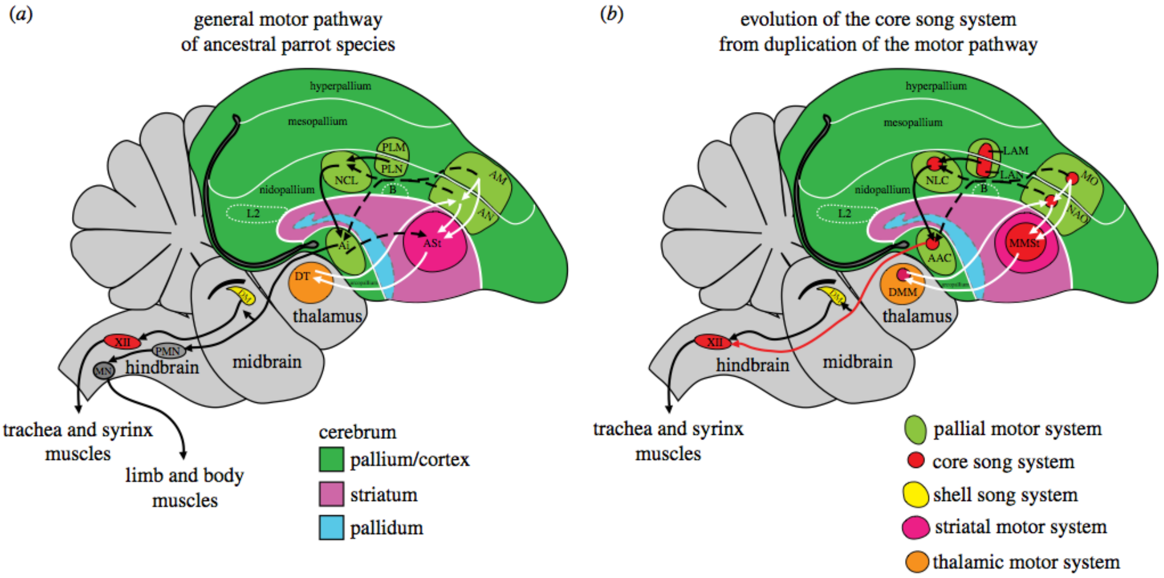


Figure 3 "Hypothesis of evolution of song system in parrots owing to sequential pathway duplications. (a) The parrot ancestral motor pathway (light green) with the posterior motor connections (in black arrows) and the anterior motor connections (in white arrows). (b) The parrot core song system (red), proposed to have evolved out of the pre-existing motor pathway through duplication." Image and text reproduced from Chakraborty and Jarvis 2015, p. 5.

The partial brain pathway duplication hypothesis of brain evolution suggests that a "core" song system evolved convergently in parrots, songbirds and hummingbirds out of this pre-existing motor system. While all three orders of song learners have a similar core song system, specialized constitutive gene expression, singing-driven gene expression, and neural connectivity tracing experiments indicate that parrots underwent an extra pathway duplication in which they now have a song system within a song system (Chakraborty et al. 2015).

The outer lying song system consists of shell regions that include both song and adjacent motor areas for two of the nuclei in the posterior pathway, NLC and AAC, as well as the nuclei oval nucleus of the anterior nidopallium (MO) and NAO in the anterior pathway. Magnocellular nucleus of the anterior striatum (MMSt) is surrounded by the striatal motor control region but was not found to have a shell.

Shell regions of the posterior pathway have specialized connectivity. NLC shell projects to AAC shell. In all avian vocal learners, the core region of the AAC has a unique projection to the brainstem vocal motor neurons (nXIIts). AAC shell in budgerigars has an additional projection to MO and NAO (Durand et al 1997). This projection synapses mostly in the core region of MO and some in the shell region of NAO. In songbirds, the posterior pathway does not project to the anterior pathway via the arcopallium (as does AAC in parrots), but rather from the nidopallium (via HVC). The other projection from the AAC shell is to the AAC core, which as mentioned previously, projects to nXIIts. AAC projects to nXIIts bilaterally and also has a unique projection to the lingual portion of nXII (Striedter 1994). Some fibers also split away from the occipitomesencephalic tract in which they descend to terminate in dorsomedial subdivision of nucleus intercollicularis of the mesencephalon, more currently known as the dorsal medial nucleus of the midbrain (DM) (Paton et al 1981). This nucleus mostly sends efferents to nXIIts, but also sends a projection to the red nucleus. The red nucleus is also a prime target for somatomotor outputs from the hyperpallium apicale of the rostral Wulst, the avian equivalent of the mammalian motor cortex (Wild and Williams 2000). This projection may be significant in parrots as it potentially mediates control of the body and limbs along with vocalization during elaborate, ritualized visual displays (Wild et al 1997).

The core and shell regions connect the anterior and posterior vocal pathways via vocal-motor pathways that run parallel to each other, but with limited intranuclear and internuclear connections between them (Chakraborty et al 2015). The connections between the anterior and posterior pathways are more different in songbirds and parrots than the connections within each pathway (Jarvis 2004). Whereas the AAC shell projects to the AAC core, but not vice versa, the core region of the MO in the anterior pathway has reciprocal connections with its shell region. NLC core and shell are also interconnected (Striedter 1994). Both MO core and shell regions project to the respective core and shell regions of NLC and AAC of the posterior pathway. NAO core and MO core also project to MMSt, analog of the songbird Area X. MMSt projects to the magnocellular nucleus of the dorsal thalamus (DMm).

Thalamic nuclei typically receive information via projecting neurons from sensory systems and then send that information to different regions of the telencephalon. Ascending connections from DMm project to both core and shell regions of NLC and AAC of the posterior pathways, as well as the shell region of NAO and the core of MO. A notable contrast is that in songbirds, DLm (analog of DMm) ascends to the analog of NAO (MAN) but does not connect with nuclei in the posterior pathway as it does in budgerigars (Striedter 1994).

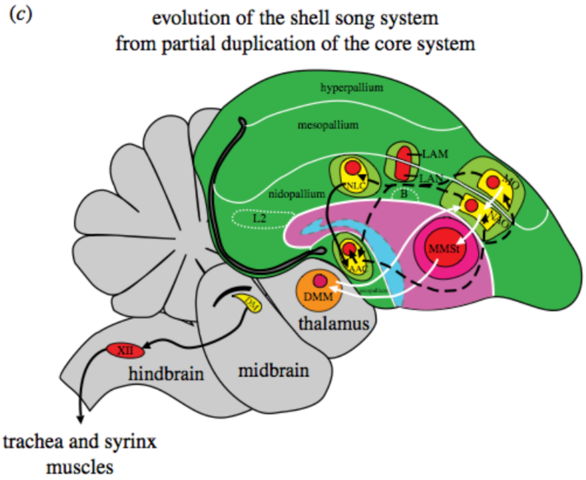


Figure 4 “(c) The parrot shell song system (yellow), proposed to have evolved out of a partial duplication of the core song system. Black arrows, posterior vocal motor pathway; white arrows, anterior vocal motor pathway; dashed arrows, connections between the two pathways; red arrow, specialized direct projection from forebrain to brainstem vocal motor neurons in vocal learners.” Image and text reproduced from Chakraborty and Jarvis 2015, p. 5.

In budgerigars, the ascending pathway from DMm could provide feedback information to the posterior pathway via connections that do not exist in songbirds and hummingbirds. The thalamic projection to posterior nuclei and the posterior projection from AAC to the cortical song nuclei is unique in parrots and may function to increase learned motor behavioral complexity over innate motor behaviors, thereby contributing to increased ability to imitate complex vocalizations as well as move to a beat. Furthering this view is the fact that shell regions appear to be larger in species with more complex and vocal cognitive abilities (Chakraborty and Jarvis 2015). As the anterior song pathway plays a role in learning and social context functions, these shell regions likely integrate information coming indirectly from the thalamus via the posterior pathway.

2.2 Eye pinning during mimicry

Tame parrots have been observed to pin their eyes in synchrony with aspects of sounds they are mimicking. Before mimicry has crystallized, pinning can be observed while parrots are listening to words that will later be produced after practice. It can also be observed while parrots are listening to a “loaded” sound that triggers a heightened state of arousal. In households, it is common for pet parrots to readily imitate emotionally charged words spoken by humans.

In the only scientifically documented case of a parrot pinning to both external and self-produced sounds, Gregory and Hopkins (1974) observe the pupils of a Yellow Fronted Amazon, Panama variety (*Amazona acrocephala panamensis*). Gregory summarizes his observations as follows:

1. The pupils contracted suddenly to about half normal size, then expanded and contracted to follow the energy envelope of words and imitated sounds of her repertoire.
2. The pupil modulation started before the utterance, with about 200 ms anticipation.
3. Occasionally, small amplitude pupil modulation would occur spontaneously, a few seconds before vocalization, suggesting internal ‘rehearsal’ for vocalising.
4. Similar pupil modulation accompanied familiar words spoken to her, and to certain sounds. These pupil changes were more variable. They occurred while she was silent but ‘attending’, looking with a beady eye. Unlike the anticipatory changes associated with her vocalisation, these pupil responses followed normal reaction-time delay to stimulus words or sounds.
5. Both for the changes associated with vocalization and responding to heard words or sounds, the pupil changes occurred only for apparently meaningful words or sounds. They did not accompany

> short loud “squawks”, believed to be innate calls. New sounds could elicit pupil responses after a few trials, as found with the Nikon camera whirr, which she soon learned to imitate. It may be noted that the distinctive whirr was special, occurring on occasions when we, and the camera captured her attention. (Gregory 1990’s, p. 2)

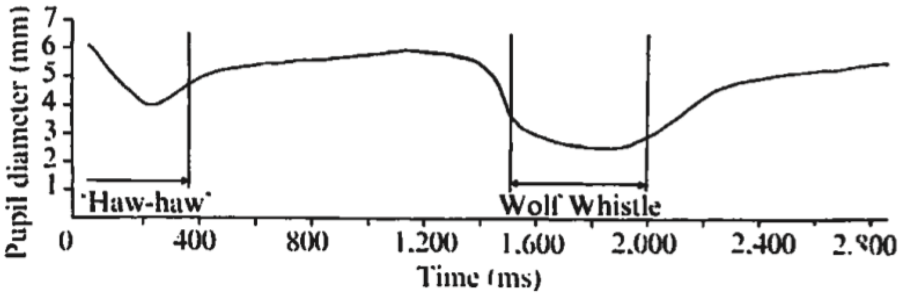


Figure 5 A sample of analyzed record (smoothed) showing constriction of the pupil immediately preceding and during vocalizations. (Gregory and Hopkins 1974)

Seraphita, the parrot in this study, seemingly had a perceptual engram that contained both the usual auditory and motor control components required for vocalizing, as well as a pupillary constriction motor component. While some pupillary activity may be voluntary in emotional contexts (although this has yet to be proven), Gregory and Hopkins’ findings indicate that understanding eye pinning associated with the song learning system, i.e. during learning and mimicry, may provide profound insight for relationships among auditory, vocal, and motor control systems, and the way behavior is learned and memories are formed and stored.

Eye pinning in Gregory and Hopkins’ study is clearly linked in some way to song learning. The first indicator that a template contains sensory and motor control components is observed when parrots are listening to sounds that they are going to mimic later on. Parrots seem to be especially drawn to imitating sounds that contain highly arousing or emotive aspects. While attending to such sounds, pupil constriction occurs during some aspects of sound but has not yet achieved the level of synchrony that is exhibited once a vocalization has crystallized. The more accurate the sound imitation, the more highly synchronized the pinning becomes (M. Kirby, pers. comm.).

When the sounds are vocalized, they are preceded by an anticipatory phase in which the pupil constricts before synchronizing with the vocalization. In addition to Seraphita, other amazons exhibit pinning while listening. Blue and gold macaws also pin in the moments before vocalizing. A 19-year old hand-raised Blue and gold macaw has been observed to pin not only before she speaks, but also before producing tricks on command (wave, dance, high 4) (M. Kirby, pers. comm).

Perhaps arousing stimuli such as novel sounds, coupled with concentration and motivation, stimulate a sensory-gated pathway responsible for remembering, calibrating, and mediating the control of replicable, desirable behaviors. Novel behaviors such as mimicking new sounds or producing a new behavior on command for a reward are products of pre-existing motor control pathways forming connections towards a novel goal-based direction. Once a representation of the desired behavior is created, higher level sensory areas of the brain must pass information to the motor regions that will be recruited to produce the behavior. Sensory feedback based on a perceptual engram encoded in the representation continues to shape the accuracy of replication during practice. As the replicated behavior becomes more accurate, a consolidated representation of the original sound or behavior and the motor activity pattern used for replication may be stored in a different region of the brain responsible for memory rather than the original region activated for processing new stimuli. Reexposure to the original stimulus may trigger activation of some aspects of the template encoded in memory. In the case of eye pinning, reexposure to the sound triggers the motor pattern coded in the memory that enacts the muscles of the iris.

2.3 Mimicry and mirror neurons

Songbird research has provided evidence that mirror neurons, or at least mirror neuron-like systems, may exist in an auditory-vocal capacity that facilitates song learning and imitation. For a brief introduction, mirror neurons are distinct neurons that have been found in certain regions of the brain in humans and non-human primates active during both an individual's observation of and execution of a behavior. They are theorized to have a role in imitative learning. In macaques, the superior temporal sulcus (STS) contains higher-order visual neurons that, in conjunction with the rostral sector of the inferior parietal lobule (PF) and ventral pre-motor cortex (F5), code the intention-based actions of others and activate the integration of the behavior into the repertoire of the observer's motor system (Jellema et al 2000, Iacoboni 2005). Intentional behaviors seem to be built up of motor acts that form prewired chains in mirror neurons where each motor act is facilitated by the motor act before it. Mirror neurons coding this cascade of behavior may allow observers to anticipate the intentions of others by coding likely future actions of the executer (Fogassi et al 2005). Primate research involving mirror neurons has mostly focused on observing others in space. A human-bonded African Grey has also been observed to imitate movement of humans using its torso, legs, wings, head, beak, and tongue (Moore 1992). Whereas the vocal imitation this bird exhibited took about three days to appear in its repertoire, movement imitations took months and were a result of consistent exposure to the behavior. Replication of this experiment has not been attempted, but research should pursue whether there may be underlying neural similarities to mirror neurons in parrots who observe intentional behaviors in visual and auditory modalities.

Two decades after the publication of “Pupils of a Talking Parrot”, Gregory wrote an informal article for his journal, Perception, and wondered, “do talking parrots have mirror cells?” (Gregory, 1990's). Auditory-vocal mirror neurons have been discovered in songbirds. HVC in songbirds is a nidopallial nucleus containing neurons that project to Area X (called HVC_X neurons). HVC seems to be “the source of precise timing signals for song patterning, the source of corollary discharge signals harnessed to allow song imitation, and a primary site where auditory signals merge with song motor representations" (Roberts et al 2010 and references therein). Area X, to which it projects, is the striatal nucleus involved in the cortico-basal ganglia pathway considered to be highly important for imitation and context discrimination in song learning.

In awake non-singing swamp sparrows, HVC_X neurons respond to playback of a single song type in the bird's repertoire and are selectively responsive to specific note combinations (Prather et al 2008). In swamp sparrows and Bengalese finches, HVC_X neurons display highly similar, temporally precise patterns of activity with action potentials that discharge at the same time in the song phrase during both singing of birds own song (BOS) and listening to BOS from a speaker (Prather et al 2008, Mooney 2014). Prather et al (2008) suggest that HVC_X activity is due to corollary discharge. These auditory-vocal mirror neurons exist in purely auditory or motor states and "could bind sensory and motor features of distinct vocal gestures, providing an efficient substrate for rapid decoding and encoding of speech". Further observations of HVC_X neurons in Bengalese finches suggest that they can encode syntactic information about the identity of individual syllables, the number of syllables repeated in a sequence, the nature of inter-syllable transitions, as well as the initiation and termination of motor sequences via the basal ganglia circuit. Of a critical note, they appear to be regulated by a gating mechanism that controls auditory drive as a function of arousal and attention (Mooney 2014).

In addition to its striatal projection via HVC_X neurons, HVC projects to the premotor arcopallial nucleus RA via HVC_{RA} neurons; however, these neurons remain unresponsive to singing and hearing of BOS and therefore are not considered to have mirroring properties. It is also worth noting that HVC_X neurons develop *in ovo*, before hatching, whereas the majority of HVC_{RA} neurons are born after hatching (Alvarez-Buylla et al 1988).

It was recently found by Roberts et al (2017) that HVC has another distinct set of projection neurons from HVC to Avalanche (HVC_{Av}) in the CM, an analog of the mammalian secondary auditory cortex. These cells "transmit vocal motor-related information from HVC_{RA} to the auditory system, play an essential role in juvenile song copying and are necessary to the adaptive modification of temporal but not spectral features of the adult's song" (Roberts et al 2017, p. 978). HVC_{Av} neurons may transmit a motor corollary discharge that serves as a predictive signal to the auditory system that can be compared to features of the auditory memory.

NLC also functions as a premotor nucleus in the posterior vocal pathway in parrots, although there are enough differences in the respective locations of HVC and NLC as well as their connectivity to the anterior song pathway that call into question whether or not they are truly homologous. NLC also responds preferentially to BOS, albeit not as strongly as HVC. It is required for parrots to speak English words (Lavenex 2000). The region of the frontal lateral nidopallium (NFl) that receives auditory projections from both auditory pathways (see Auditory and Somatosensory Connectivity for review) also receives a projection from the topographically organized somatosensory nucleus basorostralis (Bas) that contains a full body map of parrots. NLC does not receive a direct auditory projection as HVC does from Field L, however it does have access to auditory information through sparse projections from NFl/lAN and MO of the auditory pathway (see Auditory and Somatosensory Connectivity). The non-vocal motor region adjacent to NLC shell (SLN) receives auditory input from NFl/lAN. This auditory region of SLN, referred to historically in part as the supra central nucleus of the lateral nidopallium (NLs, Striedter 1994), overlaps with axon terminals from NAO shell (NAs in Striedter 1994, see new terminology in Chakraborty et al 2015), has a projection to a nucleus medial to AAC (AAm) that also has direct projections to nxIIts (Durand et al 1997), and has reciprocal connections to NFl/lAN (homolog of NIf in NCM in songbirds) (Striedter 1994), which has reciprocal connections with Field L1 and L3. Whether it has connections to lAM (homolog of Av in CM of songbirds) has not been determined. The pathways are similar enough to each other that research regarding corollary discharge and vocal-motor mirroring activity in this region of the song system should be repeated in parrots.

2.4 Early neuronal development and social exposure

While seemingly distinct behaviors, the mechanisms associated with auditory learning and imitation as well as those responsible for sexual imprinting partially overlap in their developmental timing during the sensitive period. Cross-fostering studies indicate that the timing of the development and plasticity of song learning nuclei and their projections, including those containing mirror properties, evolves in partial overlap with developing pathways associated with the social preference phase of sexual imprinting. However, the timing of the development also is dependent on tutor availability and social exposure. In zebra finches, experience rather than age determines when a song is learned; a young male remains open to learning until a suitable tutor is available (Eales 1987). Brittan-Powell et al (1997) found that parent reared budgerigars showed delayed vocal development compared to parent reared budgerigars. Budgerigars reared in isolation during the sensitive phase will not only exhibit abnormal vocalizations, they also exhibit abnormal social bonding behaviors such as warbling towards inanimate objects (Farabough and Dooling 1996).

The temporal overlap between sensitive phases of sexual imprinting and song learning processes has been a topic of interest; however, despite many conjectures that the two are related, it has been difficult to identify a direct causal linkage (Ten Cate et al 1993). Evidence of similar neuronal or mechanistic overlap has been suggested by neurobiological experiments showing that long term potentiation (LTP) and /or long term depression (LTD) and immediate-early genes *C-fos* and *ZENK* play a role in sexual imprinting and the structures involved with song learning. The effects of LTP, LTD and expression of IEG's are observed in changes in synaptic density within the sensitive period that are dependent on hormones and social experience (Bischof 2003).

Sexual imprinting consists of two separate and independent periods: a period of acquisition in which social features of an environment are learned and a preference develops, and a later consolidation period in which that social preference develops into a sexual preference that stabilizes depending on environmental conditions (Immelmann 1972). The sensory learning period for zebra finches in which a juvenile memorizes a tutor song occurs ~30-60 or 75 (Clayton 1987) days post-hatch (dph). Termination of the sensory phase seems to be attributed to vocal and sexual experiences as well as hormonal and neural maturation (Roper and Zann 2006, Schlinger and Brenowitz 2009, Gobes et al 2017). Sensorimotor learning, when a pupil uses auditory feedback to match their song to the memorized model, occurs ~45-90 dph (Roberts et al 2010). The acquisition period of imprinting begins around day 10, peaks around day 20, and ends (depending on experimental conditions) between days 40 and 60 (Bischof 2003). The onset around day 10 aligns with the visual system of the zebra finch being able to detect structured visual information (Bischof and Lassek 1985).

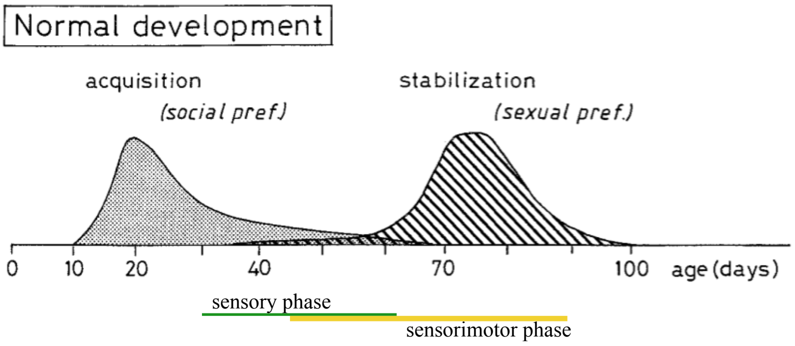


Figure 6 Zebra finch social imprinting periods. Reproduced from Bischof 2003. Song learning sensory phase, green line; song learning sensorimotor phase, yellow line.

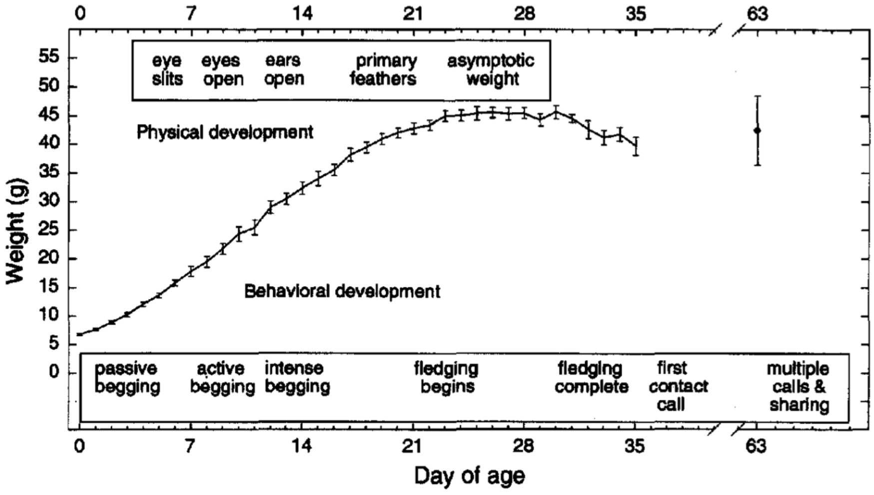


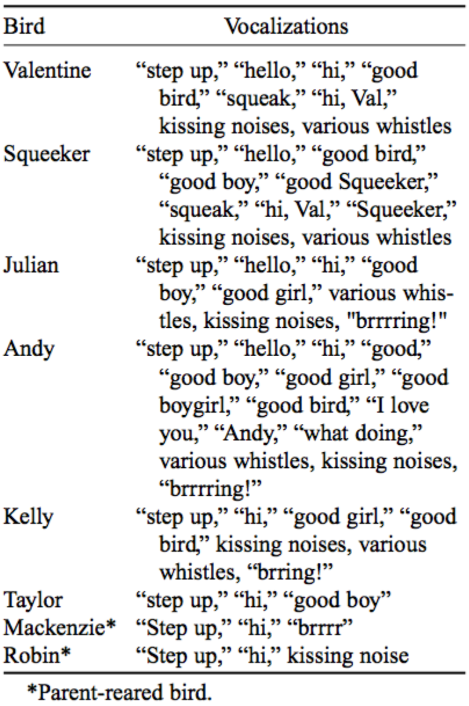
Figure 7 Budgerigar developmental phases. Reproduced from Brittan-Powell and Farabaugh 1997

The sensory period for budgerigar song learning occurs in a similar time-frame, with similar physical developmental milestones to the zebra finch. The eyes open around day 10, and the ears are able to hear almost all frequency ranges in the range of hearing by day 14 (Brittan-Powell and Dooling 2004). The nuclei of the song learning system are undergoing dramatic changes in size, volume, and cytoarchitecture. The following description of changes is summarized from Brittan-Powell and Farabaugh's work on vocal development in budgerigars:

> By one week post-hatching the NXII are well developed and have an adult-like appearance. The dorsal medial nucleus of the midbrain's (DM) boundaries are discernible from the surrounding midbrain by two weeks, whereafter little change takes place in weeks three and four.
>
> While the AAC's lateral and medial borders are visible at hatching, there is no distinction between the core and shell region until one week post-hatch. The shape of cell profiles seem to be influenced by fiber growth that transverses the AAC by three weeks. Boundaries of NLC are not observable as AAC's are at hatching, but become so by one week. At this point, a thickening of the ventricular zone is observed along the ventricular wall at the level of NLC. NLC does not become adult-like until three to four weeks post-hatching. Before its adult-like appearance, the cell profiles are densely packed with less prominent fiber bundles along the medial boundary.
>
> The anterior vocal nuclei exhibit boundary definition about a week later than the nuclei of the posterior pathway. MO becomes distinguishable by two weeks post-hatching by oval-shaped cells that surround the boundary of MO and by its lack of linearly arranged cell profiles observed in the surrounding mesopallium. It develops adult-like appearance at three weeks.
>
> NAO doesn't become easily distinguishable from surrounding regions or have adult-like organization until three to four weeks post-hatch.

While the surrounding anterior striatum is developed at hatching, MMST is not distinguished until two weeks post-hatching. It develops adult-like appearance by four weeks. (Brittan-Powell and Farabaugh 1997)

The more complex species of parrots exhibit slower developmental phases. Breeder observations suggest that hand-reared blue-naped, yellow-naped, and double yellow-headed amazons will begin mimicking human speech during the weaning period, which occurs around 12 weeks old rather than around 6 weeks as in budgerigars. African greys, who also wean around 12 weeks, have mimicked human vocalizations even earlier. According to Fox, hand-reared parrots are more likely to mimic human vocalizations than exhibit species-specific vocalizations compared to parent-reared birds. Parent-reared birds also didn't mimic human vocalizations until 6-9 months of age. Three of the six hand-raised Orange-winged Amazons in the table below began mimicking human vocalizations before they were three months old. The remaining three mimicked human speech in the presence of experimenters by four months.



Bird	Vocalizations
Valentine	"step up," "hello," "hi," "good bird," "squeak," "hi, Val," kissing noises, various whistles
Squeeker	"step up," "hello," "good bird," "good boy," "good Squeeker," "squeak," "hi, Val," "Squeeker," kissing noises, various whistles
Julian	"step up," "hello," "hi," "good boy," "good girl," various whistles, kissing noises, "brrrring!"
Andy	"step up," "hello," "hi," "good," "good boy," "good girl," "good boygirl," "good bird," "I love you," "Andy," "what doing," various whistles, kissing noises, "brrrring!"
Kelly	"step up," "hi," "good girl," "good bird," kissing noises, various whistles, "brring!"
Taylor	"step up," "hi," "good boy"
Mackenzie*	"Step up," "hi," "brrrr"
Robin*	"Step up," "hi," kissing noise

*Parent-reared bird.

Figure 8 Human vocalizations used by 3- to 12-month-old hand-reared and parent-reared Orange-winged Amazons. Reproduced from Fox 2006

"The parrots' human vocalizations were typically accompanied by excited displays such as eye pinning, head and neck feather erection, and tail fanning" (Fox 2006, p. 86-87), all of which are behaviors consistent with arousal. Hand-reared Orange-winged Amazons are also more likely to inappropriately direct both courtship and aggressive behavior associated with social preference and sexual imprinting towards humans (Fox 2006).

The anecdotal observations that human-imprinted parrots exhibit preferences for human vocalizations and mates may indicate that there is a sensitive period that lasts respectively longer into development in parrots. The plasticity observed later in their lives may be calibrated off of preferences based on early exposure, which in the case of hand-reared parrots would be human vocalizations. In songbirds, early experiences with song during development stabilize and strengthen excitatory synapses on both HVC and RA cells, analogs of NLC and AAC in parrots. During development, pronounced and spontaneous bursting activity occurs in both HVC and RA nuclei (Mooney 2014). Behavioral learning during this sensitive phase is heavily influenced by auditory exposure to a tutor and is associated with enhanced spine dynamics in the sensorimotor circuits important for learned behavior. Instructive experience stabilizes dynamic dendritic spines and strengthens synapses on sensorimotor neurons (Roper and Zann 2006, Roberts et al 2010). This has been observed mostly in HVC, but night-time bursting activity is also evident in developing RA of songbirds during sleep when neural activity patterns observed in waking behavior are reactivated and replayed (Shank and Margoliash 2008). Tutoring leads to enhanced spontaneous synaptic activity in HVC, rapid changes in vocal behavior, and a dramatic increase in spontaneous bursting in RA during initial stages of tutor-song imitation (Roberts et al 2010).

Early exposure to sound via tutors during the development of HVC and RA is critical; it is during this sensitive period that the song learning system is at its highest level of plasticity with neuronal dynamics contingent on auditory exposure. Juvenile songbirds and parrots reared in auditory isolation will sing abnormal songs based on a crude template that lacks the structure and sound of socially raised birds (Bolhuis and Moorman 2015, Farabaugh and Dooling 1996). Furthermore, the type of auditory exposure (i.e. from a conspecific vs. heterospecific tutor) plays a role in shaping neuronal development and consequently, auditory and sexual preferences of an individual after maturation.

In zebra finches, species-dependent exposure to auditory stimuli during the sensitive period affects song production and mate selection in males and females. When zebra finches are raised in a cross-fostered environment with Bengalese finches as parents, cross-fostered males produce songs that closely match the Bengalese tutors and cross-fostered females show no species-specific selectivity in prospective mates (Clayton 1987, Campbell 2009). While the long-term effects of this exposure may or may not change depending on factors later in development (mainly social exposure during first courtship (Bischof and Rollenhagen 1999, Bischof 2003)), early social exposure contributes to preexisting sensory bias in shaping social preference for context-driven vocalizations.

Social preference and sexual imprinting on heterospecifics also occurs in cross-fostered parrots in the wild. Cross-fostering of galahs (*Cacatua roseicapilla*) by Major Mitchell's cockatoos (*Cacatua leadbeateri*) leads to social preference of the foster-parents species over conspecifics to the point where conspecifics are ignored. Galahs exhibited species typical innate begging and feeding calls as well as contact/location calls to the foster parents as nestlings; however, they began to produce poor imitations of Major Mitchell's calls by 6 days out of the nest at 55 dph. Three years later, the cross-fostered galahs were observed to imitate Major Mitchell's cockatoos contact calls, albeit as a "squeakier version" (Rowley and Chapman 1986).

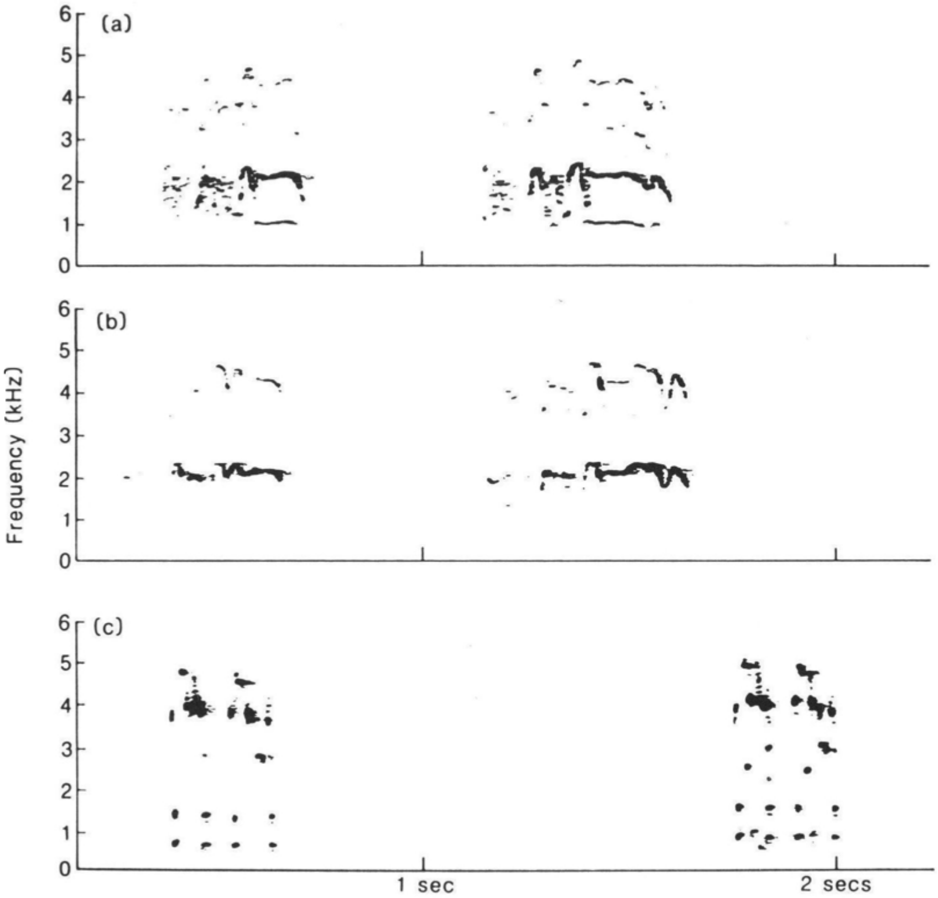


Figure 9a Sonographs of Distant Contact calls of (a) Major Mitchell's cockatoo (b) cross-fostered galah and (c) typical galah. Reproduced from Rowley and Chapman 1986

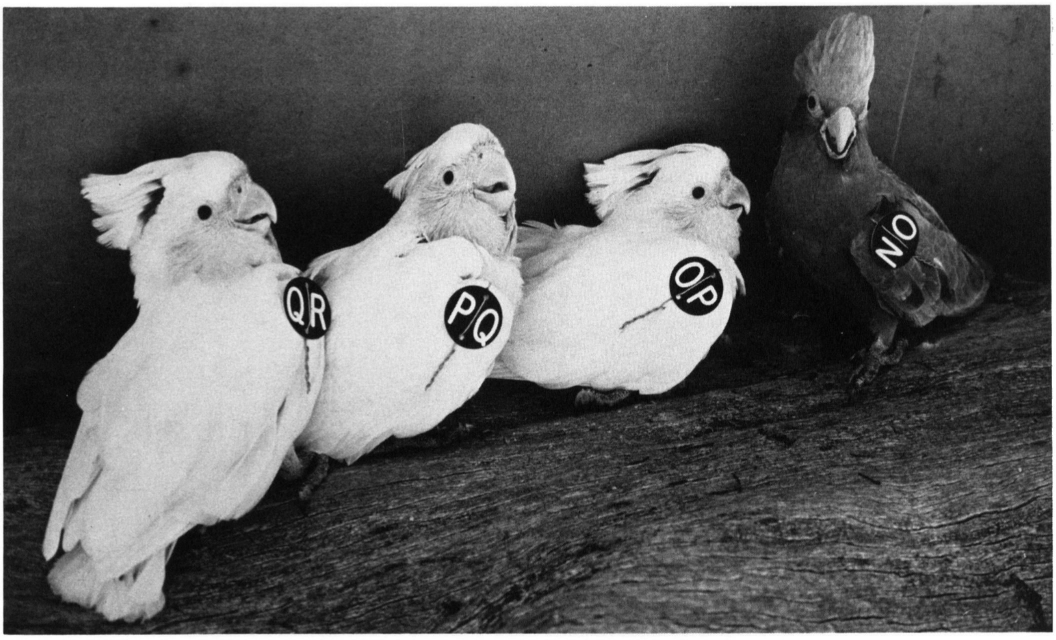


Figure 9b Major Mitchell's cockatoos and cross-fostered galah, approximately 45 days old. Reproduced from Rowley and Chapman 1986

To explain the neural correlates of cross-fostered shaping, recent research by Louder et al has elucidated different neural mechanisms that are engaged when female zebra finches process heterospecific versus conspecific songs. Early experiences in ontogeny by exposure to either conspecific (CON) or heterospecific (HET) tutors were shown to induce distinct gene expression profiles within the zebra finch auditory forebrain. While CON-tutored individuals processed CON and HET song differently, HET-tutored individuals processed CON and HET song similarly. The alpha 3 subunit member of nicotinic cholinergic receptors (CHRNA3) is known to mediate sensory gating and accounted for the similarity in CON vs. HET processing in this particular experiment. Individuals raised in a natural CON-tutor setting have down regulated CHRNA3 in response to hearing heterospecific songs; however, in HET-tutored individuals, the down regulation is diminished (Louder et al 2018). These results provide an intriguing insight into the neural basis for correlates of early social exposure and auditory processing.

Higher order auditory processing regions of the adult songbird brain exhibit preference for conspecific song. One of these regions, the caudomedial nidopallium (NCM), is characterized by significantly higher levels of ZENK mRNA when zebra finches and canaries hear conspecific calls than when they hear heterospecific calls (Mello et al 1992). In the caudal mesopallium (CM), lesions eliminated preference for conspecific songs over heterospecifc songs. This was observed by the number of sexual displays in response to songs (MacDougall-Shackleton et al 1998). New research on songbirds indicates that auditory biases and ZENK expression to species-typical songs as adults depends on exposure to a wide range of acoustic stimuli found in adult song during the sensitive phase (Diez et al 2017, Hahn et al 2015). In females raised by males singing isolate song, ZENK response as adults disappeared during exposure to unfamiliar conspecific songs (Diez et al 2017). It would be worthwhile to determine what effect early social experience and auditory exposure during the sensitive phase for song learning and social preference have on electrophysiological responses and reactivity of IEG's such as ZENK during playback of conspecific versus heterospecific calls in parrots. The lesion in CM is especially interesting as it implies that CM plays a role in processing vocalizations as they apply to preferred sexual partners. If this is the case, CM would be calibrated to distinct vocalizations heard during the social preference and sensory phase of the sensitive period. As such, it could play a role in activating circuits associated with sexually motivated behavior towards heterospecifics in imprinted birds, especially when combined with visual information regarding social preference also acquired during the sensitive period.

2.5 Pathway integration

The end of the sensitive period of development in which birds have memorized and developed species-specific vocalizations is marked by song crystallization. Some songbirds such as starlings and canaries are open-ended learners, but all species of parrots have the ability to memorize and produce new and complex vocalizations throughout their lives. Phenotypic plasticity, as defined by West-Eberhard, is “the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behavior in response to environmental conditions” (West-Eberhard 1989, p. 249). The genotype of a species can encode instructions for several phenotypes depending on experience and developmental history. Aspects of the environment have varying degrees of influence on changes in the patterns of gene expression, and early social experience, especially during the sensitive period, has been shown to play a significant role. Marler summarizes West-Eberhard’s (2003) views on plasticity well:

> The developmental plasticity of behavior can be accommodated under the same conceptual umbrella as physiology and morphology; specific cues from the environment, physical or social, engender a change of state of the organism, modifying patterns of growth, especially in the nervous system, changing motor patterns, and inducing new patterns of responsiveness to external stimuli. Even learning, the most specialized manifestation of developmental plasticity, can be viewed

> as a form of cueing by particular external stimuli, interacting with genetically based sensory and motor predispositions. (2004, p. 28)

FoxP2 is involved in the development of song learning structures. It undergoes differential expression; changing during vocalization and varying across social contexts (Knudsen et al 2015). Down regulation of FoxP2 expression is associated with novelty generation in song. 2000 other genes are co-expressed with FoxP2 in cortico-basal ganglia pathways, and recent findings in genomics imply that distinct co-expression patterns exhibit different behaviors depending on the “neurogenomic states” that the co-expression patterns exist in (Hilliard et al 2012).

When male finches practice in an undirected manner, FoxP2 mRNA is down regulated in Area X, but not when singing is female directed (Teramitsu and White 2006). The basal ganglia in the striato-pallidum of birds (including Area X and MMSt) is active during voluntary movement. In a study with zebra finches, authors compared “transcriptional patterns in tissue dedicated to Area X to those in tissue that is composed of similar cellular phenotypes but supports non-vocal motor behaviors, such as hopping and wing beating; the striato-pallidum ventral to Area X (VSP). Some non-vocal behaviors, such as courtship dances, co-occur with singing” (Hilliard et al 2012, p. 1). These two anatomically adjacent regions are functionally distinct; however, they share gene co-expression networks. While each region contains unique patterns of activity, the modules enacting these distinct functions share some of the same pathways. These findings encourage the notion that “single genes and molecular pathways are not in and of themselves specialized for systems-level neural functions or behavior, but instead unique hierarchical patterns of interactions between pathways combine to create functional specificity in particular brain regions under certain conditions” (Hilliard et al 2012, p. 2-4). The basal ganglia’s contribution to the voluntary movement of different motor control pathways and behaviors is observable due to distinct patterns of gene expression enacting behaviors via unspecialized, and in a sense “reusable” pathways.

3

Auditory and Somatosensory Connectivity

3.1 Auditory system

There are two known auditory pathways in budgerigars. They have a reciprocal connection not found in songbirds or pigeons (Farabaugh and Wild 1997). The thalamocortical pathway is the major auditory pathway that projects from the cochlear nuclei in the medulla, to the inferior colliculus of the midbrain, to the thalamic nucleus ovoidalis (Ov), to densely packed tonotopically organized neurons in Field L2 in the telencephalon (Farabaugh and Wild 1997). Field L is a major auditory region for songbirds and parrots and consists of several regions. It is considered to be analogous to the mammalian auditory cortex. In songbirds, “input from the auditory thalamus goes to subregions L2a and L2b, which in turn project to L1 and L3. Subregions L1 and L3 make bi-directional connections with two secondary auditory areas in the pallium: the caudomedial nidopallium (NCM) and the caudal mesopallium (CM)” (Theunissen and Shaevitz 2006, p. 402).

The isthmofrontal pathway is considered to be associated more so with the vocal pathway and originates in the cochlear nuclei, projects to the intermediate lateral lemniscus nucleus (LLi) also in the medulla, and then to the auditory region of basorostralis (Bas). Field L and Bas are the first nidopallial sites of auditory input. Both pathways proceed to the frontal lateral nidopallium (NFl), which is considered to be lAN of the parrot posterior vocal production pathway, although this is not entirely confirmed (see Brauth et al 2001, Jarvis and Mello 2000, Plummer and Striedter 2002). Neurons in NFl respond more selectively to a variety of stimuli, including white noise, FM sweeps, and an assortment of budgerigar vocalizations than the neurons in Bas. This increased selectivity may be an effect of the reciprocal connections between NFl/lAN and the overlying mesopallium (Striedter 1994). NFl/lAN projects to MO in the anterior song pathway (Brauth et al 2001) and along the posterior pathway to the supra central nucleus of the lateral nidopallium (NLs). It’s worth noting that the auditory projections onto NLs seem to overlap with projections that originate in the shell of NAO of the anterior song pathway (Striedter 1994). Labeled axons from NLs have terminal arborizations in NLC. The auditory responses in NLC are less than those in NLs, NFl/lAN, and Bas but are still statistically highly significant (Striedter 1994). Because NFl/lAN also projects to MO which projects to NLC, there are two potential opportunities for auditory information to make its way into the posterior vocal production pathway. Farabaugh and Wild also found that NFl/lAN has reciprocal connections to Field L1 and L3, which were originally thought to project only to a ventrolateral nidopallial area called NIVL. They suggest that the projections from L1 and L3 back to NFl/lAN may mediate auditory feedback (Farabaugh and Wild 1997).

Auditory stimulus sensitivity in parrot NLC indicates that neurons respond highest to BOS, next highest to reversed BOS, then to a contact call of another male budgerigar, and least to white noise. Neurons in NLC are similar with respect to response preferences in HVC of songbirds, however HVC responses are stronger and homogeneous throughout the nucleus. Neurons in different portions of NLC have different response preferences that respond during and prior to vocalizations (Plummer and Striedter 2000).

Different regions of the nidopallium are responsible for processing different types of auditory stimuli. NCM in songbirds receives input from Field L and serves as a large-capacity memory system that is activated by complex auditory stimuli. According to Chew et al it projects to portions of CM, which projects into the posterior pathway of the song system. Neurons in zebra finch NCM prefer conspecific stimuli. The auditory memories formed in NCM are highly specific to acoustic features of that vocalization. “The sound analysis circuit assessed by recording from NCM is very sensitive to subtle stimulus difference, which it can then memorize” (Chew et al 1996). *ZENK* is preferentially induced at higher levels by novel conspecific song, and proceeds to decrease upon repeated exposure (Mello et al 1995). Chew et al (1996) also observed a decrease in electrophysiological responsiveness in the NCM after repeated exposure. *ZENK* is also observed after hearing conspecific song in male and female European starlings (Duffy et al 1999) and male hummingbirds (Jarvis et al 2000). Hearing induced *ZENK* expression could all be part of a molecular pathway involved in forming auditory memories (Jarvis and Mello 2000). *ZENK* induction response to song is likely modulated by perceptual, attentional and/or motivation factors associated with hearing (Mello 2002).

Strong hearing-induced *ZENK* expression is also observed in budgerigars in NCM (surrounding the fields L1 and L3) (Jarvis and Mello 2000) and the regions associated with the auditory-vocal pathways such as NFl/lAN, NLs, and Bas. Brauth et al (2001) reported that NFl/lAN responds to novel contact calls with an increase in gene expression. It is hypothesized that *ZENK* "couples auditory stimulation to the synthesis of proteins involved either in storing auditory engrams or processing novel and/or meaningful acoustic stimuli relations to vocal learning" (Brauth et al 2002, p. 76). Lesions in lAN and the overlying mesopallium it shares reciprocal connections with prevented budgerigars from imitating new calls, although they retained contact calls that were learned prior to surgery (Plummer and Striedter 2002). lAN (if truly the same as NFl) also shows electrophysiological activity during call production and in response to hearing calls (Plummer and Striedter 1997). Vocally induced gene expression may represent the formation of new motor memories for vocal production after novel auditory exposure (Jarvis and Mello 2000). Alternatively, the strength of *c-fos* activated in songbird NCM upon re-exposure to a tutor's song as an adult correlates significantly with the number of song elements that birds had successfully copied from the tutor, indicating a correlation with the strength of song learning (Bolhuis et al 2001). Immediate early genes such as *c-fos* in regions of the brain that store auditory memories such as NCM and CMM may reflect the influence of *ZENK* earlier on in the learning process.

Auditory and vocal regions (NCM, CMM, HVC, and NIf) in songbirds also seem to be highly sensitive to norepinephrine (NE), a neuromodulator that tunes sensory processing systems, regulates attention and may play a role in female responses to courtship displays (Cardin and Schmidt 2004, Lynch and Ball 2008). NE projections originate in the locus coeruleus (Loc), which is known for sensory processing and regulating focused attention and attention with respect to exploring the environment. NE enhances responses to salient environmental stimuli and suppresses responses to irrelevant stimuli (Riters and Pawlisch 2007). The tendency for *ZENK* expression to be greater in response to conspecific songs versus heterospecific songs (Mello et al 1992) is abolished after treatment with DSP-4, an agent that causes pharmacological degradation of the noradrenergic system (Lynch and Ball 2008). In zebra finches, a DSP-4 treatment into dorsal NCM induced a marked BOS selectivity. DSP-4 treatment into CMM induced CON selectivity (Poirier et al 2011).

The behavioral modifications associated with NE are dose-dependent: "low levels of noradrenaline enhance NIf auditory responses, whereas high levels of noradrenaline suppress these responses" (Lynch and Ball 2008). NIf's projections to HVC represent the largest source of auditory information to the song system in songbirds and exhibits strong motor bursts that precede similar bursts in HVC and consequent song output. It also drives pre-motor like bursting during sleep (Lewandowski et al 2013). The bursts observed in these projections are less specific for BOS than those in the auditory-vocal mirroring properties of HVC neurons (Lewandowski 2013), and this threshold mechanism may emphasize the role of NE in their activity. In European starlings, norepinephrine may be an important neuromodulator for regulating the interaction between regions of the brain that regulate motivation and arousal and brain regions involved in song learning. NE associated with these interactions might guide female responses to male cues (Riters and Pawlisch 2007).

In Sara and Bouret's review of the role of Loc mediating cognition through arousal in humans, NE in the thalamus and cortex influences arousal and behavioral state and provides gating and tuning influences on sensory processing in all modalities (Sara and Bouret 2012). Projections from Loc to the amygdala are important for memory consolidation, working memory, and attentional focus, as well as attentional shifting and behavioral flexibility. It is worth noting that the posterior vocal control nuclei in parrots, NLC and AAC, both receive input from Loc, whereas HVC and RA in songbirds do not (Striedter 1994). Further research investigating the effects of NE on auditory inputs to the vocal control system in parrots should clarify the role of NE in song learning of the order.

3.2 Somatosensory system

Somatosensory information about the body and its environment is relayed to the telencephalon via projections from somatosensory nuclei in the dorsal thalamus. The telencephalon consists of motor areas with complex control mechanisms for responses to sensory input. Motor control pathway loops connect the basal ganglia and dorsal thalamus to the sensorimotor cortex, which sends projections back to the basal ganglia and to the brainstem and spinal cord. These loops contribute in part to complex and voluntary vocal control in song learning birds.

Beak mechanoreceptors are innervated by the trigeminal nerve (cranial nerve V), with one of the nerve's main targets being the principle sensory nucleus of the trigeminal nerve (PrV). PrV also receives information from the facial (cranial nerve VII), glossopharyngeal (cranial nerve IX), and hypoglossal (cranial nerve XII) nerves about the palate, tongue, and pharynx. Faunes and Wild also found that the ophthalmic nerve has afferents that terminate extensively in the ventral and dorsomedial PrV in songbirds (Faunes and Wild 2017). Four groups of birds who specialize in seed-husking and have many beak mechanoreceptors have a hypertrophied PrV: beak-probing shorebirds and kiwi, waterfowl, and parrots (Wylie et al 2015). In parrots, the hypertrophy is hypothesized to be due to tongue use for husking seeds, drinking water, picking up seeds against upper-jaw, and controlling vocalizations (Gutierrez-Ibanez et al 2010). Their lingual afferents are carried via the hypoglossal nerve to a dorsolateral portion of PrV (Wild 1981).

Efferents of PrV affect the trigeminal and hypoglossal motor nerves indirectly by terminating in the reticular formation, which sends axons to the motor nuclei. In birds, the ascending pathway of the PrV, called the quintofrontal tract, terminates in basorostralis (Bas) in the nidopallium. Bas contains somatotopically arranged information about the tongue and beak, head, wings, legs and feet, as well as an auditory component (Striedter 1994, Wild et al 1997). Bas consists of a region that receives sensory input for the tongue and beak from PrV, an auditory region whose input originates in the intermediate nucleus of the lateral lemniscus (LLI) as well as a small input from PrV (Striedter 1994), and regions mapping the wing, leg, and tail that originate in nucleus subprincipalis (sP). An ambiguous area (labeled in the diagram) may contain a vestibular representation (Wild et al 1997).

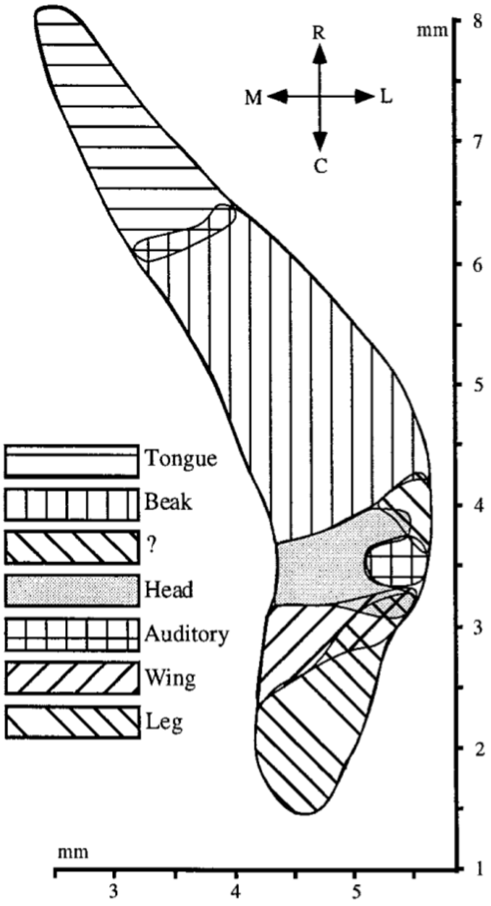


Figure 10 Bas in budgerigars.
Reproduced from Durand et al 1997

The somatosensory pathway from PrV to Bas extends to two further areas of the nidopallium- the frontal nidopallium (NF) and the caudolateral nidopallium (NCL). This ascending system plays a role in sensory control during the grasping and manipulation of objects by the beak. It has reciprocal projections to the hyperpallium. In songbirds, outputs of Bas proceed to the arcopallium indirectly through NF and NCL and exit the telencephalon from the arcopallium at the lateral intermediate arcopallium (LAI), a non-vocal motor region that controls movement (Wild 2014). It gives rise to the occipitomesencephalic tract and terminates in the spinal nucleus of CN V and its adjacent reticular formation, which is a major nexus of premotor projections to the jaw and upper vocal motor tract nuclei (Wild and Farabaugh 1996).

In budgerigars, NF, which receives input from Field L in addition to Bas, does not directly terminate in LAI, but via NFl onto NLs (Striedter 1994, Wild and Farabaugh 1996). NLs proceeds to project to the striatal motor system that surrounds MMSt (MMSt has no shell) as well as a portion of the arcopallium termed medial nucleus of the anterior arcopallium (AAm) (Striedter 1994) that lies medial to AAC. AAm also receives projections from the shell region of NAO as well as ascending projections from DMm (Striedter 1994) and contains cells that project to the lingual and tracheosyringeal portions of nxiII (Durand et al 1997). Current models for the positioning of nuclei suggest that NLC is adjacent to/embedded in the supra lateral nidopallium (SLN), a region for non-vocal movement (Chakraborty et al 2015). The title SLN encompasses NLs and NLv (Feenders et al 2008).

The complex nature of parrot social systems may recruit the use of coordinated movement of the beak, tongue and pharynx for communication. Preening conspecifics, regurgitating food, and other tactile stereotyped bill and maxilla courtship behaviors require primary sensory information from the bill. It’s possible that an increased sensory ability involved in courtship tactics and maneuvering and manipulating the muscles of the beak and tongue for husking has contributed to the ability to produce complex sounds required for mimicry, especially as psittacines are the only birds to have intrinsic muscles of the tongue.

A worthwhile study would be to analyze the PrV of other socially complex, vocal, and strong mimickers (ravens and other corvids, lyrebirds, etc.) among songbirds to identify the degree that mechanoreceptors along the beak and lingual sensory input to the PrV may contribute to the sensing, movement, and control of the tongue, beak, and surrounding musculature in order to produce complex sounds. In the Wylie study referenced above, the scatterplot of the volume of the PrV was plotted as a function of brain minus PrV volume for different orders. Eight species of songbirds were included in the study, none of which were corvids. Some corvids are known to expertly imitate other species (including humans) and have shown exceptional ability to create, manipulate, and utilize tools in the field with their beaks. Kea, who are at a basal divergence with other parrots and are known to produce distinct call types but do not seem to mimic, would also be worthwhile to compare. The vocal nuclei of the kea are lacking in the “shell” regions found in other parrots, with some researchers theorizing that these shell regions contribute to a birds’ vocal complexity (Chakraborty et al 2015). Studying the relationship and connections between PrV in vocal mimickers and these nuclei could elucidate if these sensory representations are required to produce a wide and technical variety of sounds as complex motor output. Perhaps the motor regions associated with these sensory mapped regions of the body are activated in the outer level of specialization of the parrot shell system and their adjacent motor areas during complex mimicry and courtship behavior.

Hall et al found that Bas lesions cause vocalizations to deteriorate in adult budgerigars and developing budgerigars (Hall et al 1993). In finches, pigeons, and ducks, Bas sends projections to the non-vocal motor region LAI. In parrots, the motor area surrounding NLC shell (NLs) receives input from Bas indirectly via NFl/lAN. NLs projects axon terminals into NLC, and receives projections from NAO shell. NLs also projects to the area directly medial to AAC (AAm) and the area immediately surrounding MMSt, a region that exhibits low expression of *FOXP1*. *FOXP1* is also found in NLC core and shell and is thought to be required for song acquisition in songbirds (Striedter 1994, Chakraborty et al 2015). The projections from the auditory pathway that project onto motor control regions surrounding the vocal control pathway, with an input from the anterior forebrain pathway, may be a series of connections that integrates sensory, vocal, and stored information required for entrainment and mimicry. Not only might Bas convey auditory information for learning and maintaining vocalizations to the vocal control region as Striedter suggests, but lesion-induced deterioration of vocalizations could be evidence that Bas, as a key structure in sensorimotor processing, could also facilitate the use of highly sensitive and specialized muscles in the tongue to produce vocalizations. When the representation of the beak and tongue is skewed in the budgerigars brain (by lesions in Bas), the parrot may be prevented from controlling musculature responsible for reproducing auditory templates orchestrated by the vocal control nuclei.

Analogously, superficial mechanoreceptive sensory input in humans seems to be essential in the control of orofacial movements during speech. The orofacial represention region of the primary motor cortex (Brodmann's area 4) receives a substantial portion of input from the somatosensory cortex and is thought to improve coordination and refinement of movements in great apes and humans for the manipulation of voluntary facial expressions, feeding adaptations, and speech (Sherwood et al 2005).

3.3 Entrainment

Entrainment refers to a "temporal locking process in which one system's motion or signal frequency entrains the frequency of another system" (Thaut 2015, p. 1). In behavioral biology, entrainment is referred to as the synchronization of body movement to an auditory beat. More specifically, individuals extract a pulse from periodic acoustic events and "use this inferred pulse to synchronize movements to these external events in a predictive and flexible way" (Ravignani et al 2016, p. 2). Parrots are one of the few species documented as capable of synchronizing (dancing) to an auditory beat without training (Schachner et al 2009). A recent neurobiological theory attributes this phenomenon in parrots and other animals (humans included) to neural resonance

(Molinari et al 2003, van Wijk et al 2012, Thaut 2015, Wilson and Cook 2016, Rouse et al 2016). Several studies have linked neural oscillation patterns in the auditory system to the time and frequency dynamics of rhythmic sounds stimuli (Thaut 2015), the most recent of which was a follow up with Ronan the sea lion in which the authors provide good evidence that operant beat keeping is driven by coupled oscillation (Rouse et al 2016).

All animal studies that investigate entrainment have thus far focused on how the body engages with an external auditory stimulus or beat. Several species capable of entrainment are also capable of mimicry (Ravignani 2016), however parrots are the only group displaying true imitative vocal learning and beat induction (ten Cate et al 2016). Parrots use body movements to match the frequency and phase of a musical beat (Schachner 2009). It seems likely that the abilities to entrain or mimic are products of specialized auditory-motor circuitry that facilitate temporal and spectral matching abilities. In some sense, mimicry is a form of entrainment in which an animal is manipulating its body to produce a sound that synchronizes with a sound retrieved from memory. Although entrainment advertises rhythm and beat keeping ability of an external source, mimicry is a more specialized function of complex and dynamic sound matching abilities of an internal template.

The ability to imitate accurately, or the quality of synchronization, would be a function of several conditions: 1) auditory perception, 2) reliable learning and memory of a sound formed by a significant/ arousing stimulus or consistent exposure to the sound, 3) adequate sensorimotor circuitry and anatomical structures for sound reproduction and 4) the incorporation of neural feedback during practice to hone the quality of synchronization (See Charlesworth 2012 for covert skill learning, Pepperberg 2010 for monologue speech and vocal play). Sleep is also important for strengthening neural connections involved in song learning and would fall under the category of neural feedback, albeit offline (Young et al 2017). Surely, motivation and arousal also play an overarching role in both learning and production.

There are shell regions surrounding the core nuclei of the auditory and vocal learning pathways in parrots that are embedded within or adjacent to the motor control regions of the brain (Chakraborty et al 2015). Core, shell, and surrounding activity regions all exhibit *DUSP1, c-fos,* and *ZENK*. Perhaps the surrounding movement-associated regions contain neural networks and motor control pathways that mediate courtship and social behavior and are consequently functionally linked to the embedded song learning system. Activation could involve different patterns of gene expression associated with neurogenomic states described earlier. The development and production of such mechanisms may involve temporally aligned processes driven by early experiences during sensitive periods that shape gene specialization and mirror neurons.

4

Eye Pinning

4.1 Uses in nature

Pupillary dilation in humans reflects arousal irrespective of how and why arousal occurs and is an indicator for mental effort, interest value, and system processing intensity (Mathôt et al 2013). Although pupillary activity is seen in more contexts and more elaborately in Psittacoidea than other avian orders, constriction and dilation of the pupil is observable in other species of birds with colored irides during accommodation. Pinning in aroused contexts has been observed in excited kea (who have a weakly contrasted brown iris around a dark pupil, R. Schwing, pers. comm.), aroused pigeons (Lumeij 2009, N. Rattenborg, pers. comm.), grackles during “battle or courtship” in which the iris will change from hazel to gold as the pupil constricts (Selander 1958) and bowerbirds during courtship bouts (BBC Earth 2015). Bowerbird courtship footage captured by BBC depicts stable-diameter pupil constriction in aspects of a male satin bowerbird’s (*Ptilonorhynchus violaceus*) courtship display (BBC Earth 2015b, 2:16). The most pronounced example of pupil constriction in bowerbirds occurs in orange flame bowerbird (*Sericulus aureus*) courtship displays in which the male alternately constricts his pupils (BBC Earth 2015a, :39). BBC’s Life Story footage of the flame bowerbird depicts a synchronous pupillary response to a neighboring bird’s call in the opening segment (BBC Earth 2015a, :11). Pupil constriction of varying intensity (low, medium, high, depending on the context) also occurs in threat displays and a song display that incorporates a dance component in Neotropical jays (Hardy 1974).

Intrigue surrounding eye pinning as a cognitive process grows when one considers the historical assumption that avian pupils are influenced by voluntary control in addition to classic retinal stimulation by light. It is said that this voluntary control due to striated musculature is unique to avian eyes and renders the iris useful for communication and signaling. Assessing the pupillary light reflex in birds, and particularly parrots, is problematic due to the alleged voluntary control of striated components of the iris affected by the emotional state of the bird. Consequently, parrots undergoing ophthalmic veterinary procedures need a neuromuscular blocking mydriatic agent to prevent the parrot from interfering with reflex responses.

The assumption that the pupils are under voluntary control is worth critiquing on the grounds that empirical research has yet to elucidate the actual measure or degree of voluntary control over pinning. Parrots are capable of learning behaviors through operant conditioning; however, is a parrot capable of pinning on command? An alternative theory to voluntary control could be that eye pinning is a physiological response to environmental and/or social triggers that, after reaching a threshold of arousal, initiate appropriate action patterns in accordance with that context. The interpretation that parrots have voluntary control over their pupils may be a misinterpretation of the readily observable results of a strong cognitive reaction (in the case of research and veterinary procedures, to stress) triggering a pupillary response that overrides sensory input (such as light shone during a pupillary-reflex test). This theory resembles that of the original views of animal vocalizations:

> …when the sensorium is strongly excited, the muscles of the body are generally thrown into violent action; and as a consequence, loud sounds are uttered, however silent the animal may generally be, and although the sounds may be of no use (Darwin, 1872).

Since *The Expression of the Emotions in Animals and Man,* the acceptance of animal vocalizations as content-bearing and emotion-signaling has come a long way. While countless animals produce vocalizations, eye pinning as a voluntary communicative signal is new territory in the animal kingdom. The striated musculature of the iris is a promising substrate for voluntary control, and empirically determining the mechanism, control, and extent of volition will be critical to understanding uses and limitations of the phenomenon. The following sections detail ocular anatomy as it applies to birds and when possible, specifically parrots. The goal is to review existing knowledge with the intention of guiding further research into the eye's potential use in generating effective signals for communicating mental states.

4.2 Ocular anatomy

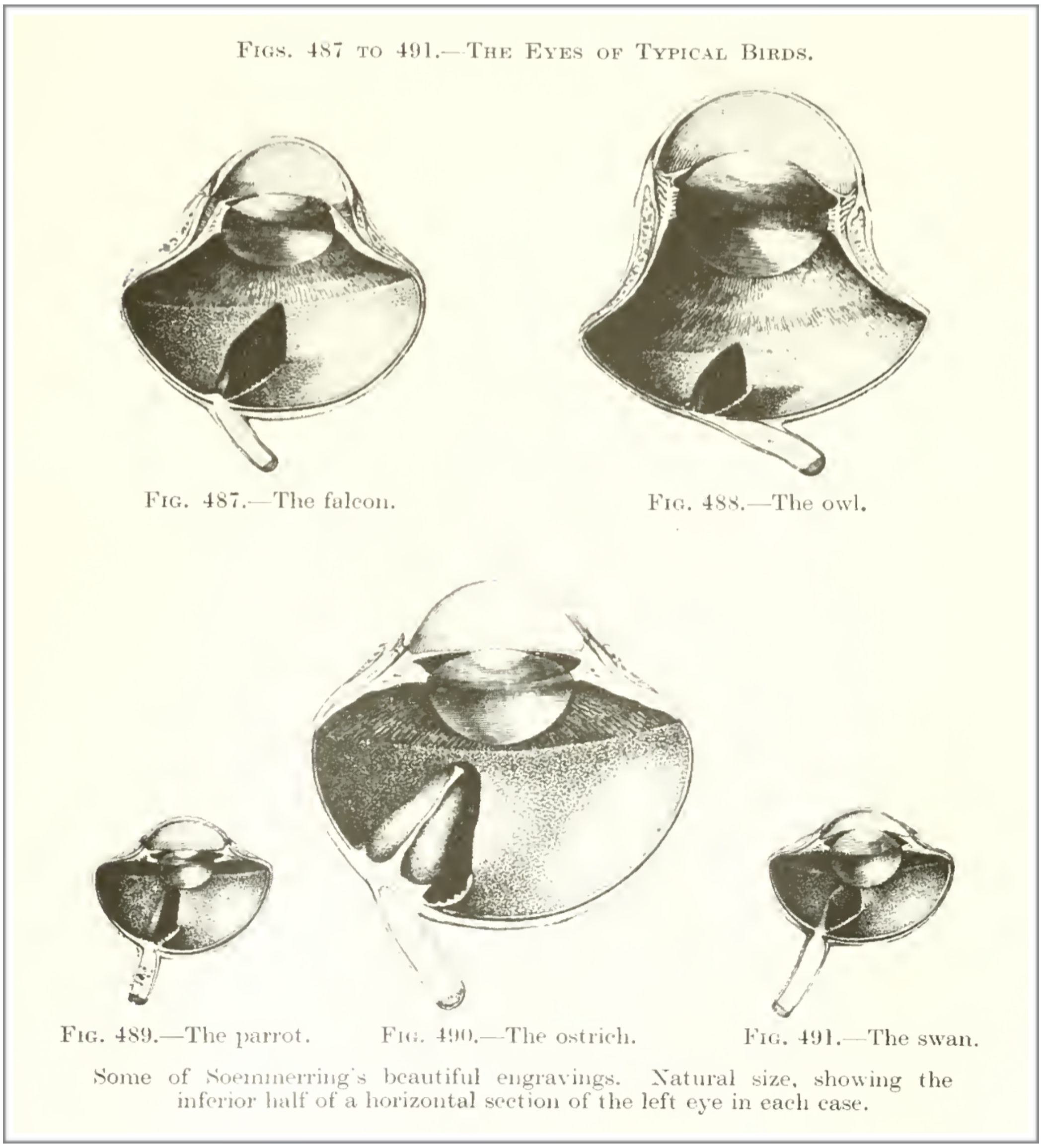

FIGS. 487 TO 491.—THE EYES OF TYPICAL BIRDS.

FIG. 487.—The falcon.

FIG. 488.—The owl.

FIG. 489.—The parrot.

FIG. 490.—The ostrich.

FIG. 491.—The swan.

Some of Soemmerring's beautiful engravings. Natural size, showing the inferior half of a horizontal section of the left eye in each case.

Figure 11 Sommering's engravings of typical bird eyes. Reproduced from Duke-Elder 1958

Birds are highly visual animals with many species having tetrachromatic, complex, and multifocal optical systems for effective flight movement and foraging. Foraging species and species that manipulate their food before ingestion must be able to adjust the focal point from distant objects or landscapes to close-up objects for use in feeding, escape behavior, social interaction, territory exploration, as well as for navigating through dense vegetation.

The eyes in birds account for approximately 50% of cranial volume of the skull, compared to less than 5% of skull volume in humans (Waldvogel 1990). The globe is partitioned into anterior and posterior segments divided by scleral ossicles that form a ring enclosed in connective tissue, providing structural stability to the eye and forming an oblate spheroid with a hemispherical posterior segment that is larger than the anterior segment (Williams 2013). There are three layers that surround the globe: the outermost layer consists of the cornea (anteriorly) and the sclera (posteriorly), the middle layer is the uvea, and the innermost layer is the retina and optic nerve. These layers surround the large, transparent structures of the eye: the aqueous humor, lens, and vitreous humor, which transmit and refract light to the retina while providing pressure to keep the globe distended (Gelatt 2014).

The outer anterior segment consists of the avascular cornea. It supports intraocular contents and refracts and transmits light by curvature and transparency into the pupil (Jones et al 2007). The area behind the cornea and in front of the iris and lens is the anterior chamber. The outer layer of the posterior segment of the globe is the sclera, a white fibrous tunic that merges with the peripheral cornea anteriorly. Like the cornea, it supports intraocular contents and maintains the shape of the eye. It contains hyaline cartilage that extends to the margin of the sclerotic ring and is the point of attachment for eye muscles.

The innermost layer of the posterior segment, the retina, consists of ten layers in birds as it does in mammals. The retina in birds is anangiotic, meaning that vasculature in the inner eye is restricted to the pecten, which is a pleated and highly vascularized structure that extends from the optic nerve head into the vitreous and is thought to supply nutrients to the retina (Pettigrew et al 1990).

The choroid lies between the sclera and the retina and is attached to the inner surface of the sclera along with the ciliary body. In conjunction with the ciliary body and the iris, it is referred to as the vascular tunic, or the uvea, and makes up the middle layer. The choroid, made up of thin-walled blood vessels and pigmented connective tissue, is a source of nourishment for the retina and serves to dissipate heat produced by retinal photoreceptors. As the choroid extends anteriorly towards the lens, it continues as the ciliary body. The iris originates from the anterior portion of the ciliary body at the ciliary processes and extends centrally over the lens as a diaphragm that encircles the pupil (Jones et al 2007).

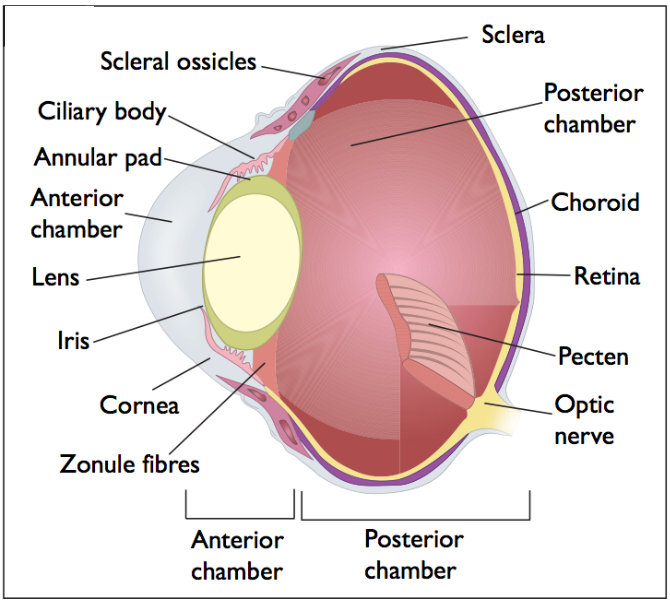


Figure 12 Anatomy of the eye. Reproduced from Doneley 2010

The sclerocorneal muscles and the muscles of the iris, in conjunction with the associated ligaments, contribute to accommodation, the process of changing the eye's refractive power to focus on objects at different distances. The iris contains striated antagonistic constrictor muscles, located primarily in the anterior two-thirds of the iris, and posterior radial dilator muscles that lie adjacent to the pigment epithelium against the lens (Glasser 1996). The constrictor muscle fibers, or circumferential muscles of the iris, form a sphincter and cause miosis while the dilator muscles cause mydriasis. The sphincter is richly vascularized and powerful. The pectinate ligament is a group of elastic fibers associated with the ciliary muscles that stretch during pupillary constriction and accommodation. When the iris muscles relax, it assists in returning the iris to its rest position and maintains the anterior part of the lens in a more flattened state (Glasser 1996). The tenacular ligament also returns the ciliary body and the posterior ciliary musculature to their relaxed states.

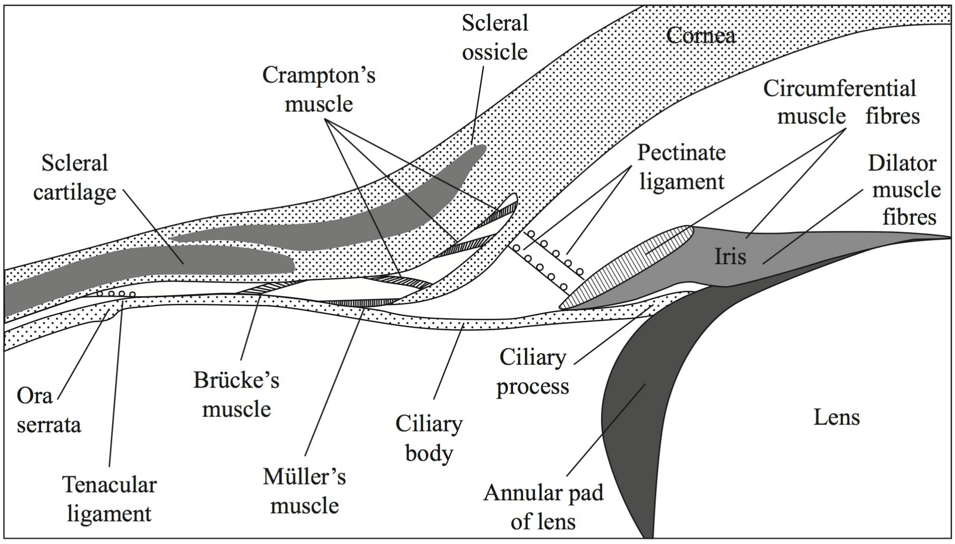


Figure 13 Muscles of accommodation.
Reproduced from Glasser 1996

4.2.1 The lens and pupillary motility

The shape of the lens may play a complex role in supporting visual processes during voluntary control of the pupil and accommodation in parrots. Because the focal length of the eye is a function of wavelength, longitudinal chromatic aberration (LCA) can degrade the quality of images being focused on the retina (Kröger 1999). Diurnal tetrapods, including humans, tend to have monofocal lenses with pupils that are small relative to the focal length of the eye. Depth of focus is long and chromatic blur isn't an issue (Gustafsson et al 2008). However, most terrestrial vertebrates, including amphibians, reptiles, and mammals, have a multifocal lens optical system in which the lens is characterized by concentric zones of different focal lengths (Malmström and Kröger 2006). Chromatic blur is decreased because each zone creates a well-focused image at the wavelength of maximum absorbance of a distinct spectral cone type on the retina (Kröger 1999). In species with a motile iris, the multifocal lens functions to reduce LCA when the pupil is fully dilated. A strongly constricted pupil blocks access to all of the zones, but creates a long depth of focus and therefore also reduces LCA.

In species with multifocal lenses and circular pupils, the pupillary light reflex or intermediate stages of pupil movement (those between fully dilated or strongly constricted) tends to shade the outer zones of the lens. In these cases, chromatic blur may degrade the image quality (Lind et al 2008). Malmström and Kröger previously determined that an adaptation for species with multifocal optical systems and motile irides is slit pupils, as they allow light to pass through each refractive zone regardless of the state of pupil constriction (Malmström and Kröger 2006).

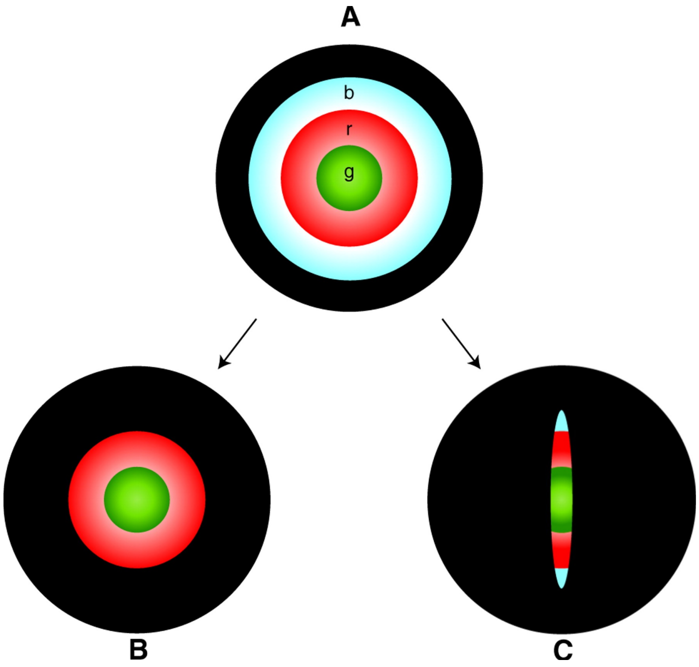


Figure 14 "The advantage of a slit pupil in an eye with a multifocal optical system. (A) The eye has three zones of different refractive powers. The zones focus light in the blue (b), red (r) and green (g) ranges of the spectrum, represented by the same colors in the figure. The iris is the black outermost region. (B) The pupil constricts circularly and the iris shades the blue-focusing zone. (C) A slit pupil allows light to pass through all zones of the optical system irrespective of the state of pupil constriction." Image and text reproduced from Lind et al 2008, p. 2753.

Multifocal lenses were first discovered in fish (Kröger 1999), but the array of species that exhibit this optical system has grown (Malmström 2006, Gustafsson et al 2008, Lind et al 2008). In research investigating optical systems in birds, multifocality was detected in 29 species in 10 out of 12 examined orders. Only five species in five orders had monofocal optical systems. Most of the birds' multifocal systems were bifocal; however, parrots were unique in that they exhibited more complex systems that involved several zones of different refractive powers (Lind et al 2008). In addition to having several complex zones, Lind et al found that parrots also have pupils that open and close within a narrow range of light intensities. Because intermediate stages of pupil movement shade the lens, it's possible that this narrow range evolved to alleviate shading. The authors termed this activity "pupil switching", and it is also seen in mice, one of the only known diurnal tetrapods with a multifocal optical system and circular pupils.

The parrot lens may have initially evolved this complex system along with the ability to see light in the UV spectrum. Pupil dynamics in Lind's study were tested in owls and parrots. Owls, who do not have UV sensitivity, did not have pupils that reacted to such a narrow range. The question remains whether switching pupils uniquely coevolved with a complex multifocal lens in parrots, or if it exists across orders as an adaptation to multifocal (or bifocal, in the case of the other avian species) lens systems with circular pupils. If it is UV specific, perhaps the species of passerines that also have the SWS1 pigment required for UV vision also utilize a switching pupil mechanism. Unfortunately, data regarding lenses of other species is lacking.

4.2.2 Pigmentation of the iris

The iris contains blood vessels, fibroblasts, nerves, collagen, epithelial cells, and extensive muscles that regulate contraction or dilation. Light entering the eye passes through the nonpigmented stroma and strikes the deeply pigmented epithelial cells on the posterior surface of the iris. As scattered pigment cells develop in the stroma, they impart color to the iris that is proportional to their density and distribution (Bortolotti et al 2003, Moses 1975).

Iris color varies among species as a result of the amount and type of pigmentation as well as the degree of vascularization (Jones et al 2007). Color changes in the iris can be observed in sexually dimorphic species, such as coloration differences between male (dark brown or black irides) and female (red irides) cockatoos, or as evidence of sexual maturation and age (brown in both cockatoo sexes before maturation). Young blue and gold macaws have dark irides that turn yellow during sexual maturation. The irides of African Grey parrots become more yellow as the bird ages and those of Amazons change from brown to red or orange when they mature (Williams 2013, Bayon et al 2008). Color changes can be observed in other orders as well (Bortolotti et al 2003, Craig and Hulley 2004, Kessel 1951, Negro et al 2017).

Pigments in the avian integument consist mostly of melanins and carotenoids. Melanins appear in feathers and bare parts that generate black, brown, gray, and chestnut hues (Prota 1992). Carotenoids generate the range of red, orange or yellow hues that are found in feathers and bare parts of birds. Iris coloration in birds is the result of carotenoid pigments found in the iris in intracellular lipid droplets. The iris also contains “iridophores” (or in those that lack iridescence, “leucophores”), which are “special pigment cells that produce structural colors by constructive interference from arrays of purine or pterin pigments” (Prum 2006). These different pigments are responsible for different coloration in various species. For example, pterin is responsible for the bright yellow iris color in Great Horned Owls (*Bubo virginianus*), purine is responsible for white iris color in Acorn Woodpeckers (*Melanerpes formicivorus*), and hemoglobin is responsible for red coloration of Phainopepla (*Phainopepla nitens*) (McGraw 2006). Although carotenoids are found in the iris, integument, and blood stream (McGraw and Nogare 2004) of avian species, the mechanisms for iris coloration seem to be entirely different from the processing responsible for coloration of the integument (Prum 2006).

Most birds obtain carotenoids through their diet and are then delivered through the bloodstream to peripheral tissues for pigmentation (McGraw and Hill 2001). Parrots are an exception to using carotenoid pigments as colorants of feathers and instead use a novel class of plumage pigments that are not found in any other organism called psittacofulvins. Psittacofulvins, like carotenoids, are lipid-soluble and produce red, orange, or yellow hues. McGraw and Nogare determined that carotenoids are circulating in the bloodstream during growth of psittacofulvin-based plumage but are selectively excluded from parrot feather follicles at the extracellular level. Both carotenoids and psittacofulvins are present in follicles, but psittacofulvins are preferentially keratanized into feathers over carotenoids. Furthermore, their lack of circulation in the bloodstream indicates that they are likely locally synthesized within the maturing feather follicle of a growing feather (McGraw and Nogare 2004).

Because psittacofulvins are synthesized at the feather follicle rather than circulatory, it is unlikely that they play a role in coloration of the iris. Psittacofulvin use in the integument over carotenoids may explain the availability for brilliantly colored irides of some species of parrots— rather than being deposited in the feathers, carotenoids are deposited in irides during maturation and may indicate developmental health.

Iris coloration in parrots is not well researched; however, in Smith's "Systematics of Parrots", Smith recorded iris coloration as well as whether or not irides contained a pericyclic ring in 81 genera. A pericyclic iris consists "of an inner, cryptically colored ring and, concentric with this, an outer, scleral, brightly colored portion" (Smith 1975, p. 38). The results of Smith's classification are overlaid with a modern phylogenetic tree depicting 79 genera from Psittacoidea (Kumar et al 2017). It is worthwhile to note for comparative purposes that in an analysis of iris coloration in passerines, 39.4% and 51.5% of genera surveyed from Southern Africa and Australia, respectively, exhibited a colored iris. Of genera surveyed from Canada, Europe, and Venezuela, 11.5%, 9.1%, and 18.6% exhibited a colored iris (Craig and Hulley 2004).

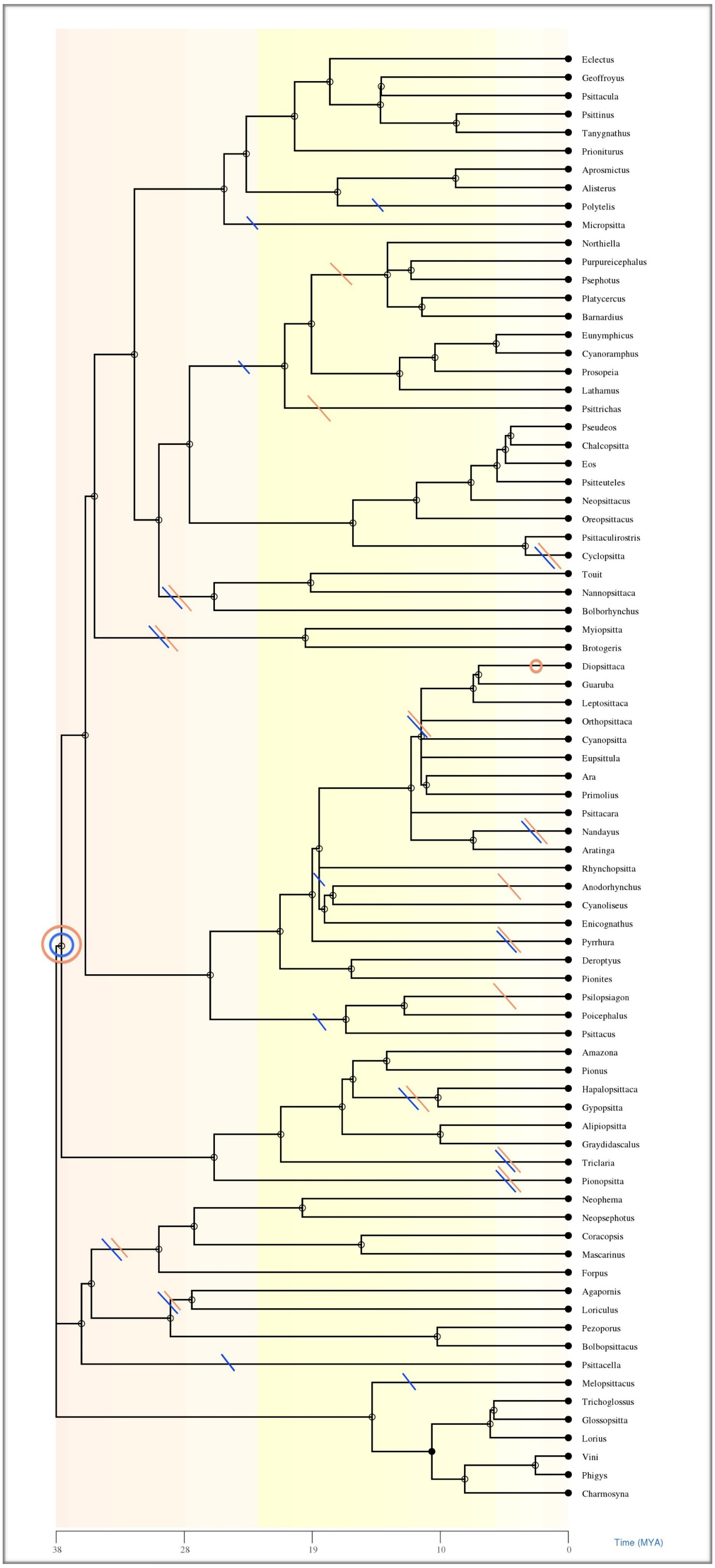


Figure 15 Iridial coloration. Data from Smith 1975. Tree from TimeTree (Kumar et al 2017).
Blue circle = percicyclic iris, Pink circle = iris coloration.
Blue line = loss of pericyclic iris, Pink line = loss of iris coloration.
Losses and gains based on parsimony.

4.2.3 Accommodation

Birds have a fluid-filled lens vesicle between the annular pad and the body of the lens that is soft and pliable, allowing accommodation to occur rapidly. A generalized mechanism of accommodation consists of muscle contractions that decrease the angle of the cornea’s curvature, deform the lens, and cause anterior movement of the lens through the pupil. Contraction occurs by two ciliary muscle groups.

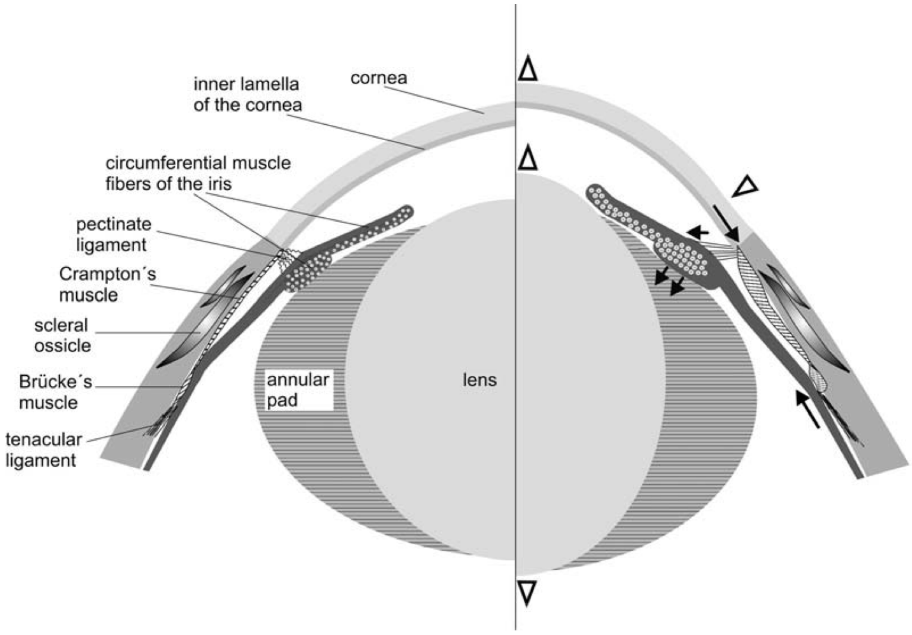


Figure 16 Mechanism of accommodation. Reproduced from Ott 2006.

The anterior sclerocorneal muscle, Crampton’s muscle, reduces the radius of the cornea’s curvature at its peripheral margin. It originates on the sclera beneath the sclerotic ring and, when contracted, bulges the central cornea outward. The posterior sclerocorneal muscle, Brücke’s muscle, also originates at the sclera but reaches back to the ciliary body to pull it forward and reduce outward tension applied to the lens by the ciliary body and tenacular ligament, an elastic tissue that connects the ciliary body to the sclera. Contraction of Brücke’s muscle pushes the ciliary body against the lens and increases its curvature, elongating it along its equatorial axis. The circumferential muscle fibers in the iris apply force against the ciliary process fused with the annular pad, which bulges the lens through the pupil (insert diagram Ott 2006). In the chick, Brücke's muscle fibers contribute to lenticular accommodation but not to pupillary constriction.

The mechanism of accommodation varies significantly depending on the evolutionary history and habitat use of a species, as does the arrangement and function of the intraocular muscles. Aquatic birds, for example, have hypertrophied ciliary muscles and a stronger lenticular accommodative ability. Corneal accommodation is not as useful because of the loss of refracting power at the water/cornea interface (Glasser, 1996).

4.2.4 Neural connectivity

In birds there is a complete decussation of nerve fibers at the optic chasm that prevents a consensual pupillary reflex from occurring. The sensory component of the eye is the optic nerve (CN II), but the motor response comes from the oculomotor nerve (CN III) which controls the skeletal constrictor muscles in the iris. Signals for pupillary constriction and accommodation reach the eye via the ciliary ganglion. The ciliary ganglion innervates the ciliary body, iris sphincter muscle, and smooth muscle of the choroid. It receives projections via CN III from the Edinger-Westphal (EW) nucleus in the oculomotor complex. In birds, CN III primarily controls skeletal muscle rather than smooth muscle (Orosz and Bradshaw 2007). EW is a cytoarchitecturally distinct nucleus that lies in the dorsal mesencephalon and can be divided into two distinct subdivisions, a medial and a lateral (Gamlin and Reiner 1991). The medial division of the EW (EWm) innervates the choroidal blood vessels whereas the lateral division (EWl), which can be further divided into a caudolateral and a rostral division, innervates the iris sphincter muscle and the ciliary body. Cells in the caudolateral EWl mediate pupilloconstriction whereas cells in the rostral EWl mediate accommodation (Reiner et al 1983).

EW receives input from the medial mesencephalic reticular formation (MRF) and a localized rostral area of the lateral mesencephalic reticular formation (LRF).

MRF projects to EWm and both regions of EWl. LRF does not project to EWm, but does send projections to both regions of EWl. A third input to caudolateral EWl comes from area pretectalis, a pretectal nucleus that receives retinotopic projections. Area pretectalis is presumed to be responsible for the pupillary light reflex. In addition to EWm's input from MRF, it receives input from the suprachiasmatic nucleus of the hypothalamus. The afferents to the areas of MRF and LRF that project to EW are not well studied and are critical for understanding the connections that contribute to eye pinning. There is some evidence that MRF and LRF receive projections from the optic tectum and areas of the arcopallium (Gamlin and Reiner 1991, see Zeier reference). The arcopallium could play a significant role, considering that stimulation of a region that receives input from telencephalic visual and visuomotor pathways produces accommodation (Gamlin and Reiner 1991).

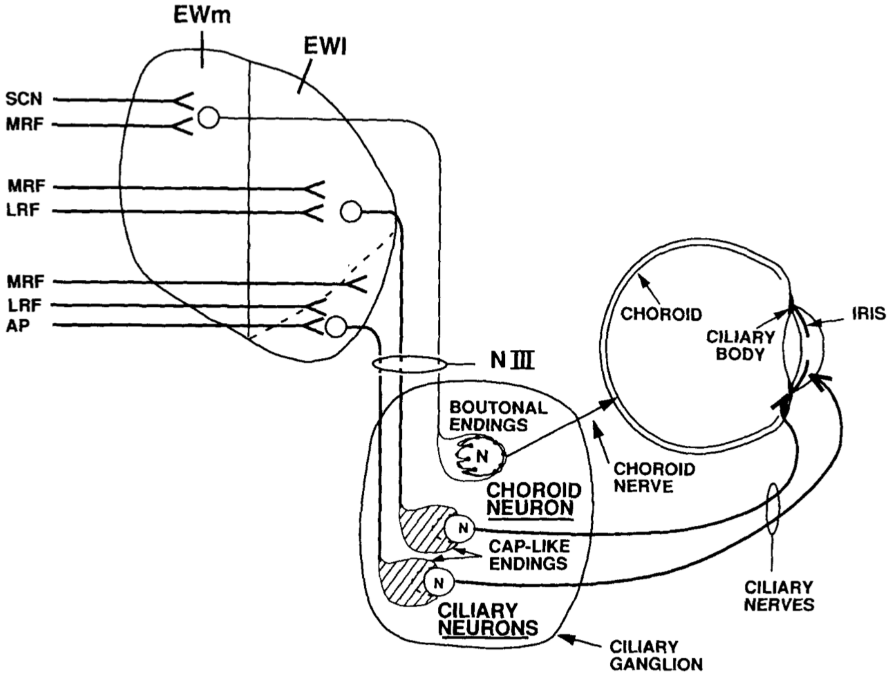


Figure 17 Sources of input to EW in a pigeon. Reproduced from Gamlin 1991.

The reticular formation is made up of clusters of neurons that fill in spaces between the sensory and motor components of the brainstem. It coordinates reflex activity, voluntary behavior, and integrates information from different senses. It is also partly responsible for regulating arousal and attention. The pathways that control movements of the musculoskeletal system carry information from the reticular formation to the spinal cord are called reticulospinal (to control limb and trunk muscles), and to the brainstem, reticulobulbar (to control cranial nerve motor nuclei in the brainstem). Mammals and birds also have corticospinal and corticobulbar pathways that work with the aforementioned pathways to provide voluntary control over muscle systems of the body and head. The reticular formation carries out coordination of the actions of eye muscles via one of its main pathways, the medial longitudinal fasciculus.

Both the lateral and medial mesencephalic reticular formation project to the caudolateral region of EWl that is presumed to mediate pupilloconstriction. I suspect that eye pinning in parrots reflects activation of this region of EWl rather than the region influencing accommodation. Activation of only this caudolateral region would potentially enable the circumferential muscles of the iris to constrict without the focus-modulating effects that accommodation affords.

4.2.5 Bony anatomy

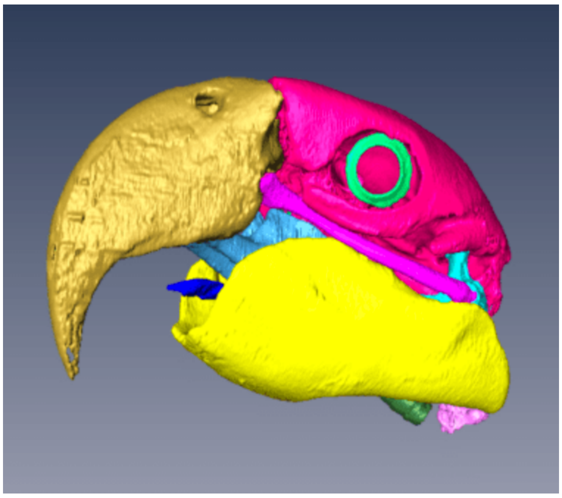


Figure 18 Digital segmentation of the bones of the head of a large macaw (Ara sp) with the sclerotic ring in green. © Avian Studios

The intermediate segment of the sclera of birds and lizards contains a ring that extends to the margin of the cornea and consists of overlapping scleral ossicles. It separates the anterior and posterior regions and is termed the sclerotic ring. The inner diameter of the sclerotic ring surrounds the corneal diameter and its fascia. Scleral cartilage within the ring serves as the site of origin for striated ciliary muscles. “Slonaker (1918, 1920) has suggested that the primary function of the [sclerotic] ring is in connection with the mechanism of accommodation. It is his view that contraction of the ciliary muscles effects an increase in intraocular pressure, thus pushing the lens farther out to accommodate for near vision. He considers that some bending of the plates is involved in this process" (Miller and Curtis 1938, p. 232). Margaret Hall's raw data on the anatomical relationships between the avian eye, orbit and sclerotic ring may provide insight into Slonaker's claims. 96% of her dry parrot specimens had a flat axial sclerotic ring length when measured (Hall 2008).

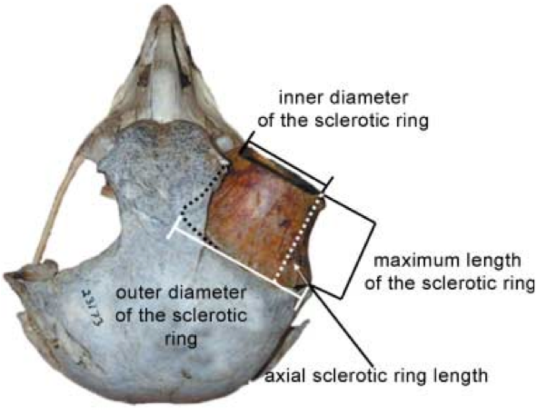


Figure 19 Axial sclerotic ring length was "calculated using Pythagoras' theory, with the maximum length of the sclerotic ring as the hypoteneuse of a right-angled triangle and half the inner diameter of the sclerotic ring subtracted from the inner diameter of the sclerotic ring as the base. Solving for the remaining side yields the axial sclerotic ring length" Text and image reproduced from Hall 2008, p. 782.

In all other orders, the dry specimens retained some axial sclerotic ring length (Hall 2008). The 0.00 mm measurement for axial sclerotic ring length was attributed to the fact that sclerotic rings tend to dry flat when the ring is relatively thin (M. Hall, pers. comm.). In some of the first research collected on sclerotic rings back in 1837, Thomas Allis asserts that "the parrot, macaw, and cockatoo have the rings particularly small and feeble; owing, I presume, to the skulls of Psittacidse being provided with perfect bony orbits, which, I believe, no other class of birds possess" (Allis 1855, p. 6). The lens of most diurnal birds has a relatively flat anterior surface. The lenses of parrots are so noticeably flat that they are almost plane (Duke-Elder 1958). In addition to flat lenses, parrots, relative to other orders, appear to have a thinner, flatter sclerotic ring. They are typically trapezoidal and overlap at the external edge of the sclera (Lima et al 2009). Given that the structure and shape of sclerotic rings varies with the degree of support and attachment needed for the ciliary musculature, and that parrot sclerotic rings are flat and feeble, there may be similarly unique traits associated with the attached musculature and elastic ligaments that provide a mechanism for striatal control of pupil constriction, allowing eye pinning to be seen dynamically and frequently in parrot behavior.

Results from Hall's comparison of avian eye shape, orbit and sclerotic ring indicate that activity pattern not only influences the soft tissue of the eye, but also significantly influences the morphology of the orbit and sclerotic ring (Hall, 2008). The fact that hard-tissue variables are associated with a bird's activity pattern shows promise in assessing relationships between unique adaptations in soft tissue of the parrot eye, including ciliary musculature, and parrot skull morphology.

On that note, Hall's findings regarding orbital size and shape cast an interesting light on a study conducted two years prior in which researchers examined the bony elements of orbits in Psittaciformes (Machado et al 2006). Little to no research has thus far addressed the curious variations in orbit anatomy in parrots. While most modern birds present an open orbit (Prince 1956), this study investigated the presence of enclosed or open orbits in parrots. An enclosed orbit refers to a fusion of the caudoventral projection of the orbital process and the rostroventral projection of the postorbital process. This fusion forms the suborbital arch and creates a 360° orbit border. Birds with enclosed orbits also have a thicker interorbital septum that separates the caudal aspects of the globes.

It was observed that some species of parrots exhibit the enclosed orbit, whereas other species of parrots exhibit the open or incomplete orbit. Interestingly, there was even variation among more closely related species, where *Ara ararauna* (blue-and-yellow macaw) and *Ara macao* (scarlet macaw) exhibited enclosed orbits, whereas *Ara chloroptera* (green-winged macaw) exhibited an open one. Among species with enclosed orbits, there was a further curious variation in that some species had shorter zygomatic processes than others. Lastly, the one and only *Cacatua sulfurea* (yellowcrested cockatoo) had a complete orbit on one side but not on the other (Machado et al 2006).

Such interesting and so far unexplainable variation in bony elements can also be observed in the number of ossicles in sclerotic rings. There appears to be much intraspecies variation in sclerotic rings in birds and orbital bone structures within true parrots (Machado et al 2006). Additionally, there is a unique relationship between orbital shape and brain shape. In Kawabe et al, brain shape strongly correlated with orbital shape. Birds with rounder, ventrally flexed brain shapes had relatively round orbits. Parrots, although closely related to songbirds and falcons, show a different brain shape from the two orders and appear to have undergone a unique evolution (Kawabe et al 2013). In a relatively new study that compared brain morphology of Neotropical parrots, a main finding was that one of the most frequently observed characteristics of Neotropical parrots is a distinctly enlarged dorsal expansion of the eminentia sagittalis, located in the avian telencephalon and frequently known as the Wulst (Carril et al 2015). Kawabe's findings indicate that the shape or size of the eminentia sagittalis changes with orbital shape. The orbital changes, referring to orbits becoming rounder and more posterolateral, and telencephalic changes, such as a dorsal expansion of the eminentia sagittalis, correlate with an integrated change of the brain shape (ventrodorsal rotation of the cerebellum and myelencephalon) (Kawabe et al 2013).

Research on the use and variation of parrot intraocular musculature and sclerotic rings, especially in comparison to orbital and brain shape, is lacking and worthwhile to study. Clearly, the variations are vast. Finding the relationships among environment, activity patterns, soft tissue, bony tissue, and brain shape in parrot species is at first glance a daunting endeavor, but dedication to determining the variables that influence one another across the parrot order could give profound insight on how physical systems evolve and drive the evolution of cognition and behavior.

4.3 Social context and selection

The use of eye pinning as a signal in agonistic, affiliative, courtship/copulatory intention and reception behaviors inherently makes the perception and interpretation of its meaning more complex. Eye pinning can indicate different levels of intensity: in a highly arousing context, the pupil is the size of pinhead and then rapidly dilated to the diameter of the eye. Constriction and dilation is more moderate in a less intense display (pers. obs., Hardy 1963).

In the case of territorial eye pinning in true parrots, components in the visual modality consist of a lowered posture, head-wagging, gaping beak, and in some species, tail fanning (pers. obs., Hardy 1963, Welle 2006). At least some species with colored irides exhibit eye pinning. Rapid constriction and dilation of the pupils may serve as a flashy display to draw attention to the face and beak. In this case, the beak is the most informative as it is the damage-inflicting component signaling “come closer and I’ll bite”.

On the positive side of the emotional signaling spectrum, a parrot experiencing pleasure while being preened fluffs out its neck feathers, pins its eyes, and flutters its eyelids in a more relaxed way. Although eye pinning is the common component underlying these two different emotional states, the differences in posture and facial expression are significant enough for a human eye to differentiate a territorial eye display from a display that indicates pleasure (pers. obs., Hardy 1963)

Courtship displays (separate from emotional displays) of some Psittacoidea involve head bobbing and eye pinning to the stereotyped frequency of a vocalization pattern (pers. obs). While most species head bob as part of their courtship display, not all have been observed to exhibit eye pinning. Those capable of eye pinning may benefit by drawing attention to the neuromuscular control involved in coordinating eye pinning, head bobbing, and patterned vocalizations. Not only would eye pinning be attention grabbing, its quality of synchronization with vocalizations would imply finely tuned neuromuscular control. Eye pinning in parrots may be incorporated into courtship displays as a motor skill advertisement signaling function in both individual and social contexts.

Sexual selection theory places emphasis on male traits that shape female response with the primary purpose of facilitating reproduction. This is certainly emphasized in species who are non-monogamous, precocial, and mostly solitary individuals. However, females of socially complex, monogamous, altricial species should take into account how a male's traits will contribute to efficient care of offspring and, in cases where parents raise the offspring together, communication between each other and flock mates. In these species a highly desirable trait would be one that signals most effectively the quality of motor skills that are used at both an individual level of function and a social level. These traits, being useful for daily survival and functioning of the individual could also be used to aid in cooperation, communication, territory defense, courtship, and other behaviors unique to socially complex groups.

The coordination required for a complex courtship dance advertises neuromuscular and motor control skills. There is "evidence that females choose their mates on the basis of subtle differences in motor performance during courtship. [Barske et al] propose that elaborate, acrobatic courtship dances evolve because they reflect motor skills and cardiovascular function of males" (Barske et al 2011, p. 1). The female may evaluate the male by his coordination as it reflects the males present state and his developmental history (Barske 2011). While in some species acrobatic courtship dances may be selected for to advertise neuromuscular coordination, songbirds rely heavily on neuromuscular coordination in male singing techniques for sex appeal.

One aspect of vocalizations that males and females in different species tune into is frequency modulation. Frequency modulation has been observed to affect social behavior in collared doves (ten Cate et al 2002). Territorial males coo with either a constant frequency or a frequency modulation that involves a jump or change in frequency to communicate territorial boundaries. Heavier males produce more modulated higher frequency coos. During playbacks, males respond more strongly to the actual change in frequency as opposed to simply responding to a higher frequency.

Lambrechts suggests that changes in frequency are more costly and therefore serve as a signal of good condition (Lambrechts 1996). Female canaries also prefer abrupt frequency falls as components of a song. Typically, females prefer songs they are exposed to while young, but in Kreutzer's studies, one strain preferred previously unheard songs that consisted of frequency falls. Frequency falls in canaries require coordination of the left and right syrinx, with the right syrinx coming into play to expand into higher frequencies. Frequency is controlled by the nervous system, meaning male neuromuscular coordination required to modulate frequency and incorporate it with a high repetition rate may signify quality (Vallet & Kreutzer 1995; Kreutzer et al. 1996; Nagle & Kreutzer 1997).

There is already some evidence that parrots prefer some aspects or qualities of sounds over others (Hoeschele and Bowling 2016). Frequency modulation may also be an attractive trait to parrots. If parrots are attracted to sounds and vocalizations that move across a wide range of frequencies the way songbirds are, the ability to produce or mimic sounds containing frequency shifts or jumps while pinning their eyes in synchrony would be an attractive trait. Vocalizations involving frequency shifts and synchronized eye pinning are observed with additional components such as stereotyped head bobbing and wing fanning frequently during courtship displays in rose-ringed parakeets (*Psittacula krameri*) (pers. obs.). The Orange-fronted Parakeets that Hardy observed exhibited an inflected cry and inflected whistle (b. in figure below) that was nearly always accompanied by pupil constriction, although this wasn't mentioned in a courtship context (Hardy 1963).

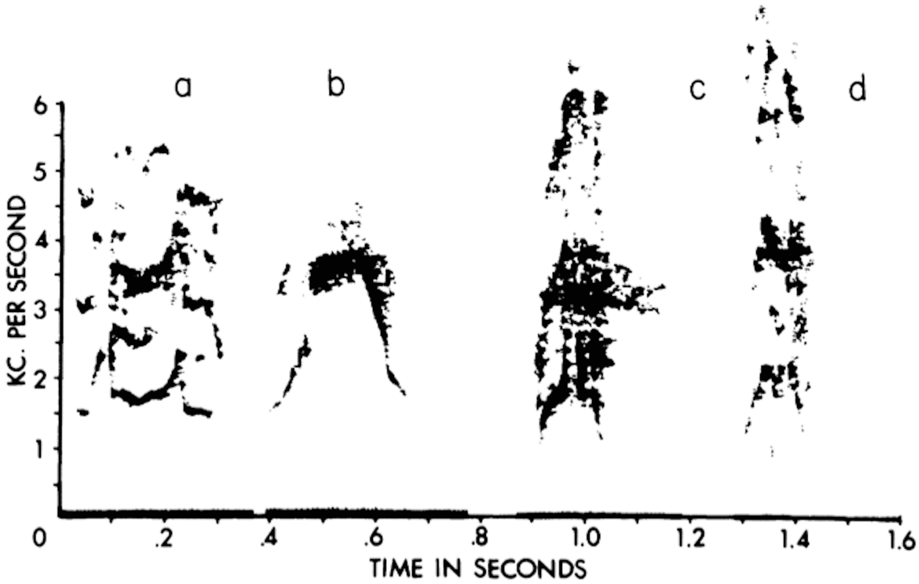


Figure 20 "Sonograms of four vocalizations of the Orange-fronted Parakeet. a, Epigamic song-like call; **b, inflected whistle**; c,d, two versions of the peach call associated with initiation of flock activity such as feeding. (All narrow band filter.)" Reproduced from Hardy 1963, p. 179.

Some lories in the genus Tricchoglossus exhibit coordinated pair duets and displays to defend their nests from other members of the flock (Bradbury and Balsby 2016). Intuitively, the quality of the male's coordination during courtship involving dance and vocalization would indicate skills that would later play a role in success of the duo's coordination during defense. As eye pinning is observed during courtship and copulatory behavior in both males and females, it may be incorporated as a signal for good coordination that may come in handy later on during vocal and/or physical defense of territory or social communication.

A link between eye pinning and courtship displays is evident. It is worth noting that pinning is incorporated into heterospecific-directed courtship displays exhibited by imprinted parrots. It cannot be a socially learned feature of courtship because it occurs in hand-raised parrots' human-oriented courtship displays. While it manifests as an innate feature of a mostly stereotyped courtship display, the mechanism behind it is flexible enough to align with temporal and spectral aspects of learned vocalizations.

4.4 Relationship to the song system

A direct connection between eye pinning and the song learning system is still speculative; however, the wealth of research on the song learning system is relevant in that it represents interaction among pathways in which sensory information is converted to motor activity. The motor commands for pupillary activity in response to auditory stimuli may occur prior to auditory information being sent to the song system. Commands may be sent as corollary discharge within the song system. Alternatively, commands may be sent via a system responsible for mediating arousal, or memory retrieval that the song system also has access to. Understanding the connectivity of various systems in the parrot brain will help direct future empirical research to define which level pupillary musculature receives input.

If a pathway containing mirror neurons exists in parrots as it does in songbirds, the parrot vocal pathway may include a motor corollary discharge signal to not just the auditory system, but also a region that activates muscles involved in constriction and dilation of the iris. This may explain eye pinning as a higher-level auditory response to hearing sounds, courtship displays involving vocalizations, and imitating songs from memory.

The previously described shell regions surrounding the core nuclei of the auditory and vocal learning pathways in parrots that are embedded within or adjacent to the motor control regions of the brain (Chakraborty et al 2015) may provide key substrate for the overlap of diverse motor behaviors during courtship and defense that incorporate contextual vocalizations. Core, shell, and surrounding activity regions all exhibit *DUSP1, c-fos,* and *ZENK*. It is possible that the surrounding movement-associated regions contain neural networks and motor control pathways that mediate courtship and social behavior and are consequently functionally linked to the embedded song learning system. As there is some degree of synchrony between the pupils and sounds heard or produced, the motor control regions may mediate motor pathways used in part to enact courtship behavior and other social interactions that incorporate eye pinning and sound production. Activation could involve different patterns of gene expression associated with neurogenomic states. We see that the main auditory region CM is activated differentially based on conspecific vs. heterospecifc/ sexual and social imprinting. Associated circuits in parrots would also likely point to regions that activate pinning during auditory or visually stimulated sexually motivated behaviors. Activation of such areas, combined with arousal, may lead to memory templates. Perhaps the loaded auditory sounds a parrot mimics in synchrony with eye pinning are the result of an auditory-motor template that formed after reaching a gated threshold dependent on NE. The development and production of the mechanisms involved with sound production and eye pinning in synchrony may involve temporally aligned processes driven by early experiences during sensitive periods that shape gene specialization and mirror neurons.

MMSt, as Area X's homolog, is part of the anterior song pathway that influences vocal learning, imitation, syntax, and use of vocalizations in social context. The nucleus itself is dedicated in part to learning vocal-motor sequences. Highly stereotyped nudging-pumping-bill-hooking behavior followed by a male turning to face the female at right angles with the male's crown and throat feathers ruffled and eyes pinning is a pre-copulatory display that frequently occurs alongside distinct vocalizations associated with courtship (Hardy 1963, Brockway 1964, Venuto et al 2000). The association may result from neuromuscular patterns activated by similarly located or activated neural pathways within the central nervous system (Brockway 1964). However, eye pinning and vocalizations do not seem to occur with the stereotypical order and consistency that the nudging, pumping, and bill-hooking movements follow. The fact that the three movements never occur in any other order may indicate that there may be a separate pathway associated with the courtship display mechanism that, under specialized patterns of gene expression, incorporates the addition of other flexible behaviors that are either under more voluntary control or mediated by different neuromodulatory systems such as vocalizations associated with courtship.

On the note of ritualized behavior, Hardy noticed in the Neotropical jays that *Cyanocorax beecheii* exhibits an intra- and interspecific threat display that involves sleeking all feathers of the head and body except for the crest feathers, which are strongly erected. The pupils are constricted displaying bright yellow irides. The same species exhibits the most developed “Sotto-voce song display” used during courtship and is the only species with a conclusive dance component. There are varying intensities in the song display, with the lowest intensity exhibiting a drooped tail, feet placed close together, the head directed diagonally upward, and the pupil slightly constricted. In a medium intensity, the tail is slightly raised, the back straight or slightly arched, feet more widely spaced, the bill directed at a steeper diagonal, and the pupil more constricted. In high intensity, the tail is raised at a diagonal, back arched, bill pointed almost vertically, the pupils constrict to a pinpoint, and the feet clasp and unclasp as a dance on the perch. The head is also waved about slightly and passing food back and forth with the directed female may or may not occur (Hardy 1974).

5

Conclusion

John William Hardy's highly detailed observations of budgerigar, Orange-fronted Parakeet, and Neotropical Jay's agonistic, affiliative, courtship and copulatory behaviors provide insight into the origin of eye pinning as a communicative signal. Although it is demonstrated widely and obviously in the majority of Psittacoidea genera, the trait is one that has likely been passed from a common ancestor of the Neotropical jays, bowerbirds (both Passeriformes) and Psittaciformes. The use of eye pinning in ritualized contexts involving body movement and vocalizations in both orders provides insight into the speculation that the courtship, pupillary activity, and song learning pathways either overlap or have evolved out of the same rudimentary pathway. Comparison with eye pinning during courtship in pigeons provides an interesting and further removed perspective as they do not have a song system.

Incorporating eye signals into agonistic and courtship displays must provide some sort of benefit to individuals although the extent of its use and interpretation as a signal has remained unstudied. Iris coloration, dependent on a multitude of factors including health and diet, sexual maturity, and season and breeding phase, has likely been selected for as an indicator of fitness. What remains unclear is why Psittacoidea have such colorful irides when Strigopoidea and Cacatuoidea have dark irides. Cockatoos have feather crests that are also said to be under voluntary control and are raised for communicative purposes to indicate alert, excited, or agitated states. Perhaps the resources necessary for deposition of carotenoids or other diet-exclusive pigments were unavailable in their specific habitats, and the sensorimotor pathway for feather control strengthened as it enabled communicative success and drove more elaborate crests.

The mirror neuron and corollary discharge propositions in song learning and pupillary pathways in parrots are highly speculative. However, the similarities and differences in the songbird and parrot song systems lay ground that parrots may have mirror neurons associated with another song nucleus and potentially a more dynamic mirror system than that of songbirds, albeit thus far unidentified. Early social interaction and experience in developing parrots may influence the development and calibration of such mirror neurons. These neurons, being a product of early social interaction and fine-tuned by early exposure to sound, would fire after reaching a threshold that involves arousal and memory. An enhanced sensory system and sensorimotor processing ability, perhaps associated with an enlarged PrV, could potentially drive the accuracy of replicated behaviors.

Perhaps the most interesting and in some ways simplest question still remains: is eye pinning in parrots a voluntary behavior? Whereas pinning in pigeons, bowerbirds, and even *C. beecheii* exists as part of highly ritualized displays, parrots do seem to have a greater sense of autonomy. Does eye pinning fall under an innate, stereotypical courtship or territorial display pathway? Or, does it's association with song learning, of which many parrot vocalizations are remembered and reproduced contextually and voluntarily, mean that it too can be generated contextually and voluntarily? Answering such questions about seemingly stereotypical behaviors in such an intelligent and complex species may have profound implications for how we interpret communicative signals.

Interdisciplinary reflection

The goal of this thesis was to investigate a unique behavior in parrots using an interdisciplinary approach and a theoretical perspective. Inspiration for the topic originally occurred while I was volunteering at an animal rehabilitation center (ARCAS) in Guatemala back in 2011. While cleaning an aviary, I caught the eye of a hormonal male who subsequently spewed every Spanish catcall in his repertoire in my direction. This classy fellow, a heavily imprinted yellow-naped amazon, wooed me with his Spanish words and nobly defended my ankles when the other amazons in the cage crept up with their heads crouched and beaks open to bite my ankles and shoelaces. After driving the competition away, this parrot gazed directly at my face and rapidly constricted and dilated his pupil, displaying his brilliantly colored iris. I was taken aback by the beautiful iris as well as how direct and deliberate the behavior was.

A preliminary search through my college database upon return delivered no scientific literature regarding this behavior. What I did learn is that it is colloquially known by breeders and bird owners as “eye pinning”. After a much more time consuming and thorough review during this project, I was able to find that eye pinning has been mentioned in literature few times, usually as a casual observation mentioned briefly while describing aspects of behavior and patterns in regard to aggression and courtship.

I reviewed empirical observations to identify all of the contexts in which eye pinning occurs. Because empirical observations are limited, I supplemented with anecdotal observations from personal experience, bird owners, veterinarians, and bird researchers. The contexts in which the behavior was used in both types of observations aligned. Eye pinning occurs socially and most emphatically in courtship and aggression in parrots and almost always indicates some heightened level of arousal (all parrot owners I’ve spoken with claim it occurs when the parrot is excited). It eventually became clear that this behavior has been observed in other orders during courtship and aggression, leading me to believe that the neurological pathway for this pupil activity is conserved from an ancestral order. However, only in parrots is it observed when a bird is exploring a novel object, feeding, or listening to/producing sound.

The behavior appears to have a dominant social component. This necessitated the introductory review on parrot social ecology. The unique and complex social structure of many parrot species also correlates to unique brain morphology and characteristics associated with those ecological traits. I merged ecology and brain morphology in the introduction to draw inferences between unique ecology, unique brain structure, and unique behaviors.

The behavior is further explored through descriptions of the song, auditory, and somatosensory systems. The review of these systems involved a deep dive into neurobiology. Whether it is determined that eye pinning is voluntary or not, the auditory systems involved in processing both simple and complex stimuli play an early role in its production as made evident by auditory and vocal synchrony. This same concept applies to the song and somatosensory systems, which likely play more of a later role as part of the production pathway. Due to the synchronicity of eye pinning and its use in hierarchical stereotyped displays, the three systems are in a position to develop based on environmental changes or responses and feedback. They are relevant to any empirical study that will focus on this phenomenon and knowledge of them will be useful in tracing the behavior.

Veterinary resources provided the most useful information for ocular anatomy. Knowledge of anatomy will also be useful for empirical research of the behavior. A comparative approach of the reviewed structures can help trace the evolution of these structures and how they have changed over time, as well as whether or not there is a direct relationship with eye pinning in parrots or other orders.

The interdisciplinary approach used for reviewing different aspects of eye pinning was critical for a first attempt at defining a unique behavior in a multidimensional way. Biology, ecology, social ecology, anatomy and morphology, veterinary science, neuroscience, and neurobiology all played a role in guiding the content of this review. This serves as the first interdisciplinary review of its kind on the behavior. Researchers from a wide array of disciplines can access it to be used as a baseline resource for parrot research regarding not only eye pinning but any of the systems described within. Future empirical studies can either focus on a specialized aspect of the behavior (e.g. whether or not avian irides are under voluntary control) or continue broadly (e.g. catalog the pinning behavior and contexts, iridial structure, and iridial color of as many parrot species as possible for use in a phylogenetic analysis). Researching this behavior will help discern the fascinating evolution of unique biological systems and behavior and their relationships to complex and unique environments. I hope that empirical research on this phenomenon soon comes into play.

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