

makes it less effortful and automatic. To find the type of learning that has reliably produced exceptionally high performance for centuries, Ericsson, Krampe, and Tesch-Römer turned to the domain of music (Figure 1). They found that the key to improvement is 'deliberate practice', namely engaging in practice activities assigned by a teacher with a clear, specific goal of improvement and where the practice activities provide immediate feedback and opportunities for repetitions to attain gradual improvements. They found that professional violinists and the best students at an international music academy in Berlin had spent an average of 10,000 hours of solitary deliberate practice by age 20, which was around 2,500 and 5,000 hours more than two groups of less accomplished violinists at the same academy. This finding rejected the popular view that more 'gifted' musicians needed less practice.

In the last 20 years the search for deliberate practice activities has been extended to numerous domains, such as medicine, nursing, ballet, sports, SCRABBLE, scientific research, psychotherapy and teaching. Current research is now finding relations between the amount of engagement in particular intensive practice activities and desired beneficial changes in the brain and other parts of the body. Future research aims to develop a detailed understanding of how designed practice activities can build complex physiological adaptations and mental representations that are associated with increased superior performance among professionals and increased achievement among amateurs.

Where can I find out more?

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Primer

Selective attention in birds

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The natural world constantly inundates our senses with an abundance of information. Selective attention enables us to navigate this abundance intelligently by selecting the information that is most relevant, at each moment in time, for differential processing and decision-making. The attributes of attention have been studied in humans for over a century. In his influential 19th century treatise, *The Principles of Psychology*, philosopher and psychologist William James defined attention as: "... the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought ... It implies withdrawal from some things in order to deal effectively with others." (James, 1890). James' definition elegantly captures two key hallmarks of attention: the enhanced processing of task-relevant information (target information) and the suppression of task-irrelevant information (distracting information).

Over the past decades, behavioral scientists have developed sophisticated psychophysical tasks that quantify these hallmarks of attention. One popular task involves cueing a subject to attend to a particular location, and comparing her ability to detect or discriminate stimuli at the cued location ('targets') versus stimuli at other, uncued locations. The consistent observation across many studies is that spatial cueing increases perceptual accuracy (d' , a performance measure based on signal detection theory) in detecting or discriminating targets and decreases the reaction time to respond to targets at the cued location versus at other, uncued locations. Consequently, these two metrics (increased accuracy and decreased reaction time) have become recognized as the

quantitative signatures of attention in humans.

In this Primer we shall consider the evidence for selective attention in birds, and outline what we know of the underlying neural mechanisms and behavioral advantages of such selective attention.

Behavioral evidence for selective attention

Given that selective attention serves the basic function of enabling animals to behave intelligently in a complex, unpredictable world, it is likely that this capacity appeared early in evolution. It has been well documented that our close relatives, old world monkeys such as macaques (*Macacca mulatta*), have this capacity. How about our more distant relatives? Do birds (class *Aves*), for example, which diverged from us more than 250 million years ago, also have selective attention?

Birds certainly exhibit a variety of behaviors that apparently require selective attention. For example, birds of prey, such as falcons (*Falconiformes*), eagles (*Accipitriformes*) and owls (*Strigiformes*), display impressive abilities to locate and track well-camouflaged prey across large distances, and capture it 'on-the-wing' with remarkable precision in both space and time. Alternatively, birds that forage on the ground, such as chickens (*Galliformes*) and pigeons (*Columbiformes*), as well as tree-foragers, such as songbirds (*Passeriformes*), exhibit similarly remarkable feats of selective spatiotemporal stimulus processing, as they repeatedly make rapid, accurate decisions about the next target for pecking while searching highly cluttered environments for food. In both cases, birds must select one out of many potential targets, analyze the target's identity and location, and ignore irrelevant, distracting stimuli.

Surprisingly, laboratory studies that have investigated the capacity of birds for selective attention have produced controversial or inconclusive results. A large body of early studies investigated the capacity of birds to attend to stimulus features (feature-based attention). For example, in highly cited work (Reynolds, 1961), pigeons

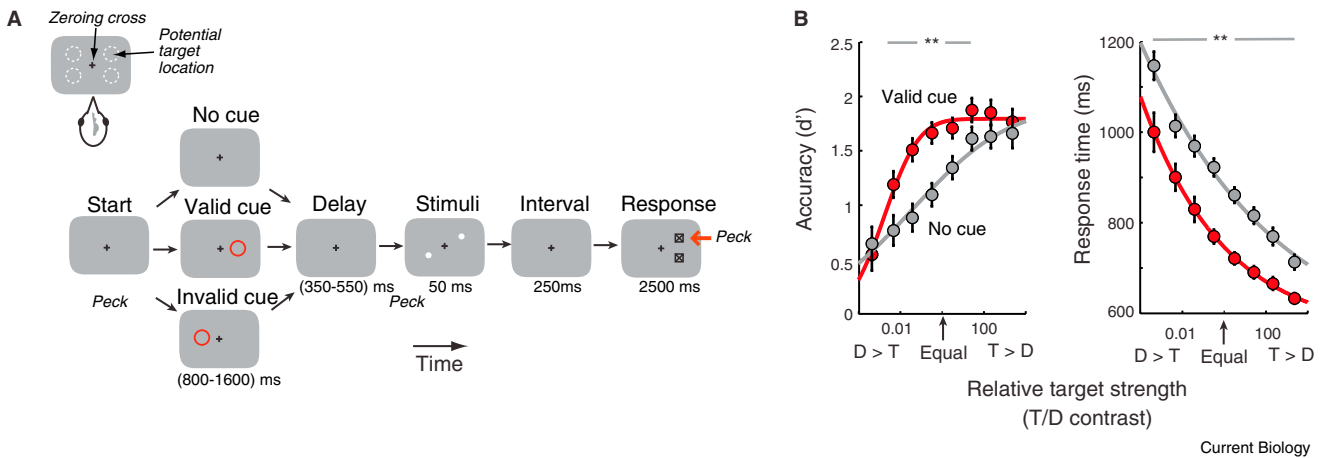


Figure 1. Behavioral evidence for selective attention.

(A) Chickens were trained on a target localization task that required them to report the vertical location of a target stimulus in the presence of a task-relevant, distracting stimulus. The bird initiated a trial by pecking on a 'zeroing cross' at the center of a touch-sensitive video screen. After a variable delay, the bird pecked again to trigger the appearance of a stimulus array consisting of two briefly flashed (50 ms) stimuli (positive contrast 3° dots) in opposite hemifields, one to the left, the other to the right. The location of each stimulus varied randomly between two possible locations, above or below the visual horizon. The locations of the two stimuli were independently sampled, and upper and lower locations were tested with equal probability. The two stimuli were identical except in contrast, which was varied randomly and independently for each stimulus. After the stimulus array was extinguished (250 ms interval), two response boxes appeared to one side. The side of the response boxes designated *post-hoc* which of the stimuli was the 'target' and which the 'distracter'; such tasks are referred to as 'filtering' tasks. In filtering tasks, the distracter is always a potentially task-relevant stimulus, so that an additional stimulus (here, the response boxes) is necessary to distinguish the target from the distracter. Birds were rewarded for indicating the location of the target by pecking on the response box closest to the target's location (red arrow). On interleaved trials, a spatial cue (middle panel) was presented on the horizon for a variable duration and was extinguished before the stimulus array appeared. The cue predicted the side of the upcoming response boxes and, therefore, identified the target stimulus with 100% validity. However, the cue was completely uninformative about the vertical location (elevation) of the target. In other sessions, behavioral performance was measured with 90% valid and 10% invalid cues (bottom panel). (B) (Left) Psychometric functions of localization accuracy (quantified as d' , a signal detection theory measure) without and with a valid spatial cue, as a function of relative target strength (target to distracter contrast ratio). Gray symbols: performance in uncued trials; red symbols: performance in cued trials (N = 199 sessions in three birds). Lines: cumulative Gaussian fits; error-bars: standard error of the mean. (Right) Response times without and with a spatial cue, for correctly localized trials as a function of relative target strength. Lines: Power law fits. In both panels, asterisks denote significant differences (in accuracy or response time) between the cued and uncued trials ($p < 0.01$). Figure modified with permission from Sridharan *et al.* (2014).

were reinforced for pecking on targets that combined two features (for example, color and shape). In later trials, when the features were presented individually, birds pecked almost exclusively on targets with only one of the two features (for example, color ignoring shape). The results were interpreted as indicating that the birds had attended selectively to only one of the two features (color, for example). However, a follow-up study has questioned this interpretation (Wilkie and Masson, 1976). Other studies have attempted to investigate the capacity of birds to select particular locations (spatial attention). For example, pigeons were shown to be able to anticipate the location of an upcoming target based either on the statistics of target presentation or on the validity of a spatial cue. However, these studies measured the effects of cues in terms of faster reaction times to the cued location, rather than as improvements in perceptual accuracy (d'). Crucially, faster

reaction times do not distinguish the effects of selective attention from those of motor preparation to respond to the cued location. Thus, the evidence for attentional phenomena in birds was tenuous, at best.

The controversy remained unresolved until recently, when quantitative behavioral protocols for measuring d' , modeled on protocols developed for measuring attention in primates, were applied to birds (Sridharan *et al.*, 2014). Chickens were trained to perform a spatially cued localization task (Figure 1A). The task required the birds to localize and report the vertical position of a visual target in the presence of a task-relevant distracter. The behavioral effects of cueing resembled signature effects of attention in primates: target localization accuracy (d') increased and response times decreased in a space-specific manner (Figure 1B). Spatial cueing also greatly reduced the performance deficits induced by

distracting stimuli and, furthermore, significantly increased the bird's confidence in its decisions. Thus, consistent with our intuition, birds do, indeed, have selective attention, and the behavioral phenomenology of spatial selective attention is remarkably similar in birds and primates.

Neural circuits and mechanisms for controlling attention

The similarities in spatial attention between birds and primates, measured behaviorally, suggest that the neural mechanisms underlying attention appeared early and have been conserved through evolution. Is there evidence for this?

Extensive literature on the neural circuits that control attention in the primate brain has identified two key systems: a forebrain system comprising the prefrontal cortex (including the frontal eye field; FEF) and the posterior parietal cortex, and a midbrain system comprising the superior colliculus (SC) and a set of

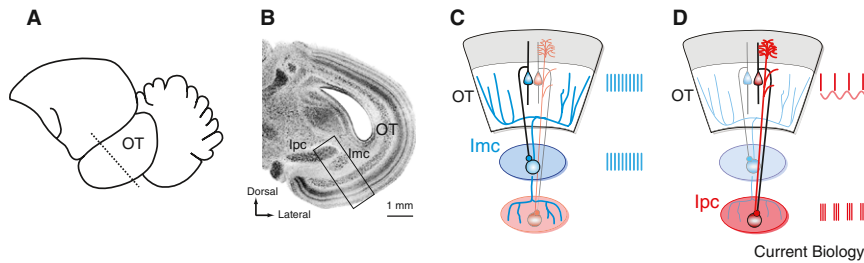


Figure 2. Neural circuits and mechanisms for controlling attention.

(A) A schematic, lateral view of the chicken brain comprising the forebrain, midbrain (including the optic tectum, OT) and the cerebellum. (B) A brain section, cut in the transverse plane (dotted line in panel A), showing the tegmental nuclei lpc and lmc relative to the multi-layered OT. Rectangle: portion of the OT–lmc–lpc circuit that is schematized in panels C and D. (C) In one specialized circuit, lmc neurons receive topographic, multimodal input from layer 10b in the OT space map and send high-rate, GABAergic inhibitory output (blue) to all portions of the space maps in both the OT and the lpc, except the portion of the OT that provides input. This unusual pattern of interconnections enables each focus of activity in the OT space map to powerfully suppress responses in all other portions of the space map and, thereby, generate a spatially localized representation of the highest priority location in the environment. (D) In another specialized circuit, lpc neurons, which are cholinergic (red), receive topographic input from layer 10b neurons in the OT space map, and they project topographically back to the OT. lpc input increases the gain of sensory responses, in a space-specific manner, across OT layers, including those that provide ascending activity to the forebrain. When activated by a salient stimulus, the recurrent OT–lpc circuit generates rhythmic oscillations in the local field potential (LFP) at gamma frequencies (25–90 Hz). This midbrain-generated gamma rhythm is regulated by mechanisms that are remarkably similar to those observed in the mammalian forebrain, and may constitute a selection signal that powerfully influences information processing in the forebrain pathway.

interconnected nuclei in the midbrain tegmentum.

The vast majority of research on primate attention has centered on the forebrain (frontoparietal) system. In contrast, the forebrain attention system in birds has not yet been studied as intensively. Brain areas in birds thought to be equivalent to prefrontal and extrastriate visual areas in mammals have been proposed based on anatomical connectivity, neurotransmitters, and effects of lesions on behavior. But none of these structures has been studied electrophysiologically in birds that are engaged in attention-demanding tasks. The most thoroughly understood structure in the avian forebrain attention system is the forebrain gaze field, called the archipallial gaze field (AGF) in birds, analogous to the FEF in mammals. The avian AGF and mammalian FEF exhibit similar patterns of anatomical connections with sensorimotor and premotor structures. Both the avian AGF and mammalian FEF play a necessary role in working-memory-dependent gaze control. Electrical microstimulation of either the AGF or FEF evokes saccadic changes in gaze direction (overt movements of the head or eye). In addition, sub-saccadic electrical microstimulation

of either structure causes space-specific, attention-like modulation of sensory neural responses. Finally, electrical microstimulation of the FEF shifts the locus of spatial attention in behaving monkeys; the equivalent experiment has not been conducted in birds.

Although research on the forebrain system in mammals has elucidated the phenomenology of neural activity during attention tasks, it has provided little insight into how attention actually works at the level of specific neural circuits and computations. In contrast, research on the midbrain system, which has been highly conserved across vertebrate evolution, has yielded circuit level, mechanistic insights.

The contribution of the midbrain system to the control of spatial attention has been demonstrated in monkeys. The superior colliculus (SC), the major node in the midbrain network, is a multimodal integration center that receives both ascending sensory information and descending sensory, decision, and motor planning information from the forebrain, and it combines this information into a unified topographic map of space. It sends descending output to premotor structures in the brainstem that orient gaze and

ascending output to structures in the forebrain that influence target selection for attention. In monkeys, there is growing evidence, based on focal electrical microstimulation and pharmacological inactivation, for the causal involvement of the SC in the performance of spatial attention tasks.

The structure in birds that is homologous to the mammalian SC is called the optic tectum (OT; Figure 2A). The OT and all other components of the midbrain selection network are far more differentiated in birds than in mammals, reflecting a spatial segregation of specialized neural circuits into separate layers in the OT and into separate nuclei in the midbrain tegmentum (Figure 2B). This high degree of architectural differentiation and organization in birds may reflect the adaptive advantage of being able to make rapid and reliable decisions during flight and landing. For investigating the mechanistic role of the midbrain in attention, the spatial segregation of these specialized circuits provides unique advantages in terms of recording from, manipulating, and analyzing the computational contributions of the various circuits.

Two specialized circuits in the avian midbrain network have been particularly well studied. One circuit comprises the OT and the lmc (nucleus isthmi pars magnocellularis), an inhibitory tegmental nucleus that uses GABA (gamma-aminobutyric-acid) as its neurotransmitter (Figure 2C). This circuit mediates the competitive selection of the highest priority stimulus as well as the global suppression of neural responses to all other, non-selected stimuli. Another circuit comprises the OT and the lpc (nucleus isthmi pars parvocellularis), a cholinergic tegmental nucleus (Figure 2D). This circuit enhances neural responses to selected stimuli and amplifies rhythmic neural activity at gamma (25–90 Hz) frequencies, the same range of frequencies that is modulated in the mammalian frontoparietal system during attention tasks. These circuits perform distinctive spatial and temporal transformations on neural activity that may underlie the behavioral hallmarks of attention: distracter suppression and target enhancement.

Advantages of birds for studies of visual attention

Birds provide unique advantages for studying the neural mechanisms of visual attention. The specialized circuits of the midbrain network, which are best studied in birds, have been conserved across vertebrate evolution. In addition, diurnal ground-foraging birds, such as chickens and pigeons, possess highly developed visual systems. The eye of these species contains four or five cone opsins (depending on the species) for color vision, and the spectral sensitivity range (visual wavelengths ~400–600 nm) is similar to that of the human eye. The spatial acuity of birds is also comparable to that of humans, although raptors, such as eagles and hawks, exceed this capacity by at least an order of magnitude. Because of their excellent spatial acuity and color vision, birds can be trained on visual attention tasks that employ complex stimulus arrays.

Moreover, birds exhibit a natural behavior that enables decisions to be reported rapidly and precisely in space and time. Ground and tree-foraging birds use pecking to obtain food and to explore objects in the environment. They engage in this behavior repeatedly, hundreds of times each day. Operant conditioning of pecking behavior is simple and enables precise quantification of perceptual decisions in birds, comparable to the quantification of foveating eye saccades in primates.

Among birds, chickens are particularly advantageous as a model for research. Chickens have been domesticated, making them easy to handle even as adults. They are inexpensive and readily available in large numbers. In addition, they are a precocial species, and even newborn hatchlings exhibit complex visual discrimination and attention-dependent behaviors that can be readily conditioned (see Supplemental Movie S1). These properties enable research not only into the various aspects of attention, but also into the developmental maturation of these capacities and the neural circuits that underlie them.

Finally, the Trans-NIH Gallus initiative describes the domesticated chicken as “the premier non-mammalian research model organism” (<http://www.nih.gov/science/models/gallus/>).

The complete chicken genome has been sequenced, leading to the availability of a variety of cutting-edge molecular and genomic resources, and creating unprecedented opportunities to develop a fine-grained map of the molecular architecture of the chicken brain. Together, these emerging research tools and the amenable behavioral and neural characteristics of the domestic chicken offer a powerful model system for linking molecules and circuits to high-level functions, including selective attention.

At the same time, measuring spatial vision and attention behavior in birds poses unique technical challenges. Unlike primates, birds lack dexterous forelimbs and they do not execute consistent orienting eye-movements independently of head movements. Instead, as mentioned previously, they orient their beaks. Thus, behavioral measurements that require spatially accurate reporting of decisions cannot be easily performed with the head immobilized, as in primates. As a result, when the head and eyes are free to move, their positions must be monitored in real time to ensure that stimuli are presented at consistent spatial locations in the visual field. Strategies for stimulus presentation in head-free visual tasks include adjusting stimulus position and size relative to the bird’s direction of gaze monitored in real-time, or synchronizing the presentation of stimuli during stable and stereotyped epochs of gaze fixation that occur naturally following a peck.

Concluding remarks

Over the past century, major strides have been made in characterizing the phenomenology of attention in humans. As a result of this research, a variety of attention disorders, such as attention deficit disorder, autism and schizophrenia, can now be reliably diagnosed. However, the etiologies of these disorders remain poorly understood. Developing targeted therapies for treating such disorders requires a mechanistic understanding of how attention works at the level of cells and circuits.

The demonstration that the phenomenology of spatial selective attention is remarkably similar in birds and primates opens up new avenues for research into the neural

mechanisms that control attention. The brains of birds and primates share many neuroanatomical and functional features. Like primates, birds (especially chickens) are readily trained to perform behavioral tasks that yield precise, quantitative measures of decision-making. In contrast to primates, they are readily available and, hence, tractable for developing and applying cutting-edge experimental techniques. We expect, therefore, that research on avian species will greatly accelerate the discovery of neural mechanisms that underlie attention.

Supplemental Information

Supplemental Information includes a supplemental movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.12.046>.

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