



Figure 2. Images of an animation at different times of a helical path.

The helical path is described by its curvature, k , and the torsion with a k/τ ratio of four which is suitable for both organisms. The *Chlamydomonas* eye (τ negative, left handed) and the dorsal side of *Platynereis* larva (τ positive, right handed) are facing inward. The normal vector, n , points directly toward the helical axis. The direction of the helix, the net cell motion, is parallel to the Darboux vector [11], $\Omega(s) = \tau(s) t(s) + k(s) b(s)$, where s is the length along the trajectory. Note this is in the t - b plane.

detect low light levels. Six, the spectral sensitivity of the eye should match the color of the incident light most useful for the behavior. The measured spectrum suggests an organism adapted to relatively deep waters. Seven, the eye must be integrated with the response mechanism of the cell for rapid communication of the signal. As beautifully shown by Jékely *et al.* [7], the photoreceptor cell acts as its own motor neuron directly innervating via cholinergic synapses and exclusively inhibiting neighboring ciliated cells. Although the synapse is probably by chemical diffusion, the postsynaptic cells most likely respond electrically to rapidly control the cilia.

Eight, the eye must have proper phasing of the response. Jékely *et al.* [7] report at least an 80 ms delay to response, which must be compensated by an equal phase advance. Because all rhodopsins respond to the change in, rather than absolute, light intensity, the response occurs as the edge of the field of view of the eye comes into the light beam. The edge field is enhanced by the tubes of receptor being oriented perpendicular to the cell surface, which minimizes sensitivity toward the normal and maximizes it toward a wide angle. Inadvertently, this optical trick may have made it easier to evolve polarization sensitivity since by shrinking the tube diameters rhodopsins are forced into greater orientation along the long axis of each tube as seen for many invertebrate eyes [14]. Probably the two eyes were also better to evolve stereovision.

The new paper by Jékely *et al.* [7] reminds us that there is a fascinating interplay between physical constraints and evolutionary design for phototaxis, which as a byproduct, via many additional steps [15], led to eyes like our own.

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Tropical Ecology: Riparian Corridors Connect Fragmented Forest Bird Populations

Landscape corridors connecting habitat patches may help overcome the genetic and demographic problems of small and isolated populations. An elegant field experiment shows that some Costa Rican forest birds will use 'riparian' (river margin) corridors to get back home, but they can be picky about corridor quality.

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Increasing human-domination and fragmentation of tropical forests has made landscape and population connectivity a critical issue for

biodiversity conservation [1]. To test the extent to which animals use corridors between habitat fragments, one promising approach is to move them away from their territories and radio-track their efforts to return, but

this labor-intensive methodology has rarely been used in developing countries [2,3]. Gillies and St. Clair [4] have broken new ground by conducting the first direct experimental test of dispersal ability and corridor use in tropical forest birds.

The researchers removed barred antshrikes (*Thamnophilus doliatus*) and rufous-naped wrens (*Campylorhynchus rufinucha*) from their territories in Costa Rican dry forest and used radio tracking to map their return paths [4]. After capture in a mistnet, a radio transmitter was attached to each bird (Figure 1), which was immediately translocated across pasture, riparian forest or fencerows to a location 0.7-1.9 kilometers away.

The birds could return back across pasture, along fencerows or through 'riparian' corridors (forested rivers). At riparian corridor translocations, antshrikes had 80% return rate, whereas this declined to 60% and 40%, respectively, for fencerow and pasture translocations. For wrens, there was no significant difference between treatments. At pasture and fencerow translocations, 80% of antshrikes used indirect forested routes to return, two crossed open pastures, and none used fencerows. However, only one out of 13 wrens, a species tolerant of open habitats, returned through forest, the rest traveling through fencerows or pastures in equal number. Both species crossed significantly fewer gaps while returning along riparian corridors than along fencerows or across pastures, but wrens crossed twice as many gaps as antshrikes.

I spent a week with Gillies in July 2000 and these birds' responses were apparent even then: barred antshrikes mostly stuck to remnant forests, mainly along riparian corridors, whereas rufous-naped wrens often made a run for it by flying across a pasture. What struck me was the difference between Gillies' Guanacaste location and my Costa Rican field site near Panama. Compared to Guanacaste's open and dry forest, the Las Cruces premontane forest is dense, humid, and gets four meters of rain per year. This is more representative of the less seasonal and more diverse forests that comprise the majority of tropical forests worldwide. These humid forests harbor thousands of bird, amphibian and other vertebrate species which, compared to these two species, are more sedentary, more forest-dependent, and more threatened. Their ability to use corridors is virtually unknown.

To put things into perspective, Stiles [5] lists both study species as forest-generalist/non-forest birds that are forest-independent. Of Costa Rica's approximately 700 land bird species, Stiles [5] considered 60% more forest-dependent than barred antshrikes and rufous-naped wrens. That most of Gillies and St. Clair's [4] birds returned to their original territories means they are reasonably mobile for tropical forest birds. Many forest-dependent species would not be so lucky, even if their lives depended on it. In a literal test of this, Moore [6]



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Figure 1. One of the barred antshrikes (*Thamnophilus doliatus*) in the study is about to be radio-tracked after translocation.

removed from their territories individuals of ten Panamanian forest land bird species with different ecological requirements and forest dependence. He released them over Lake Gatun, Panama to measure how far they could cross a gap. The birds were highly motivated as the alternative was to drown (Moore saved them when they fell in). Nevertheless, most birds in forest-specialist families like antbirds could not cross even 100 meters of open water. Only 10% of Western Slaty-antshrikes, a forest interior species, could cross a 200 meter gap. Over half of the birds could not cross 100 meters. Similarly, in Brazilian Amazon, translocated antbirds would not cross a 250 meter gap to return to their territories [2].

Barred antshrike gives the classic bird call of the Neotropics, a scolding ha-ha-ha-ha-ha-ha-ha-ha-WAEYK that is heard from Mexico to Paraguay. Even though they are forest specialists in Guanacaste, in the Neotropics, these birds are generally considered to be forest independent [5], common in forest edge and disturbed forest. A widespread forest edge and thicket specialist rarely seen inside humid forests, this species has adapted well to the open, dry forests of Guanacaste. Despite its reluctance to cross gaps in this study, the barred antshrike is one of the more gap-tolerant species

of its superfamily Furnarioidae, which represents the main radiation of forest-interior birds in the Neotropics [5]. Unlike the barred antshrike, 87% of Costa Rican furnarioid species are forest-dependent [5], also reflected in their sensitivity to forest fragmentation [7]. It would be valuable to conduct a similar experiment with species restricted to the tropical forest interior, as these specialized species suffer most from the fragmentation and isolation of their populations [2,8].

Landscape connectivity is critical in tropical agricultural countryside where forest fragments harbor hundreds of species that rarely, if ever, leave the forest. In Guanacaste, where centuries of cattle raising practices have removed ~75% of the native forest that once covered the entire region [4], most of the remaining forest outside protected areas is found along fencerows and rivers. Nevertheless, 50–150 meter wide riparian corridors and 15–30 meter wide fencerows of this study are wider than many riparian strips and fencerows seen in the tropics, including my study area in southern Costa Rica [9]. Considering that both bird species tested are forest-independent birds [5], more sensitive tropical forest species that often have access to narrower corridors likely experience greater isolation and its consequences.

Playback experiments in Chilean temperate rainforest demonstrated that corridors <10 meters were not used by forest understory birds and only corridors >25 meters were used constantly [10]. In Honduras, more forest bird species and individuals were recorded in belts 50 meters or wider [11]. In Australian rainforest, lemuroid ringtail possums require corridor widths of at least 200 meters [12]. In Amazonian tropical forest, corridors <200 meters wide are prone to edge effects, and bird and mammal species richness declines in riparian corridors less than 400 meters wide [13]. These data hint that ideal tropical forest corridor width may be inversely correlated with seasonality and directly correlated with regional species richness. Wide corridors also serve as habitat in their own right and can harbor similar communities of litter frogs and small mammals as continuous rainforest [14]. Two rows of trees do not a corridor make, and in corridor ecology, width is as important as length.

The study birds, especially wrens, regularly used stepping stones like remnant trees to get back home [4]. Countryside biogeography [15] has shown that increased tree cover in tropical countryside not only improves the mobility of forest-restricted species, it also provides critical habitat for many other forest species that persist in these landscapes [9,15,16]. Since 2002, we have radio-tracked nearly 450 birds of ten native forest species persisting in the agricultural countryside of southern Costa Rica. Although riparian strips cover only 4.6% of our study area, forest generalist silver-throated tanagers used them 23–38% of the time [9]. Remnant trees, which provide stepping stones and fruits, were used 31–48% of the time, despite covering 1.4% of the landscape. Forest-dependent white-throated thrushes used riparian strips 29–35% and remnant trees 6–25% of the time [9]. For some species, however, riparian habitat is not just an option. Worldwide, a quarter of tropical river specialist bird species are near threatened, threatened or extinct (my unpublished data).

Birds themselves can connect landscapes with their ecological services such as pollination or nutrient transfer [17]. These services can

decline in isolated forest fragments that lose their ‘service providers’ such as seed dispersers [18] and insectivores [7]. Therefore, higher landscape connectivity, via corridors [18] or increased tree cover in agricultural areas [16] can have the added benefit of restoring some of these ecosystem services.

Corridors are likely to become more important as many species face range shifts in response to climate change [19], but there is little knowledge on the role of corridors in a changing climate [20]. Mobility does decrease the chance of extinction in birds, as sedentary birds are 2.6 times more likely to be threatened or near-threatened with extinction than long-distance migrants [8]. By forcing many species to move to areas with suitable climate and vegetation, climate change will make mobility, connectivity, and corridors even more critical. Sedentary birds, which include most bird species [8], are five times more likely to go extinct from climate change than long-distance migrants [19].

Riparian corridors also provide local ecosystem services by protecting watersheds for people and domestic animals, by reducing erosion, and by providing shade and recreational areas [9]. Some tropical countries, like Costa Rica and Brazil, have legislation that protects riparian corridors [13,14]. Enforcement is a different matter, however, and riparian corridors are often much narrower and more degraded than what is ideal for forest species [9,13]. Cattle also degrade riparian vegetation and make corridors less suitable for native wildlife [9].

As tropical landscapes become increasingly human-dominated, deforested, and fragmented, riparian corridors are becoming disproportionately important in connecting and harboring populations of tropical forest organisms. Gillies and St. Clair [4] have made an important contribution, but much more is needed. Our knowledge of corridor use by tropical species is biased towards common species, mobile endotherms, distributional studies, and one time snapshots. We need more experimental studies in the tropics, focused on a wider range of taxa, representing threatened, sedentary, and forest-dependent organisms, while covering climatic and elevational gradients. In most

tropical countries, riparian conservation laws are lacking, insufficient or not enforced. We must combine a better understanding of corridors with science-based conservation and superior enforcement to effectively conserve these critical lifelines. Equally importantly, local people need to be more involved with, informed about, and benefit from corridor conservation efforts in the tropics.

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Visual Attention: The Thalamus at the Centre?

New work shows that spatial attention modulates visual responses of single neurons in monkey thalamus, providing empirical support for a long-standing theoretical prediction that specific thalamic nuclei play a key role in controlling the spotlight of visual attention.

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Until recently, visual attention and awareness in primates were thought of as purely cortical phenomena. But functional magnetic resonance imaging (fMRI) signals in the human lateral geniculate nucleus (LGN) of the thalamus are correlated with fluctuations in both visual attention and visual awareness [1,2]. Such findings are surprising, given the location of the thalamus very early in the visual processing pathway, and have sparked a renewed interest in the functional properties of the primate thalamus. Critical, but previously unresolved questions include whether such modulation of fMRI signals reflect changes in firing rate of individual LGN neurons rather than feedback signals from cortical areas, and more generally what the precise functional relationship is between the different nuclei that comprise the primate thalamus. McAlonan *et al.* [3] have provided important new data that not only conclusively demonstrate that visual attention can modulate visual responses of single cells in monkey LGN, but also provide significant new insights into the functional relationship between different components of the visual thalamus.

The vast majority of visual information from the retina passes through thalamic relay cells in the lateral geniculate nucleus of the thalamus before reaching visual cortex. Most axons connecting the thalamus and cortex in either direction pass through the thalamic reticular nucleus (TRN), a thin shell surrounding the dorsal thalamus that contains

almost exclusively GABAergic neurons. Both thalamocortical and corticothalamic neurons emit excitatory collaterals within the TRN that are organised in both a spatiotopic and modality-specific fashion, and TRN cells send strong inhibitory projections to thalamic relay cells [4,5]. Thus, the inputs to the TRN are excitatory, but its outputs to the same thalamic relay are inhibitory (Figure 1). This suggests a possible modulatory role for the TRN in controlling thalamic activity, and led Francis Crick to suggest many years ago [6] on theoretical grounds that the TRN might play a key role in directing visual attention.

Nearly twenty-five years later, McAlonan *et al.* [3] recorded from visually responsive neurons in the TRN and LGN of awake behaving macaque monkeys performing a simple spatial attention task. The monkeys fixated on each trial, were centrally cued to attend to one of two visual stimuli, and then judged whether that stimulus subsequently dimmed. One of the stimuli was placed in the receptive field of the recorded neuron and so the effects of attending to that stimulus on visually evoked responses could be compared with when the same stimulus was ignored. Attention significantly increased visually evoked responses in the LGN, and this increase was independently observed in both magnocellular and parvocellular LGN neurons. Critically, however, neurons in the TRN showed the opposite pattern of modulation: directing spatial attention to a stimulus led instead to *decreases* in the firing rate of TRN neurons with receptive fields covering that stimulus. This inhibitory effect of

attention in TRN was somewhat more modest than the increases in LGN but was nevertheless highly significant. This pattern of modulation was not observed prior to stimulus onset, but only began in the initial 100 milliseconds after the stimuli appeared. Intriguingly, the modulation was transient, disappearing in the next 100 millisecond epoch, but LGN cells also showed a second, later period of modulation that could not be identified in TRN cells.

The receptive fields of LGN (and TRN) cells are very small, and so detailed analyses of eye tracking data were able to rule out the possibility that these findings could arise from systematic confounding by large or small eye movements. Further evidence that these effects derived from the top-down effect of spatial attention came from the observation that these response modulations were only seen on trials when the monkeys correctly detected the dimming of the peripheral target, and thus only on trials where spatial attention was correctly directed to the cued stimulus. Taken together, these findings show that attention leads to a spatially specific biphasic modulation of thalamic responses to visual stimuli: an initial attenuation of TRN and enhancement of LGN responses, followed by a slightly later enhancement restricted to LGN neurons.

These findings show that single neurons at very early anatomical stages of the visual pathway are already modulated by spatial attention. Moreover, the comparison of LGN and TRN modulation provides new insights into the functional relationship between different elements of local thalamic circuitry. One intriguing possibility, consistent with Crick's [6] prediction, is that the reciprocal early modulation of visual responses in both TRN and LGN reflects a causal influence of the TRN on the LGN. According to such a proposal, the topographically organised inhibitory collaterals from