

Dispatches

Physiology: Woodpecker skulls are not shock absorbers

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Woodpeckers are well-known for their audible percussive wood drilling. A new study shows that these birds benefit from their small size and key skull features to safely hammer at wood for insect food and nesting excavations.

From a human's perspective, banging one's head against solid objects, such as wood, suggests the potential for a concussive knockout blow and significant risk of brain damage. Indeed, concussive brain injury resulting from vehicular impacts and falls, as well as head impacts during sporting competition, is well recognized^{1–3}. This has led to many safety requirements for operating motor vehicles and cycling, including seat belts, air bags and helmets, as well as improvements to shock-absorbing materials^{4,5}, which mitigate the rapid increase in energy transmitted to a person's head and, most importantly, their brain, following a collision impact. As a widely successful family of birds, woodpeckers rely on repeated hammering on trees with their head and beak powered by trunk and neck muscles to feed on insects and their larvae, excavate food caches and nests, signal conspecifics of their territory, as well as for mating (Figure 1). Past work has reported conflicting interpretations regarding the adaptations and risks that woodpeckers face pursuing this unique habit. Some have argued specific adaptations favoring 'cranial kinesis' (movement between the upper beak and skull)⁶ and shock absorption^{7–9}. Proposed adaptations of woodpecker skulls for shock absorption have been argued as bioinspiration for improved design of shock-absorbing materials^{4,5}. However, an inherent problem with shock absorption is that any reduction of the impact energy between the bird's beak and the wood reduces the beak's penetration and hammering effectiveness. Now, in a study in this issue of *Current Biology*, Van Wassenbergh and colleagues¹⁰ report experimental

measurements based on high-speed video recordings of three woodpecker species, combined with computational mechanical modeling of the woodpecker skull, to assess the role of shock absorption in relation to their drilling performance.

When a woodpecker's chiseled beak collides with the surface of a tree, it must either safely absorb the energy of the collision without damaging its brain or other structures, or the duration and amount of energy imparted to the skull and brain must be within safe limits. Past work examining human (and primate) head trauma related to motor vehicle accidents and falls³ has shown that the duration of impact and the magnitude of acceleration imparted to the skull and brain are the key variables that determine whether traumatic brain injury occurs. Increased duration and increased acceleration combine to increase the risk of brain injury. Earlier work based on high-speed film recordings of an acorn woodpecker (*Melanerpes formicivorus*) pecking into a tree⁷ showed that the duration of impact was extremely short: 0.5 to 1.0 msec, with the beak and head moving at 6–7.5 m/s and decelerating over a range of 635–1525 g (where g is the acceleration due to gravity). Subsequent theoretical analysis by Gibson¹¹ examined the risk for concussive brain injury in the acorn woodpecker and related species based on a scaling analysis of the relative brain size and mass of woodpeckers compared with humans. Gibson's analysis argued that the small size of woodpeckers, as well as the orientation of their brain within the skull, significantly reduces the risk of concussive brain injury for woodpeckers,

allowing them to withstand 11 to 20 times greater head and brain acceleration than much larger humans. As a result, due to their small size woodpeckers appear to have evolved the ability to withstand repeated collisional impacts with a safety margin of 6–7 times below the level that would cause them brain injury. Nevertheless, small size alone may not fully explain the ability of woodpeckers to resist repetitive hammering with their beak and head, as other small birds and animals are susceptible to concussive impacts that can leave them dazed or unconscious for a time¹².

Following up on these earlier studies, Van Wassenbergh and colleagues¹⁰ carried out high-speed imaging of three woodpecker species, combined with high-resolution μ CT scans of the woodpecker skull and computational mechanical modeling, to test for evidence of shock absorption between the beak and skull of woodpeckers. As with earlier studies, movements of the skull based on motion of the eye were assumed to accurately track motions of the brain within. Their modeling approach also allowed them to simulate variation in earlier proposed viscoelastic connections that exist between the beak and skull, as well as the spongy bone of the skull itself that surrounds the braincase, which could contribute to shock absorption. Their high-resolution kinematics showed no evidence that the skull's deceleration differed from that of the beak penetrating the wood. By modeling variation in the spring stiffness between the beak's attachment to the skull, they also showed that increases in energy dissipation due to reduced spring stiffness, which would reduce the impact energy imparted to the





Figure 1. Female pileated woodpecker (*Dryocopus pileatus*) pecking on wood.

As a diverse family of birds, woodpeckers, including the pileated woodpecker shown here, drill into wood to excavate insects and larvae for food, to create nests and food caches, or for mating and territorial signaling. Powered by their trunk and neck muscles, the head and chiseled beak impact the wood, imparting kinetic energy to penetrate the wood. Little to no energy is lost by shock absorption, making their hammering highly efficient. They avoid concussive brain injury due to their small size, extremely brief impact duration, and adaptations of their brain and skull that reduce the risk of trauma.

skull and brain, necessarily resulted in reduced kinetic energy of the beak's impact and wood penetration. In other words, any increase in energy absorption to reduce impact on the brain would reduce the hammering effectiveness of the woodpecker's beak.

Based on their computational model, Van Wassenbergh *et al.* also estimated intracranial pressures likely experienced by the woodpecker's brain in relation to that of a human resulting from head impact. This analysis showed that intracranial pressures that cause concussion-mediated brain trauma to humans and primates relevant to vehicular accidents³ were two to three times lower in woodpeckers, based on the measured decelerations and short durations of their impact during pecking. As the authors note, spongy bone in the front and rear of the braincase likely serves to resist impact forces without

causing skull failure, rather than absorbing impact energy through elastic deformation as previously proposed.

Van Wassenbergh *et al.*'s results¹⁰ confirm the earlier theoretical modeling work carried out by Gibson¹¹, demonstrating that the level of head and brain deceleration that woodpeckers repeatedly experience drilling into wood is well below that which would likely cause them brain injury. However, it should be noted that repeated sub-concussive shocks to the brain may lead to traumatic brain injury, based on post-mortem evidence obtained from contact sport athletes^{1,2}. Nevertheless, no evidence of shock absorption was found. Further, owing to energy conservation alone^{7,10}, none would be expected if natural selection favored effective hammering performance, in which the energy delivered by trunk and neck muscles is converted to impact energy to penetrate wood. In addition to their small size, which significantly increases the level of brain deceleration that woodpeckers can withstand over extremely brief impact durations, other features of their braincase and skull likely contribute to the ability to hammer away at wood without incurring injury. These include tight packing of the brain within the braincase by means of reduced cerebrospinal fluid to minimize brain motion relative to the skull⁷ and an enlarged frontal area of the brain that reduces the stress imposed on brain tissue¹¹. Recent evidence of p-tau proteins observed in the brains of woodpeckers, but absent in red-winged blackbirds (as control)¹³, which are found post-mortem in humans who suffered concussive brain trauma², intriguingly raise the question of whether woodpeckers suffer some brain damage through a lifetime of wood pecking — or do they manage this without a biological cost? Finally, many woodpeckers have long tongues to extract food deep within crevices, which are driven by remarkably long hyoid skeletal-muscular elements that wrap around the posterior and dorsal surfaces of the skull. Although their role in stabilizing the head for drilling has been speculated¹⁴, no evidence exists to support that they contribute to protecting the brain from damage.

An open question not yet addressed is how the neuromuscular system of woodpeckers has been tuned to

coordinate trunk- and neck-powered movements of the head and beak to hammer in a straight-line trajectory, which facilitates stable head movements to reduce the risk of concussive shock of the brain. What muscles are used and how are they coordinated?

In any event, the extremely common belief publicized in a range of ornithological websites, as well as serving as motivation for bioengineers seeking to develop bioinspired improvements to light-weight shock-absorbing materials, appears to be misguided and wrong — in other words, 'pecking up the wrong tree'. At their small size, natural selection has evolved a highly effective stiff energy transmission mechanism for repeated hammering by woodpeckers to find and store food, create nests, and signal conspecifics. Enjoy their busy pecking as you make your way through the woods!

DECLARATION OF INTERESTS

The author declares no competing interests.

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Association learning: Dopamine and the formation of backward associations

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<https://doi.org/10.1016/j.cub.2022.06.007>

The activity of dopamine neurons is critical for the ability to learn and update cue–reward associations. New work in rats shows that dopamine transients are also critical for the formation of backward associations in which the reward precedes the neutral stimulus.

A central research question asks which neural processes facilitate the learning of associations between cues in the surrounding environment and biologically significant outcomes. Cognitively, this process is thought to be driven by ‘prediction error’: the difference between the actual value of the reward and that expected in the presence of the cue(s). Although activity of midbrain dopaminergic neurons has long been considered a close neural correlate of prediction error, the seminal finding that generated this hypothesis¹ and much subsequent work has relied on experimental preparations in which cue presentations precede reward delivery, whereas associations between neutral cues and rewards can form through a multitude of temporal arrangements. For instance, as illustrated in [Figure 1](#), if you were to regularly eat ice cream on your way to the cinema (because you pass your favourite shop on the way), but only buy popcorn once you arrive, you would likely form both *forward* cue–reward associations between the cinema’s cues and popcorn, as well as *backward* reward–cue associations between the cinema and ice cream. The cinema could even become

a specific inhibitory cue for ice cream, as once you arrive you learn that it will be a certain amount of time before you will eat ice cream again. Dopamine’s role in forming cue–reward associations is well established, but its role in forming reward–cue associations has been unclear. As they report in this issue of *Current Biology*, Seitz *et al.*² have now demonstrated such a role by optogenetically inhibiting dopaminergic neurons in the ventral tegmental area (VTA) of rats during a Pavlovian backward conditioning procedure.

To enable the targeted inhibition of dopamine neurons with temporal precision, Seitz *et al.*² injected an inhibitory halorhodopsin (NpHR) virus and implanted optic fibres into the VTA in transgenic rats expressing Cre-recombinase under control of the tyrosine hydroxylase promoter, used to ensure the specific transfection of dopamine neurons. Backward conditioning procedures began with rats receiving intermixed presentations of two palatable rewards — pellets and maltodextrin solution — each followed by unique auditory cues presented 10 seconds later. All animals received a green light delivered to the VTA for 2.5 seconds at the onset of each cue

presentation, effectively inhibiting the activity of VTA dopamine neurons for the NpHR-injected group but not for the group injected with a control virus containing only enhanced yellow fluorescent protein (group eYFP).

Following backwards conditioning, rats were next trained to respond on one lever for the pellet reward and on a second lever for the maltodextrin reward in the absence of optogenetic inhibition. This procedure allowed Seitz *et al.*² to probe the content of the learned associations. To do this, they gave rats a Pavlovian-to-instrumental transfer (PIT) test in which both levers were extended but no food rewards delivered. In control rats, the presentation of each cue drove responding on the lever that had been associated with the alternative outcome. Specifically, the backward cue that had followed pellet presentations increased responding on the maltodextrin lever, and the maltodextrin backward cue increased responding on the pellet lever, suggesting that each cue had become inhibitory of the outcome it preceded. Optogenetic inhibition of VTA dopamine transients during backwards conditioning abolished these effects, indicating that the ability of

