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RESEARCH ARTICLE

Neuromuscular coordination of movement and breathing forges a hammer-like mechanism for woodpecker drilling

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ABSTRACT

Drilling and tapping behaviors in woodpeckers have long garnered significant attention, given their extreme, high-impact nature. However, how these birds integrate neuromuscular and respiratory systems to produce such high-force, high-frequency behaviors remains poorly understood. Here, we combined electromyography with measures of respiratory air-sac pressure and syringeal airflow to investigate the neuromuscular and ventilatory mechanisms of forceful pecking in downy woodpeckers. We found that both types of pecking behaviors tested engage skeletal muscles across the head, neck, hips, tail and abdomen. In-depth analysis of EMG timing and activity point to a hammer-like model associated with drilling, whereby head and neck muscles contract to create a stiffened cephalo-cervical lever arm that efficiently transfers kinetic energy from the swinging bill into the wood. Moreover, hip flexors help power protraction of the head and body for drilling, whereas tail muscles presumably help brace the bird's body against the tree. Respiratory analyses show that woodpeckers actively exhale with each bill strike of the substrate, resembling the 'grunting' behavior that human athletes use to stabilize their core and enhance force output. These effects persist at high tapping frequencies, indicating that individuals take mini-breaths between successive taps. Altogether, our results highlight the way motor and respiratory systems are leveraged to facilitate the production of extreme behavior, which hinges on biomechanical specializations and extraordinary performance abilities.

KEY WORDS: *Dryobates pubescens*, Pecking behavior, Electromyography, EMG, Motor performance, Mini-breaths

INTRODUCTION

Many animals perform routine tasks using behavior that requires specialized and/or extreme motor performance. Examples include basilisk lizards that can run across standing water to escape predators (Glasheen and McMahon, 1996), amphibians that catapult their tongues to capture prey items (Deban et al., 1997), and fish that rapidly vibrate their swim bladder to create loud 'boat whistles' for underwater communication (Remage-Healey and Bass, 2005). These behaviors are not only striking in terms of their biomechanics, but they also offer powerful insights into how motor systems can evolve to meet remarkable functional demands (Carrier et al., 1998; Dial and Biewener, 1993; Jayne and Lauder, 1995; Roberts and Marsh, 2003). Studying such behavioral extremes may reveal key organizational principles that underlie processes of motor control.

A compelling case study of extreme motor performance is offered by the woodpeckers (Picidae). These birds use their bills to forcefully 'peck' woody substrates to excavate nests, forage, and communicate through specialized behaviors such as drilling, tapping and drumming (Schuppe et al., 2021). Here, we focused on two specialized pecking variants in woodpeckers, drilling and tapping, as they are the focus of most prior biomechanical work (Gibson, 2006; Liu et al., 2015, 2017; May et al., 1979; Vincent et al., 2007; Wang et al., 2011; Wassenbergh et al., 2022). We define drilling as individual, forceful pecks employed for foraging or excavation, whereas we define tapping as repetitive strike sequences at frequencies around 10 Hz. Notably, tapping is slower than the classic 'drumroll' (16 Hz in downy woodpeckers) that individuals perform to compete with rivals for breeding territories (Schuppe et al., 2021). Work that has examined the mechanical basis of drilling and tapping suggests that woodpeckers weighing less than 100 g perform these behaviors with remarkable force as high as 19.6 N, corresponding to 20–30× body weight (Liu et al., 2017). Because of the mechanical force woodpeckers experience in generating these behaviors, most prior work has examined the morphological and physiological specializations of the skull, bill, neck and pectoral girdle that enable woodpeckers to withstand repetitive head impacts and safely execute drilling (Farah et al., 2018; Jenni, 1981; Lee et al., 2014; Liu et al., 2017; May et al., 1979; Tobiansky et al., 2021; Wang et al., 2011; Wassenbergh et al., 2022).

To date, little is known about the neuromuscular control of drilling and tapping in woodpeckers. Such control is undoubtedly critical, because drilling and tapping require exquisite timing, force modulation and coordination across multiple body regions to both generate and withstand extreme impact forces. Many who have considered this topic did so by focusing on the longus colli ventralis (LCv), a neck muscle that powers head protraction in birds and other taxa (Snively and Russell, 2007). In woodpeckers, the LCv appears highly specialized. For example, its posterior belly is hypertrophied and extends up the ventral vertebral column via long tendons that insert close to the base of the skull. This design likely improves the muscle's mechanical advantage by effectively lengthening the lever arm that drives forward head movements (Jenni, 1981). Likewise, the woodpecker LCv expresses high levels of transcripts for proteins that mediate myocytic calcium flux, which likely increases the tissue's contraction–relaxation cycling frequencies (Schuppe et al., 2018). Yet, muscles beyond the LCv are also likely involved in the actuation of drilling and tapping; for instance, prior work suggests

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that hip musculature may contribute to power generation during drilling, whereas tail muscles may provide bracing that stabilizes the body during forceful strikes (Schuppe et al., 2021; Vincent et al., 2007).

The respiratory mechanics that support drilling and tapping are also poorly understood, leaving an incomplete picture of how woodpeckers integrate breathing with these extreme behaviors. This is significant because prior work implies that coupling of breathing and motor activity can improve efficiency or manage mechanical constraints in rhythmic activities such as running, flying and singing (Deban and Carrier, 2002; Funk et al., 1997; Suthers et al., 1999). This coupling even extends to high-frequency repetitive behaviors, where respiration is synchronized one-to-one such as during singing or galloping (Bramble and Carrier, 1983; Goller, 2022). A particularly intriguing question is whether woodpeckers exhale 'through' the moment of impact or momentarily arrest exhalation. This question is nicely addressed in the human performance literature, where work suggests that individuals intentionally exhale through impact-driven and propulsive behaviors to increase performance (Callison et al., 2014; Ishida et al., 2016). This strategy forcefully spikes intra-abdominal pressure, boosting stability and measurably enhances propulsive velocity. Given that woodpecker drilling and tapping can impose some of the highest instantaneous decelerations recorded in vertebrate musculoskeletal systems (e.g. >400 g) (Wassenbergh et al., 2022), it is possible that woodpeckers coordinate their breathing to support the extreme nature of drilling and tapping. Doing so would likely aid these birds in stiffening their axial column at the moment of contact for efficient kinetic energy transfer between the bill and the tree, similar to the efficient kinetic energy transfer via axial stiffening during running in mammals (Deban and Carrier, 2002).

To address the knowledge gaps outlined above, we investigated the neuromuscular and respiratory basis of drilling and tapping in downy woodpeckers (*Dryobates pubescens*). We combined electromyography (EMG), air-sac pressure recordings and measures of syringeal airflow to identify the system-wide coordination of muscular and respiratory mechanics that are associated with forms of forceful and rapid pecking behaviors such as drilling and tapping. EMG is an especially powerful tool for elucidating how motor systems coordinate muscle activation to optimize behavioral performance (Daley and Biewener, 2003; Roberts and Marsh, 2003; Wainwright and Bennett, 1992). EMG studies can be easily integrated with pressure and airflow recordings to reveal how respiratory processes coordinate with behavioral activity (Cooper and Goller, 2004). Thus, our study was designed to test the hypotheses that: (i) muscles across the head, neck, abdomen, hips and tail are coordinated to actuate drilling; (ii) these muscles are repeatedly and rhythmically recruited in synchrony to drive rapid tapping; and (iii) breathing is exquisitely timed with these behaviors, coupling expiration to the moment of impact to enhance stability and performance. Altogether, by uncovering the neuromuscular and respiratory bases of these behaviors, our study provides insight into how woodpeckers manage the substantial mechanical demands of drilling and tapping through the exquisite, whole-body coordination of neuromuscular and respiratory systems.

MATERIALS AND METHODS

Animals

We conducted this experiment at Brown University in Rhode Island, USA, with locally captured downy woodpeckers *Dryobates pubescens* (Linnaeus 1766) (*n*=8). Downy woodpeckers were the most locally abundant and accessible woodpecker species in our study region. We caught these birds via passive mist netting and quickly transported them to our nearby laboratory, where they were provided suet, seed, mealworms, puppy chow and water *ad libitum*. We gave all individuals at least 2 weeks to habituate to laboratory conditions before taking part in the experiment. All work outlined herein was completed with the approval and permission of the United States Fish and Wildlife Service, and the Rhode Island Department of Environmental Management and Brown University Institutional Animal Care and Use Committee (no. 23-01-1001).

Handling and surgery

We followed previously published surgical protocols to implant EMG electrodes, pressure cannula and/or flow probes (Cooper and Goller, 2004; Franz and Goller, 2002; Fuxjager et al., 2017; Goller and Daley, 2001; Mackelprang and Goller, 2013; Plummer and Goller, 2008; Young et al., 2017). In all cases, we first anesthetized birds using isoflurane (2–4% in O_2). For EMG electrodes, we made a small (<1 cm) incision in the skin above the muscle of interest, in which we inserted a pair of wires that had the insulation stripped from the tips (≈0.5–1 mm). Two small holes were made in the outermost fascia with the tips of sharp forceps, and the electrodes were inserted 1–2 mm apart. Once implanted, we fastened the tips of the electrode wires in place using a small dab of Vetbond™ tissue adhesive. We then coiled a small amount of wire around the implantation site to provide enough slack that prevented electrodes from dislodging when birds moved. We carefully routed the two wires subcutaneously to the small backpack. Accordingly, we collected EMG activity data from a range of neck and head muscles [longus colli ventralis (LCv), longus colli dorsalis (LCd), flexor colli lateralis (FCl) and musculus complexus (MC)], abdominal muscles [musculus obliquis externus abdominus (MOEa)], leg muscles [iliotibialis cranialis (IC) and iliofibularis (IF)] and a tail muscle [M. depressor caudae (MDc)] (see Figs 1 and 2A below). Electrodes were made of either stainless-steel wire (California Fine Wire, SS 304; 25 µm) for small muscles (MC, MOEa and MDc) or silver wire (A-M Systems, Ag, 76.2 µm) for larger muscles (LCv, LCd, FCI, IC and IF). In total, we recorded EMG activity from three to four individuals per muscle, across a total of eight birds.

We also recorded changes in air pressure in the anterior thoracic air sac to assess respiratory dynamics when birds performed their behavior (*n*=6 birds). To do so, we fitted a flexible silicone cannula (Dow Corning, 1.65 mm o.d., 6 cm length) ≈5 mm into the distal end of the anterior thoracic air sac directly below the last rib. We then stabilized the cannula by suturing it to the rib cage, and sealed the incision site with Vetbond™ tissue adhesive. We connected the cannula to a piezoresistive pressure transducer (Fujikura FPM-02PG; Fujikura, Tokyo, Japan) positioned on the bird's backpack (see below). For two individuals, we also conducted tracheal airflow recordings to determine whether the syringeal valves were open or closed when birds drilled and tapped. We therefore mounted a microbead thermistor (Thermometrics, type BB05JA202, 0.125 mm diameter) in small stainless-steel tubing (3–4 mm long) directly above the syrinx (Suthers and Hector, 1982). To do this, we made a tiny incision in the connective tissue between two tracheal rings through which the probe was inserted and then closed with tissue adhesive. These thermistors are heated to a constant temperature by a feedback circuit (Hector Engineering, Ellettsville, IN, USA), and they measure flow by quantifying the proportional levels of current needed to maintain the thermistor's temperature as air is blown across it. Direction of airflow (inspiratory versus expiratory) is determined in conjunction with the valence of air-sac pressure. Once EMG electrodes, pressure cannula and airflow probes were in place, we sealed the incision site using a combination of surgical sutures and

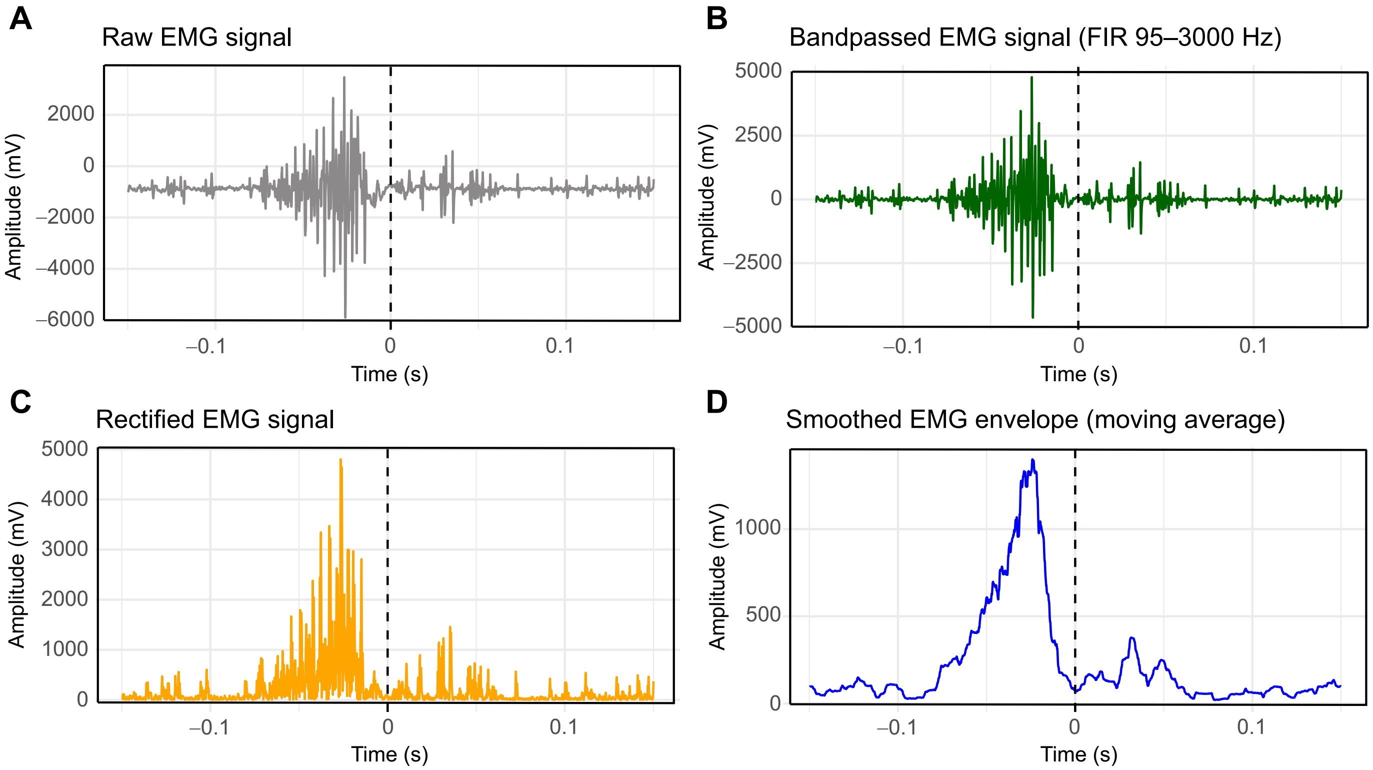

Fig. 1. Processing pipeline for electromyography (EMG) signals. Example of processing from (A) raw EMG signals using longus colli ventralis during a hard peck to (B) the bandpassed signal, (C) the rectified signal and finally (D) its smoothed EMG envelope. The example here is the same signal across all four steps of processing.

tissue adhesive. Individuals then received meloxicam as an analgesic immediately and up to two times per day for 3 days post-surgery as needed based on observations of normal feeding and other behaviors.

At the end of the surgical session, we connected our measurement devices to the small backpack that was custom-fitted to each bird (Cooper and Goller, 2004; Franz and Goller, 2002; Fuxjager et al., 2017; Goller and Daley, 2001; Mackelprang and Goller, 2013; Plummer and Goller, 2008; Young et al., 2017). The backpack itself consisted of flexible elastic straps that wrapped around the wings, which were attached to an elastic base that gently sat atop the thorax. The base had a small Velcro tab, on which we placed a series of micro-connectors that attached recording wires and cannula. Once these connections were made, we removed birds from anesthesia and allowed them to recover under supervision.

Data collection

Soon after recovery, we transferred each bird to an observation chamber that was designed for unobstructed video recording of drilling and tapping behavior. Accordingly, one wall of the chamber was made of clear plexiglass, and one end of the chamber held a large vertically positioned piece of hardwood on which birds could cling, drill and tap. Once in the chamber, each pair of electrodes on the birds was connected to an amplifier by a small 4-conductor shielded wire (Alpha Wire Company, 1102 Multicolor, Elizabeth, NJ, USA) that could attach to the backpack. We then routed this wire out of the chamber along counter-balanced lever arm, which helped ensure that slack from the wire never accumulated to entangle the bird.

We amplified EMG signals with a Brownlee 410 amplifier (Brownlee Precision, San Jose, CA, USA), using a multichannel A-D converter (NI USB-6212; National Instruments) to run signals into a nearby laptop. We then recorded data using Avisoft-Recorder (Avisoft Bioacoustics, Berlin, Germany), with an 8 kHz sample rate. In most cases, we recorded four separate channels simultaneously: air-sac pressure, two EMGs and the light pulse for file synchronization (see below). We collected recordings of voluntary behaviors during daylight hours between 07:00 and 8:00 h for recording sessions up to 30 min. Multiple recording sessions were conducted for each bird to collect recordings of all relevant behaviors. Note that for two individuals, we recorded air-sac pressure, syringeal airflow and the light pulse at a 44.1 kHz sampling rate. Once all data had been collected, EMG implants were removed under anesthetic isoflurane, the birds were banded and provided meloxicam once more, monitored for 48–72 h and then were released back to their site of capture.

Importantly, we synchronized all physiological measures to high-speed videography (250 frames s^{-1}; JVC SDXC) collected as birds were drilling and tapping. As such, we paired the closure of an electrical circuit with an LED illumination trigger to a separate channel associated with EMG, pressure and/or flow recordings. Then, we used Adobe Premiere Pro (video; Adobe Inc., San Jose, CA, USA) and Praat (EMG; praat.org) to match pulses of blinking light in our behavioral videos to their corresponding squares waves in the recording files. Given the 250 Hz frame rate of the videos, our alignment precision was 4 ms.

Analytical approach

For our analyses, we extracted instances of head turning, drilling and repetitive tapping from our synchronized video and recording files. We defined head turning as instances in which birds rotated their entire head left or right, without any visible sign of protraction or retraction. We defined drilling as a pecking event, in which birds protracted their head until their bill made contact with the substrate.

From these events, we then classified two types of pecks: soft and hard. We called soft pecks instances in which the bird protracted its head from a set position, whereas we called hard pecks instances in which birds visibly cocked their head backward immediately prior to protracting their bill forward. We defined repetitive tapping as instances in which birds pecked the substrate repeatedly, typically at a frequency of ≈8–10 strikes s^{-1}. Such tap trains ranged from two to nine successive pecks. For all these drilling and tapping events, we measured times of protraction initiation, contact with substrate and retraction termination (n=780 events across eight birds and eight muscles).

Processing of EMG signals

In our analysis, it was important that signals from different trials shared common reference points so that sampling intervals were identical across behavioral events. We therefore clipped each of these events to a common time window of 300 ms, which was centered around the timing of contact with the substrate (i.e. when the bird's bill struck the wood). We then resampled data in the recordings to a fixed time vector, as this alignment ensured that signals from different trials shared common reference points and had identical sampling points for comparisons (Fig. 1A). The few missing or sparse data segments were interpolated so that each trial yielded complete and comparable data across the entire time window.

Next, we corrected files for different gain settings, and we bandpass filtered files using a finite impulse response with a Hamming window of 95–3000 Hz (Fig. 1B). We rectified the data (Fig. 1C) and transformed it with a Hilbert transformation to obtain a signal envelope (Fig. 1D). To smooth rapid fluctuations and create a cleaner representation of overall muscle activation, we applied a moving average (5 ms) to each envelope. Such smoothing helped emphasize broader activation trends, while reducing small, transient spikes. For visualization purposes, we normalized all signals within a given muscle×behavior pair between 0 and 1, averaging their amplitudes at each time point. To determine whether each implanted muscle was active during the behaviors of interest, we visually inspected all EMG envelopes, which allowed us to compare the timing of activation for muscles involved in head and body protraction before the strike, stabilization during the strike and retraction after the strike.

To compare patterns of muscle activation across behavioral traits, we calculated root-mean-square (RMS) values of our signal envelopes. RMSs reflect the overall intensity of muscle activity and thus are correlated with the amount of muscle recruitment (Fuxjager et al., 2017). Accordingly, to make the RMS calculation, we squared, averaged and then square root transformed each envelope in the sample time window. Finally, trials or behaviors of interest were filtered to remove outliers (e.g. beyond 1.5× the interquartile range) and normalized across trials to facilitate comparisons across individuals. Because replication varied by individuals, random intercept models with individual bird ID were used for each combination of muscle×behavior. We determined marginal means and standard errors and performed Tukey *post hoc* tests to compare behaviors within each muscle and determine significant differences in activation. Note that we did not compare between muscles, given the potential variation in EMG electrode placement and impedance.

Processing of respiratory pressure and syringeal airflow signals

Respiratory pressure signals were detrended using a robust loess regression to correct for any deviation from a resting baseline, which may be caused by extreme pressure events (such as defecation). We then subtracted the estimated baseline from the original signal so that fluctuations around zero reflect the 'true respiratory cycle', where positive values represent expiratory pressure and negative values represent inspiratory pressures. Syringeal airflow signals were detrended so that the lowest value in each exemplar was set to zero, because the data from the thermistor bead do not indicate the direction of the airflow. Because syringeal airflow was always paired with respiratory pressure, the direction of airflow can be determined from the valence of air-sac pressure. For example, when air-sac pressure crosses zero and becomes sub-atmospheric, air flows inward. This direction then reverses when flow reaches zero and the corresponding air-sac pressure increases at the start of expiration.

To determine respiratory rates during various behavioral events and while at rest, we applied a peak detection analysis to our detrended pressure signals. Specifically, raw pressure data were first smoothed using a 2-ms moving average to reduce high-frequency noise. Peaks were then identified by setting a detection threshold at the 85th percentile of the smoothed signal, enforcing a minimum 55 ms interval between successive peaks, and excluding detections near the signal boundaries. Respiration frequency was automatically calculated as the number of accepted peaks in the detection minus 1 and then divided by the time interval between the first and last peak. Troughs were similarly detected, instead using a 15th percentile threshold. To ensure the reliability of these measurements, we visually confirmed respiratory rates by overlaying original and smoothed signals with marked peaks and troughs. These validated estimates of respiratory frequency were subsequently used in two linear mixed-effects models, with bird ID as a random intercept to (i) compare quiet respiration with respiration during repetitive tapping, and (ii) test the association between respiratory and strike rates. For the former comparison, we calculated estimated marginal means and a corresponding pairwise t-test. To determine the association between respiratory rates and strike rates, we calculated the Pearson correlation coefficient from our mixed-effects model.

Circular analysis of EMG and kinematics in repetitive tapping

We evaluated kinematics of repetitive tapping by determining contact-to-contact phases from EMG recordings. We assigned peak events to their appropriate contact interval based on temporal order. The fractional position of each peak within its interval was then converted to a phase angle (0–360 deg). To account for differing numbers of replicates per individual, and because there is no widely used frequentist mixed-effects model for circular distributions, we employed a cluster bootstrap procedure using bird ID as the clustering variable. In each bootstrap iteration, birds were sampled with replacement, and all corresponding replicate measurements were retained to ensure that the estimated 95% confidence intervals for the circular means accurately reflect the between-individual variability. This approach minimizes the influence of individuals with a larger number of replicates on the overall uncertainty estimates. Only the first five cycles were retained for kinematic timing analyses, as the sample size dropped dramatically for strike cycles beyond this point. From here, we used a Watson–Wheeler circular omnibus test to determine whether strikes performed in sequence varied in the phase in which they were performed (Batschelet, 1981). We applied this statistical test because it assesses whether independent samples of directional data (strikes in a sequence for our purposes) share the same underlying distribution and detects deviations in mean direction. Using a similar peak detection analysis and linear mixed-modeling approach to the one described for respiration, we analyzed linear changes in peak EMG amplitude across strikes for each muscle.

RESULTS

EMG activation and intensity

To assess how muscle action is coordinated across the body to support woodpecker drilling, we aligned muscle EMGs to the precise time at which the birds' bills contacted the wood substrate (Fig. 2A,B). Most muscles showed a singular burst of activity either prior to this moment of impact (e.g. the LCv, MOEa, MDc and IC) or concurrent with it (e.g. the LCd, MC, FCl and IF). Interestingly, some muscles also showed secondary bursts of activity. The IF (hip extensor) and MDc (tail protractor), for example, showed small peaks in activity prior to the muscles' major burst in activity, both of which occurred before or during the protraction period. These muscles may potentially contribute to repositioning the bird's body in preparation for drilling behavior given they precede protraction (IF) or occur at protraction initiation (MDc). Meanwhile, the MOEa (abdominal muscles) showed relatively equal-sized bursts of activity during protraction and at the point of contact. Finally, the LCv (head protractor) showed a secondary burst of activation after the moment of impact, while the bird was retracting its head. This activation may reflect subtle adjustments of head position or part of cranial kinesis to help loosen the bill from the wood after impact (Lyons et al., 2023).

Following our initial appraisal of how muscle activity aligned with drilling, we validated that neural activation of these muscles was in fact attributable to this behavior, rather than reflecting artifacts of transient movement. Accordingly, we compared root mean square (RMS) values derived from the muscles' EMG envelopes during drilling events with both head rotation events (positive control) and baseline values (negative control). We found significant differential activation among behaviors for all muscles (ANOVA, $P<0.001$; Fig. 2C, Table 1), whereas *post hoc* analyses revealed two distinct patterns of differential activation. First, axial muscles of the head and neck (LCv, LCd, FCl and MC) showed increased activity during head rotation events, relative to baseline. However, activity was still significantly lower than the activity observed during drilling ($P\leq0.008$; Fig. 2C, Table 1). Second, trunk and appendicular muscles (MOEa, MDc, IC and IF) showed increased activity only during drilling ($P\leq0.001$), with no evidence of an activity increase during head rotation ($P\geq0.35$; Table 1). Note that we did not compare RMS values between muscles, given that differences in EMG electrode placement and impedance can confound effects that may emerge.

Next, we evaluated which muscles might fine-tune power production associated with drilling. Therefore, we compared RMS values associated with soft and hard pecks, focusing specifically on muscles that showed distinct activation peaks during the head protraction phase of the behavior (LCv, MOEa, MDc and IC). All four muscles showed differential activation in our comparisons (LCv: $F_{2,65}=150.8$, $P<0.001$; MOEa: $F_{2,21.1}=7.7$, $P<0.001$; MDc: $F_{2,22}=17.2$, $P<0.001$; IC: $F_{2,36.1}=33.2$, $P<0.001$; Fig. 2D). However, only the IC (hip protractor) showed differential

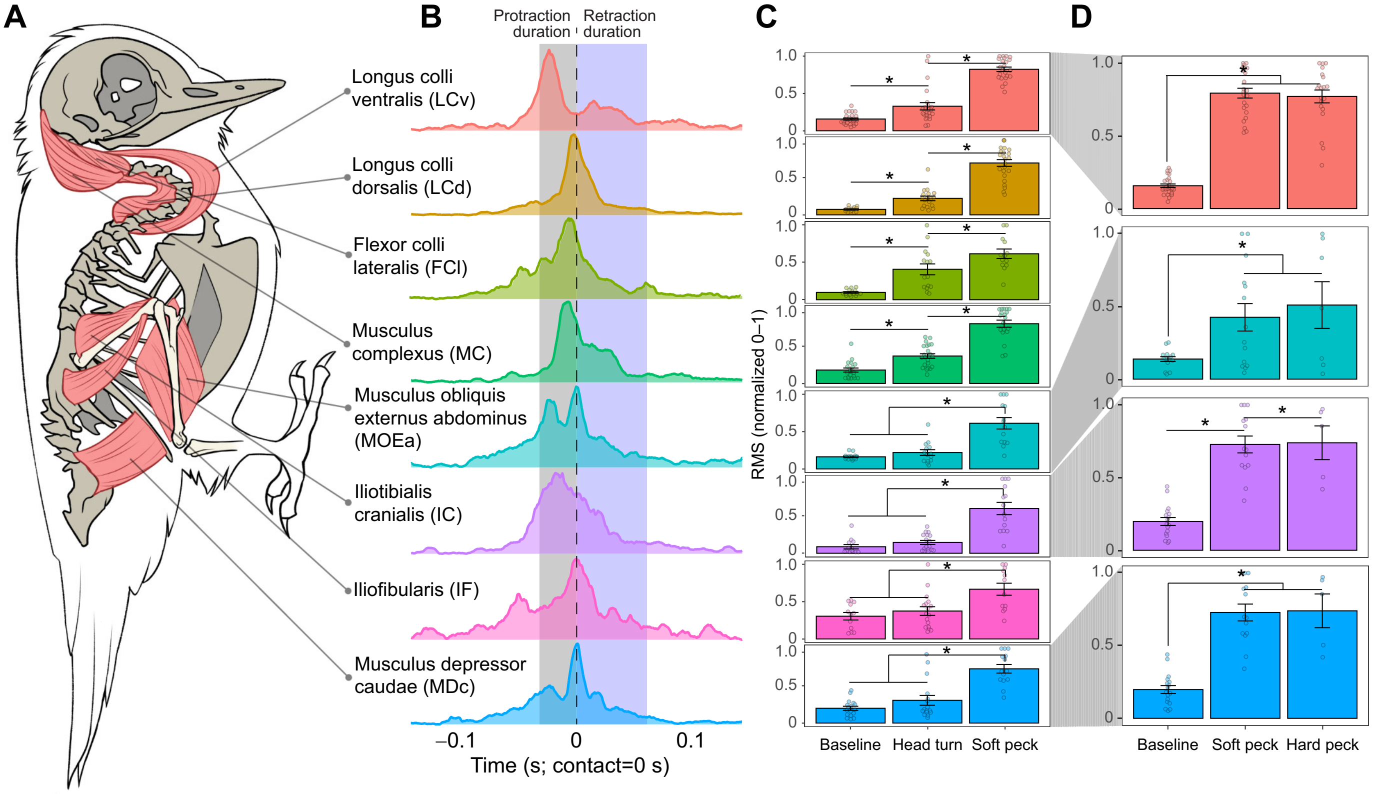

Fig. 2. Patterns of muscle activation during soft peck drilling behavior. (A) Skeletal muscles targeted in our study and (B) associated electromyography (EMG) envelopes collected during soft pecks (averaged across birds). Gray shading reflects average head protraction time (s), whereas blue shading reflects average retraction time (s); both are relativized to time of impact denoted by dashed black line. (C) Variation in EMG intensity (root mean square, RMS) from each muscle when birds do nothing (baseline), turn their head or softly drill (see Materials and Methods). (D) Variation in EMG intensity when bird perform soft versus hard pecks. C and D show estimated marginal means±1 s.e.m. Asterisks denote significant differences between groups (*$P<0.05$). Individual data points (replicates) are shown with opaque circles for $n=4$ birds for LCv and MC and $n=3$ birds for the LCd, FCl, MOEa, IC, IF and MDc.

Table 1. Tukey pairwise *post hoc* comparisons of differential EMG activation (determined by root mean square value) comparing different behaviors within each muscle

			Post hoc P-value		
Muscle	Overall effect *F*-value	Overall *P*-value	Head turn versus baseline	Soft peck versus baseline	Soft peck versus head turn
LCv	106.3 (2, 70)	<0.001	↑ (0.001)	↑ (<0.001)	Peck>Head (<0.001)
LCd	97.4 (2, 51.1)	<0.001	↑ (0.008)	↑ (<0.001)	Peck>Head (<0.001)
FCl	21.7 (2, 40)	<0.001	↑ (<0.001)	↑ (<0.001)	Peck>Head (0.04)
MC	78.7 (2, 56.3)	<0.001	↑ (<0.001)	↑ (<0.001)	Peck>Head (<0.001)
MOEa	28.9 (2, 39.2)	<0.001	n.s. (0.43)	↑ (<0.001)	Peck>Head (<0.001)
MDc	27.8 (2, 44)	<0.001	n.s. (0.35)	↑ (<0.001)	Peck>Head (<0.001)
IC	29.4 (2, 41)	<0.001	n.s. (0.71)	↑ (<0.001)	Peck>Head (<0.001)
IF	11.5 (2, 36.1)	<0.001	n.s. (0.54)	↑ (<0.001)	Peck>Head (0.001)

Upward arrows denote increased activity from baseline and n.s. denotes *post hoc* comparisons where no significant difference was found between behaviors. LCv, longus colli ventralis; LCd, longus colli dorsalis; FCl, flexor colli lateralis; MC, musculus complexus; MOEa, musculus obliquis externus abdominus; MDc, M. depressor caudae; IC, iliotibialis cranialis; IF, iliofibularis.

activation between soft and hard pecks ($P<0.001$). In this case, activation was significantly greater for hard pecks compared with soft pecks, whereas activation in both these instances was greater than baseline ($P<0.001$). For the other three muscles (LCv, MOEa and MDc), activation was indistinguishable between soft and hard pecks ($P\geq0.176$), but greater than baseline ($P\leq0.05$).

Respiratory dynamics and tracheal airflow

To assess how respiration was coordinated with drilling, we synchronized EMG recordings from abdominal muscles (MOEa) and recordings of air-sac pressure with behavior at the moment of impact (n=3 individuals). We also synchronized respiratory pressure with measures of syringeal airflow in two other individuals to determine whether birds might breathe out or hold their breath through impact as they drill and tap (Fig. 3). To ensure the exemplars in Fig. 3 were representative of the broader dataset, we averaged time-matched coordination of abdominal EMG, respiration and airflow across events and individuals from pecking behaviors (Fig. S1). Overall, we found that expiratory pressures were tightly coordinated with abdominal EMG activation across drilling types, as well as during quiet respiration and defecation (Fig. 3A–D). Interestingly, during drilling events, we found that expiratory air-sac pressure is increased compared with quiet respiration, but the syringeal valves did not close (as indicated by the presence of airflow during soft and hard pecks; Fig. 3A,B). With respect to drilling itself, our results showed that soft and hard pecks exhibited a notably consistent pattern in air-sac pressure. That is, prior to the bill's impact with wood, expiratory pressure is increased in coordination with the burst of EMG activity in the MOEa. Upon impact, we consistently saw a small, short decrease in air-sac pressure, which was accompanied by a proportional dip in tracheal airflow (Fig. 3A,B). Notably, after this dip, expiration increased again, suggesting that the birds 'grunt' during the drilling strikes. Importantly, we included defecation as a control behavior because it involves elevated expiratory pressure. In songbirds, the elevated pressure during defecation is generated by increased activation of expiratory muscles and closure of the syringeal valves, such that there is no expiratory airflow (Cooper and Goller, 2004; Young et al., 2017). Our results suggest that defecation follows the same principle in woodpeckers (Fig. 3A,B).

Muscle activation during repetitive tapping

We next evaluated how EMG activation of each muscle was coordinated across the course of repetitive striking behavior. For all muscles in our study, we found no difference across taps in the relative time between peak activation and moment of bill impact ($P>0.123$ for all muscles; Fig. 4). In other words, it appears that the timing by which each muscle is activated consistently aligns with behavioral output regardless of the number of strikes produced in a tap train. By contrast, we found that EMG amplitude significantly increases across strike cycles within a tap train, at least for most muscles ($P<0.05$ for LCd, MC, MOEa, MDc, IC and IF; Fig. 5A,B). We did not observe this positive effect in the LCv and FCl ($P>0.79$ for both muscles; Fig. 5A,B). These results indicate that most muscles are activated more strongly to support subsequent pecks in longer sequences of rapid pecking. Sensitivity analyses confirmed these results by showing that the observed effects appear genuine rather than being biased by the unequal sampling of different woodpeckers performing tapping bouts of different lengths leading to uneven sampling across muscles and birds (Table 2).

Respiratory dynamics of repetitive tapping

Finally, given our results showing exquisite coordination between drilling and respiration, we assessed the nature of this coordination in the context of tapping. This is a compelling question, considering that songbirds interlace rapid respiratory pulses (i.e. mini-breaths) throughout their vocal displays, or songs. In a similar vein, we found that woodpeckers continue to exhale during each tap event within a tap train (Fig. 6A). Therefore, respiration rates significantly increased when birds were tapping to roughly 9 breaths s^{-1}, which is more than triple the average quiet respiration rate of roughly 2.8 breaths s^{-1} ($t_{1,114.9}=20.8$, $P<0.001$; Fig. 6A,B). To this end, our results showed that neither respiration rate ($F_{5,70.7}=0.51$, $P=0.77$; Fig. S2A) nor tap rate ($F_{5,70.2}=0.35$, $P=0.88$; Fig. S2B) differed based on the number of taps in a sequence. Thus, we found that respiration rate was positively correlated in a 1:1 ratio with the tap rate ($r=0.94$, $P<0.001$; Fig. 6C).

We did not find any evidence that the amplitude of expiratory pressure changed across taps in a series ($F_{5,189.79}=1.855$, $P=0.10$; Fig. S3), and neither did inspiratory amplitude ($F_{4,133.18}=1.551$, $P=0.19$; Fig. S3). However, although the duration of expiratory pulses (EP) remained consistent across taps in the series ($F_{5,179.09}=1.173$, $P=0.32$; Fig. S4A), the duration of inspiratory pulses (IP) did vary on average ($F_{5,195.35}=10.141$, $P<0.001$; Fig. S4A). Specifically, the IP preceding the first strike was significantly longer than the second and third IPs (Tukey $P<0.01$ for each), and the second IP was also significantly shorter than the fourth IP (Tukey $P=0.008$). When comparing all IPs with EPs, we found no significant difference in duration ($F_{5,383.92}=0.0008$, $P=0.977$; Fig. S4B), but when excluding the large IP that preceded the first strike, IPs were significantly shorter than EPs ($F_{5,330.35}=5.2627$, $P=0.022$; Fig. S4C).

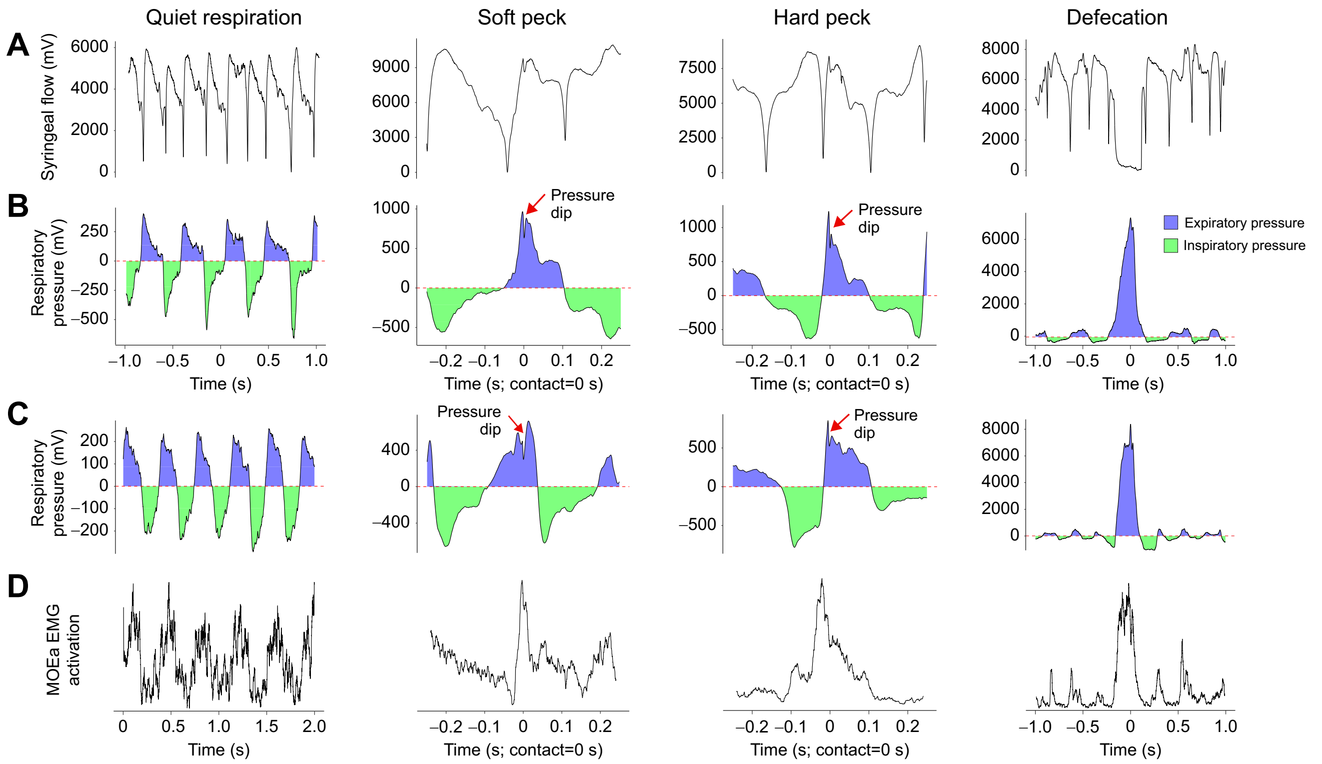

Fig. 3. Integration of respiratory and muscular activity during drilling and control behaviors. Synchronized measures of (A) syringeal airflow, (B,C) air-sac pressure and (D) EMG from musculus obliquis externus abdominus (MOEa). Plots are representative examples. Airflow and pressure data in A and B come from the same individual, as do pressure and EMG data in C and D. Time is synced by contact time at 0 s. In B and C, positive amplitude denotes expiratory pulses (blue), and negative amplitudes denote inspiratory pulses (green). Dips in respiratory pressure are noted in B and C with red arrows.

DISCUSSION

Our results reveal the physiological mechanisms driving drilling and tapping behaviors in downy woodpeckers. First, from a neuromuscular perspective, we show that both behaviors recruit muscles across the woodpecker body plan, to which muscles of the head, neck, hips, abdomen and tail contribute. Some of these muscles appear to drive rapid forward movement of the head and neck, which characterize drilling (e.g. the LCv, IC and IF). At the same time, other muscles appear to play supportive roles either by retracting and positioning the head (e.g. the FCl, MC and LCd), or by stabilizing the neck and body (e.g. the MOEa and MDc). Importantly, we demonstrate that drilling and tapping emerge from the integrated action of seemingly diffuse muscle groups across the body and coordination with respiration, highlighting complex motor control across multiple physiological systems to produce these extreme behaviors.

From a respiratory perspective, we show that drilling and tapping are tightly integrated with a bird's breathing patterns. Indeed, individuals exhale as they drill by contracting their abdominal muscles to increase air-sac pressure, while releasing stale air through the trachea. We found no exceptions to this phenomenon, nor evidence of variation in the way expiration is coordinated with drilling. Moreover, our results even show that woodpeckers synchronize small exhalations to each strike (1:1) at rapid frequencies (≈9 Hz) while tapping, and these expiratory pulses are followed by short inspirations. This behavior closely mirrors the way songbirds take mini-breaths during bouts of singing (Goller, 2022). Overall, these results provide further support for the notion that drilling and tapping in woodpeckers – as extreme forms of pecking behavior – engage the entire body in tight muscular and respiratory coordination.

Neuromuscular mechanisms of drilling and tapping – a woodpecker hammer

Why does the nervous system exquisitely coordinate muscle systems across the body to support drilling and tapping? The answer likely relates to fundamental mechanical and biophysical properties that help birds produce these two behaviors. Namely, we hypothesize that whole-body muscle coordination creates the biomechanical equivalent of a hammer, whose movements need to be integrated in concurrent behaviors, such as maintaining position and contact with the substrate and aiming at the target. Human hammering involves a kinetic chain of events, where the movement of the shoulder and elbow provide gross power, and the wrist acts as a distal joint to modulate speed, accuracy and stiffness at the point of impact. Crucially, hammer handles function as rigid lever arms to amplify kinetic energy, which requires muscular stiffening, especially at the wrist, to prevent energy loss upon impact (Cote et al., 2008). In woodpeckers, the head and bill may function similarly as a hammer head, whereas the neck likely serves as the rigid lever arm that swings around joints in the lower axial skeleton and hips. Based on observed EMG activation patterns, muscles driving protraction during drilling (e.g. the LCv and IC) likely supply the effort necessary for generating kinetic energy in the bird's head, whereas muscles such as the FCl and MC presumably stiffen the neck and head along their vertical axis. In theory, this latter effect should enhance the ability of the neck to function as an effective lever arm by allowing efficient energy transfer from the bill to the substrate and reducing energy absorption to the bill and body. Support for this idea comes from the fact that neither the FCl nor the MC protract the head and neck, meaning that they are unlikely to help move the head forward per se (Snively and Russell, 2007).

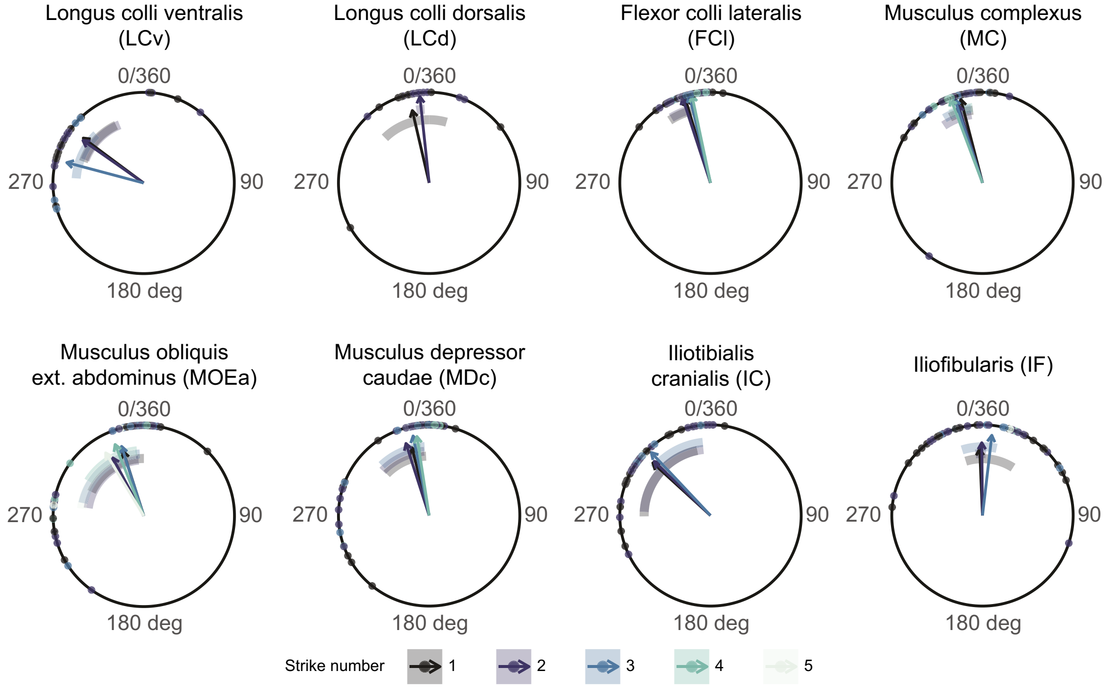

Fig. 4. Timing of EMG muscle activation within repetitive tapping cycles. Circularized repetitive tapping cycles demonstrate how long before contact (0/360 deg) each muscle reaches peak EMG activation. The length of each arrow represents that strike's uniformity (*r*=0–1) and each colored ribbon represents the 95% confidence interval around the degree orientation of each arrow. Individual data points (replicates) for repetitive tapping are shown along the circle for *n*=3 birds for the LCv, LCd, FCl, MC, IC and IF and *n*=2 birds for the MOEa and MDc.

Moreover, we found that both of these muscles are activated near the time of contact, and only slightly prior to activation of the head retractor muscle (LCd, see below). In other words, this neck stiffening appears functionally analogous to wrist stiffening during human hammering.

With this model in mind, our results also suggest that post-impact retraction of the head occurs through coordinated recruitment of the LCd (head and neck retractor) and the IF (hip extensor). Both muscles peak in activation precisely when bird's bill impacts the wood. Notably, the overlapping activations of these retractors with the waning recruitment of the muscular protractors likely smooths the transition of head movement from going forward to going backward. This is akin to the partially overlapping recruitment patterns of antagonistic muscle pairs in bird wings, which helps ensure smooth and rapid transitions between the upstroke and downstroke of a wingbeat (Dial, 1992; Tobalske and Biewener, 2008; Tobalske et al., 2010).

The MDc (tail flexor) appears to have a complex function as a brace, potentially facilitating transitions between strike protraction and retraction (Bock, 1999; Liu et al., 2015). This suggested function is based on the muscle's activation peaks: the first occurs during a ramp-up of recruitment in the protraction phase, whereas the second, larger peak occurs upon contact, concurrently with the LCd and IF. Kinematically, it appears the tail flexes to contact the substrate during protraction and may then stabilize the hip joint and helps anchor the body against the substrate when the bill hits the wood. In this way, we expect that the tail's bracing function may promote more 'fluid' oscillations between phases of movement, particularly for repetitive strikes (Schuppe et al., 2021).

Neuromuscular mechanisms of power production for drilling

Woodpeckers are known to adjust how hard they drill and tap. Individuals will sometimes gently peck at trees and shrubs to probe for insects they can eat, but they can also vigorously excavate cavities in fresh wood to build nests (Schuppe et al., 2021). Our results suggest the IC (hip protractor) is at least one regulator of the differential power that underlies these differences in drilling. Indeed, we found that IC recruitment is greater when birds perform hard pecks compared with when they perform soft pecks. Past work indicates that such differences in EMG activity can correspond to proportional difference in muscular force production (Dial and Biewener, 1993; Hof and Gazendam, 2006; Josephson, 1999; Niebuhr et al., 1993; Richards and Biewener, 2007; Roberts and Gabaldón, 2008); thus, by increasing IC recruitment for hard pecks, birds might generate greater protractive force for more powerful drilling. Interestingly, we did not find differences in activity in other muscles that are thought to potentially influence drilling power, including the LCv and MDc. However, it is quite possible that the limited variation we observed reflects the specific context of our experimental setup (i.e. drilling on a single substrate type). Future work testing across a broader range of substrates or ecological conditions may reveal variation in recruitment for these muscles that was not apparent here.

Neuromuscular mechanisms associated with repetitive tapping behavior

Repeated muscle recruitment during tapping revealed that each muscle activates at a consistent time relative to the strike, but also that EMG amplitudes for most muscles progressively increased across strikes in each tapping sequence. Such a pattern aligns with prior work from repetitive and rhythmic tasks in other taxa, where increasing EMG amplitudes often compensate for cumulative muscular fatigue or mechanical energy losses that may inherently alter inter-muscular coordination and timing during repetitive motion (Gates and Dingwell, 2011). For instance, human hammering studies show that despite consistent rhythm, muscles progressively increase activation

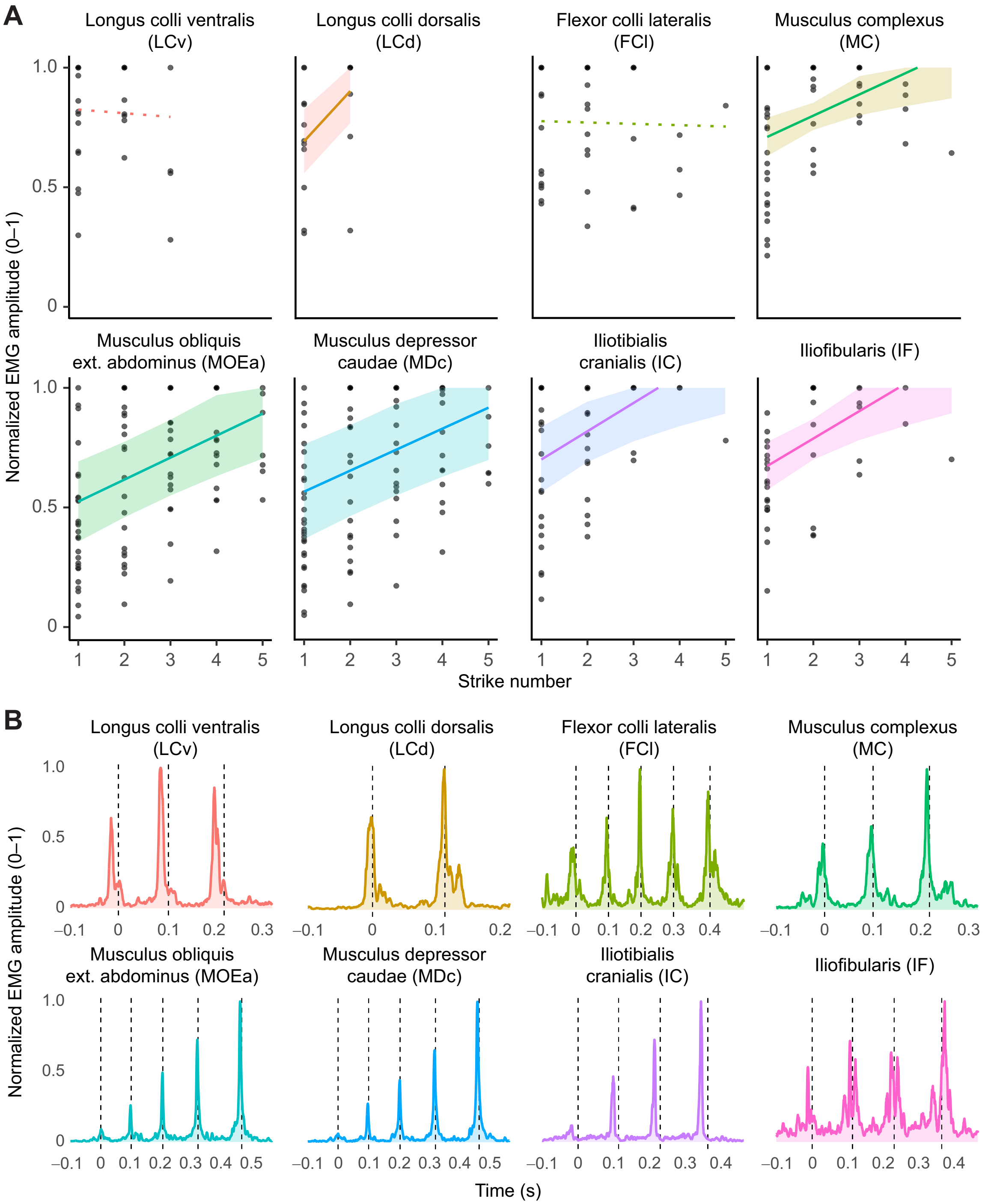

Fig. 5. Changes in muscle activation across successive taps. Graphs show normalized peak EMG amplitude for all muscle for successive taps in a tap sequence (see Materials and Methods; *n*=3 birds for the LCv, LCd, FCl, MC, IC and IF and *n*=2 birds for the MOEa and MDc). (A) Solid regression lines denote statistically significant ($P<0.05$) relationships between strike number and relative amplitude, whereas shaded regions denote 95% confidence intervals. (B) Normalized EMG envelopes for single, representative tapping events in each muscle. Points of contact are shown by vertical dashed black lines. Time zero on each graph represents the timing of first contact for each exemplar.

amplitudes to counteract fatigue and maintain consistent strike force and accuracy (Côté et al., 2005, 2008). Similarly, in animals that perform other forms of cyclic behavior, such as flying or chewing, stable motor timing is frequently accompanied by EMG amplitude scaling to ensure performance stability despite physiological or mechanical challenges (Altshuler et al., 2010; Vinyard et al., 2008). Our current results support this view by suggesting the possibility that woodpeckers use similar mechanisms to sustain neck stiffening and strike production while tapping. Such coordination may help individuals not only maintain important features of this behavior related to strike force and/or precision, but also its acoustic properties (e.g. relative amplitude; Rutter et al., 2025).

Notably, the LCv and FCl did not show increased amplitude across strikes despite tight timing in EMG activation across strikes.

Table 2. Sensitivity analyses of EMG peak amplitude trends across taps in tapping bouts for each muscle

Muscle	Strike truncation	Truncation *P*-value	Jackknife dropped strike position	Jackknife *P*-value	Bootstrap slope [95% CI]	Permutation upsampling *P*-value
LCv	2	**0.040**	1	**0.004**	–0.073 [–0.231, 0.117]	0.798
	3	0.793	2	0.240		
			3	**0.040**		
LCd	2	**0.042**	–	–	**0.218 [0.032, 0.392]**	**0.038**
FCl	2	0.273	1	0.275	–0.0067 [–0.0851, 0.144]	0.862
	3	0.479	2	0.897		
	4	0.742	3	0.769		
	5	0.876	4	0.469		
			5	0.742		
MC	2	**<0.001**	1	0.065	–0.00741 [–0.134, 0.140]	**0.003**
	3	**<0.001**	2	**0.009**		
	4	**<0.001**	3	**0.035**		
	5	**<0.001**	4	**0.002**		
			5	**0.001**		
MOEa	2	**<0.001**	1	0.297	**0.0754 [0.0303, 0.122]**	**<0.001**
	3	**<0.001**	2	**<0.001**		
	4	**<0.001**	3	**<0.001**		
	5	**<0.001**	4	**<0.001**		
			5	**<0.001**		
MDc	2	**<0.001**	1	0.585	**0.0651 [0.0124, 0.117]**	**<0.001**
	3	**<0.001**	2	**<0.001**		
	4	**<0.001**	3	**<0.001**		
	5	**<0.001**	4	**<0.001**		
			5	**<0.001**		
IC	2	**0.043**	1	0.380	0.0301 [–0.0806, 0.158]	**0.004**
	3	**0.005**	2	**0.008**		
	4	**0.001**	3	**0.020**		
	5	**0.003**	4	**0.015**		
			5	**0.001**		
IF	2	**<0.001**	1	0.682	0.00506 [–0.149, 0.125]	**0.002**
	3	**<0.001**	2	**0.002**		
	4	**<0.001**	3	**0.007**		
	5	**0.001**	4	**0.004**		
			5	**<0.001**		

For the first analysis (columns 2 and 3), we iteratively truncated the final strike from each series and recalculated the linear regression with length and associated *P*-value shown. For the second sensitivity analysis, we performed a 'leave-one-out' jackknife resampling for cross-validation with *P*-values from removing each specific strike reported (columns 4 and 5). Third, bootstrap slope estimates (with 95% confidence intervals) are shown once per muscle to summarize balanced–sampling stability (column 6), and empirical *P*-values from 1000 permutations of strike labels test against a null of no ordering effect (column 7). Bold *P*-values denote significance at $\alpha<0.05$, and bootstrap slopes with confidence intervals that do not overlap zero are likewise in bold.

This may be due to the postural nature of activation for these muscles, where they operate at peak activation immediately and across repetitive movements, much like the stable activation of the soleus in walking compared with running relative to the much more variable change in muscle activation displayed by the gastrocnemius (Hof and Gazendam, 2006). Given the variability in tapping bouts performed by each bird, we performed multiple sensitivity analyses, which suggested statistical robustness for these results (Table S2).

Respiratory basis of drilling and tapping

By comparing MOEa (abdominal muscle) activation timing with respiratory dynamics, we demonstrated that woodpeckers exquisitely couple their beak strikes to expiratory pulses. Notably, expiratory pressure increases rapidly to near maximum just before the time of beak contact. We noticed a consistent, brief dip in expiratory pressure coinciding precisely with substrate contact, highlighting a potential reflexive mechanism to enhance core stabilization, akin to human expiratory strategies during impact behaviors (Ishida et al., 2016). Then expiratory pressure briefly returns to a near maximum amplitude before decreasing into inspiration during the retraction phase of the drill. Together, this pattern of 'breathing out through the strike' seems indicative of grunting behaviors observed to increase force production in the human performance literature for tasks such as striking a tennis ball. This type of breathing pattern is known to generate greater co-contraction of trunk musculature and lead to improved spinal and torso stability to potentially boost power output without an oxygen cost (Callison et al., 2014). Similar patterns of co-contraction have been shown across numerous bird species during flight and locomotion (Boggs et al., 1997, 2001; Mackelprang and Goller, 2013). This differs slightly from the 'Valsalva maneuver' shown during explosive weightlifting, where the chest cavity is pressurized by closing the airway (Hackett and Chow, 2013). Indeed, we confirm that the airway (syrinx) remains open during drilling by monitoring tracheal airflow, contrasting with Valsalva-like contexts such as defecation, where syringeal valves close to pressurize the thoracic cavity. In terms of the slight airflow dip right at the point of contact, we suspect this is related to the 'grunt' pressurization we observed in the air-sac pressure. Specifically, it is possible that the deceleration generated by impact is transmitted from the neck to move the sternum slightly forward in a manner that briefly expands the air sac and therefore passively reduces expiratory pressure and airflow.

Along with repeated muscle recruitment during tapping, we found a one-to-one relationship between each peck and respiratory

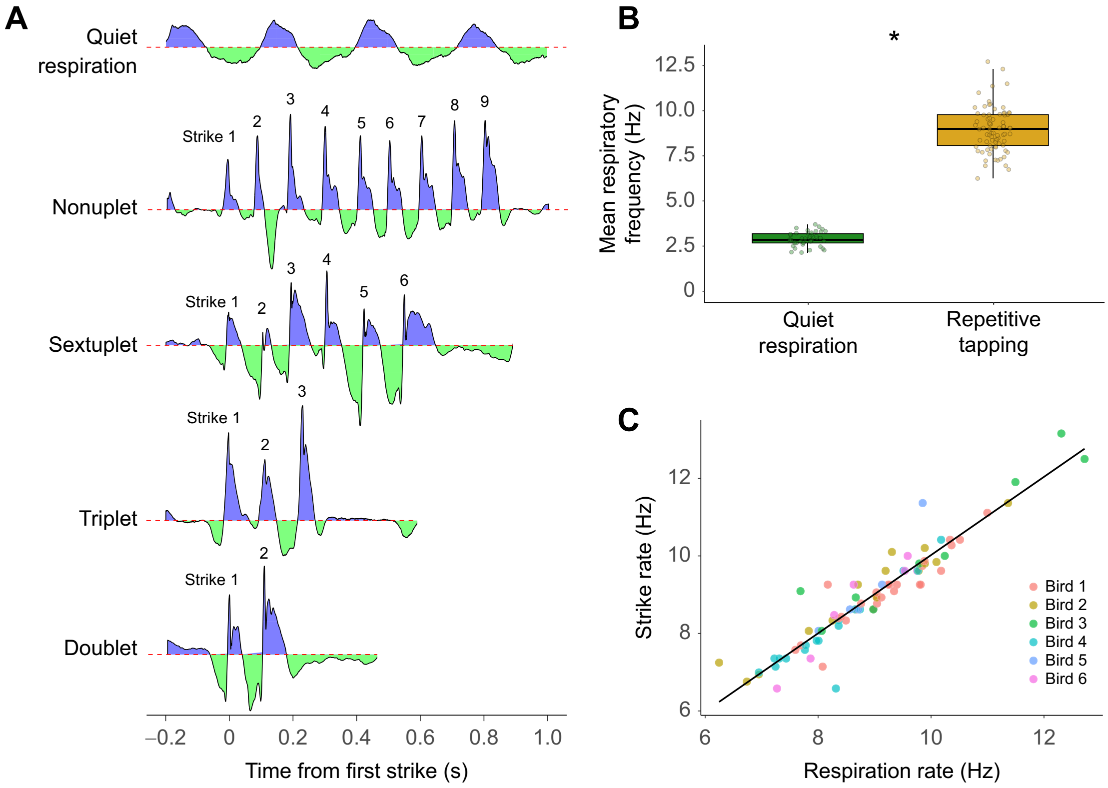

Fig. 6. Respiratory coupling with repetitive tapping behavior. (A) Respiratory pressure cycling during quiet respiration compared with tapping. Expiratory pulses are blue (positive pressure), and inspiratory pulses are green (negative pressure); timing is aligned to contact time of first strike. (B) Comparison of quiet respiration rate to respiration rate during agonistic tapping. Boxplot lines represent data quartiles with thick line at the median; asterisk denotes a significant difference (**P*<0.05), and individual data points are shown for *n*=6 birds. (C) Correlation between strike rate (Hz) and respiration rate (Hz) shows a 1:1 relationship.

cycle. Repetitive taps ranged up to 13 Hz, with inspirations as short as ≈40 ms. Although the inspiratory air-sac pressure peaks are not as great as those found during songs of many birds (Hartley and Suthers, 1989), the rapid switch between expiration and inspiration characteristic for song also appears for woodpecker tapping. The ability to replenish the air through these mini-breaths allows birds to sing long song sequences, facilitating vocal performance; hence, the evolutionary origin of mini-breaths has been widely associated with selection for rapid trill production (Goller, 2022, 2025; Hartley and Suthers, 1989). Our discovery that woodpeckers employ similar mini-breath-like respiratory behavior when tapping potentially implies a broader evolutionary context for the origin of this trait. Much like songbirds, woodpeckers must maintain oxygenation and pressure regulation while performing their high intensity behavioral displays. During drumming, peck rate is even higher than during tapping. If a similar coordination between pecking and respiration occurs during drumming, mini-breath respiration may have a more universal evolutionary origin. Future studies should explore the neural and muscular control of mini-breathing in a comparative framework to clarify whether this respiratory trait represents a vocal precursor, a display-derived mechanism and/or a more flexible respiratory adaptation repeatedly co-opted for high-performance display functions.

Whole-body coordination and its relevance to motor skill

As we indicate above, our results show that drilling and tapping are whole-body behaviors that require precise, concerted activation of multiple muscular systems throughout the body. Moreover, this activity involves direct coordination of the respiratory system to exquisitely time ventilation with behavioral output. Often, studies that explore the neuromuscular basis of behavior – including most complex behavior – focus on only one or two muscular actuators (Cooper and Goller, 2004; Dial and Biewener, 1993; Fuxjager et al., 2017; Hof and Gazendam, 2006). Although this work has revealed important details about adaptive motor control, it is typically unable to capture the holistic coordination of such processes, which integrate multiple physiological systems in behavioral performance (e.g. timing ventilation and the activation of multiple muscles across an organism's body plan as we have done here).

With this perspective in mind, it is clear that drilling, tapping and presumably drumming behaviors in woodpeckers require significant motor skill. This term refers to how 'well' an animal performs a specific task, and it is often evoked to explain how certain social displays might provide honest information about an individual's condition, quality or developmental integrity (Byers et al., 2010). Specifically, our study lends credence to the notion that displays involving drilling and tapping likely require precise neuromuscular coordination of the entire body, and variation in the timing of a specific muscle's activation has the potential to impact how skillfully an animal can perform its display. As such, our study provides a framework for quantifying the neuromuscular and respiratory coordination underlying these behaviors, offering a pathway to assess how individuals execute their characteristic social drum displays. In downy woodpeckers, field studies suggest that faster and longer drums signify greater territorial prowess, and thus we suspect that the manner in which muscular coordination facilitates this behavior might reflect greater motor skill (Schuppe and Fuxjager, 2018).

Conclusions

In summary, we describe the neuromuscular and respiratory basis of drilling and tapping in downy woodpeckers. Such extreme behavior hinges on the tightly coordinated activation of multiple motor systems throughout the body, including those that govern the head, neck, hips and tail. These systems also appear to exquisitely coordinate ventilation with drilling and tapping behavior, likely enhancing their performance. This work therefore reveals important insight into the physiological basis of an elaborate behavior, showing its production is a whole-body endeavor that requires great motor command.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.D.A., F.G., M.J.F.; Data curation: N.D.A., S.O., M.C., F.G., M.J.F.; Formal analysis: N.D.A., T.J.R., F.G., M.J.F.; Funding acquisition: N.D.A., M.J.F.; Investigation: N.D.A., F.G., M.J.F.; Methodology: N.D.A., F.G., M.J.F.; Project administration: M.J.F.; Resources: F.G., M.J.F.; Software: N.D.A.; Supervision: F.G., M.J.F.; Validation: N.D.A., T.J.R., F.G., M.J.F.; Visualization: N.D.A., F.G., M.J.F.; Writing – original draft: N.D.A., M.J.F.; Writing – review & editing: N.D.A., S.O., M.C., T.J.R., F.G., M.J.F.

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Data and resource availability

Data and code are publicly available via figshare at doi:10.6084/m9.figshare.29469872. All other relevant data and details of resources can be found within the article and its supplementary information.

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