

Dance Choreography Is Coordinated with Song Repertoire in a Complex Avian Display

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Summary

All human cultures have music and dance [1, 2], and the two activities are so closely integrated that many languages use just one word to describe both [1, 3]. Recent research points to a deep cognitive connection between music and dance-like movements in humans [2, 4–6], fueling speculation that music and dance have coevolved [2, 7, 8] and prompting the need for studies of audiovisual displays in other animals [9, 10]. However, little is known about how nonhuman animals integrate acoustic and movement display components [11, 12]. One striking property of human displays is that performers coordinate dance with music by matching types of dance movements with types of music, as when dancers waltz to waltz music. Here, we show that a bird also temporally coordinates a repertoire of song types with a repertoire of dance-like movements. During displays, male superb lyrebirds (*Menura novaehollandiae*) sing four different song types, matching each with a unique set of movements and delivering song and dance types in a predictable sequence. Crucially, display movements are both unnecessary for the production of sound and voluntary, because males sometimes sing without dancing. Thus, the coordination of independently produced repertoires of acoustic and movement signals is not a uniquely human trait.

Results and Discussion

Dance can be coordinated with acoustic display in multiple ways. In humans, the simplest method involves dancing in time to music where the visual accent of the dancer's movements is aligned to the accent (or beat) of the music [13]. A more sophisticated form of display is temporal coordination of repertoires of movements with repertoires of music, so that specific movements occur predictably with particular types of music. For example, 19th century ballet consists of both a repertoire of movements and a repertoire of music, and the two are combined nonrandomly. Thus, a waltz section of a ballet is easily distinguished by either the type of music played or the movements of the dancers [14]. Similarly, a solo flamenco performer matches types of arm movements to types of percussive music produced with her feet. Here, arm movements are not essential to sound production and the performers control how arm movements are combined with sound. Such performances are challenging, requiring

performers to remember repertoires of both music and dance, to remember how they relate, to recall this information, and to overcome the physical challenges of skilled motor performance.

Do nonhuman animals coordinate a repertoire of acoustic signals with a repertoire of independently produced display movements? The simultaneous expression of visual and acoustic signals is common in solo animal displays [11, 12, 15–17]. Display movements can produce sounds [18–22], and thus visual and acoustic signals are necessarily synchronized. In contrast, there is only equivocal evidence of coordination between a repertoire of acoustic signals and a repertoire of display movements independent of sound production (e.g., [23, 24]). In birds, there are tantalizing but untested descriptions of coordination between complex repertoires of song and display movements (or “dance”) [25–29]. Three quantitative studies have analyzed the interaction between just one type of movement and one type of vocalization [30–32], but the only study to test for a relationship between repertoires of dance and song structures was inconclusive [24]. Thus, there is currently no compelling evidence of coordination between independent repertoires of sound and display movements in nonhuman animals.

We have obtained evidence that the superb lyrebird, *Menura novaehollandiae*, an oscine passerine, coordinates repertoires of song types with repertoires of independently produced dance movements. Like many birds, male lyrebirds display to females with both song and dance. Lyrebirds have a promiscuous, lek-like mating system lacking in paternal care [33]. Adult males advertise vocally with a large repertoire that can exceed 90 song types [34], comprising song types exclusive to lyrebirds and extreme levels of accurate mimicry of the vocalizations of other species of bird [33–35]. Males also have a spectacular visual display involving the inversion of their tail over their heads, revealing the striking underside of their elaborate tail feathers (Figure 1). In addition, they perform a dance display on circular mounds that they have built on the forest floor [33]. This solo dance display is accompanied by song and is the prelude to mating [33] but has never been formally investigated.

To determine the relationship between song and dance in the superb lyrebird, we filmed dance displays of 12 males performing in the wild (see [Experimental Procedures](#) for details). We also observed and recorded males to determine whether dance movements were necessary to produce songs. We first characterized the acoustic component of dance displays.

Songs accompanied all dances. Despite males possessing a very large repertoire of song types, we identified only four song types produced while dancing (Figure 2). Each of the song types A, B, and C involved the production or repetition of a subunit of song, a “syllable,” the structure of which was unique to each song type (Figure 2). Song type D contained repetitions of one or more syllables from a set of eight syllables (Figure 2; see also [Figure S1](#) available online).

To investigate the relationship between song and dance, we first identified the beginning and end point of each song type within a dance display. For the time period delineated by the duration of each song, we assessed the movement of the

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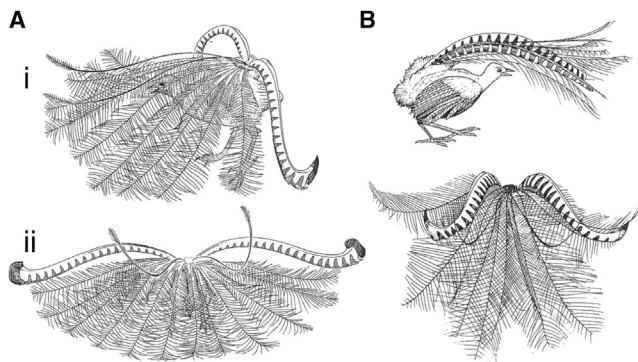


Figure 1. Inverted Tail Postures in Dance Displays by Males

Tail in (A) “Wide” and (B) “Narrow” position with (i) side view and (ii) front view (see also [Movie S1](#)). Drawings by Peter Marsack and reproduced with permission from [33].

singing male, scoring the movement or posture of the legs, wings, and tail ([Figure 2](#)). Leg movement consisted of one of three mutually exclusive categories: (1) steps, “S”; (2) jumps or deep bobs, “J”; or (3) none, “N”. Steps within the dance were usually distinctive “dance steps,” with males stepping sideways. A male’s wings were either motionless (“No flaps”) or flapped (“Flaps”). The male’s tail feathers were either fully fanned over his head, so that the outermost feathers, the striped lyrates, were at 180° to each other (“Wide”: [Figure 1A](#)), or closed, so the angle between the lyrates was less than 90° (“Narrow”: [Figure 1B](#)). Just as a song type is a set of acoustic characters, so dance is a set of movements and postures. In order to treat both song and dance equivalently in our analysis, we combined the scores of leg movement, wing movement, and tail position into a single factor, “gesture,” so that each of the 12 possible sets of movements corresponded to a different gesture. We then examined the association between each song type and each type of gesture (see [Experimental Procedures](#) for details).

Our analysis revealed that each of the four song types within the display was associated with one particular gesture ([Figure 2](#); [Table S1](#); [Movie S1](#)). The gesture accompanying song A consisted of steps, often to the side, with wings motionless and a wide tail ([Figure 1A](#)). In contrast, the male’s tail was narrowed ([Figure 1B](#)) while he sang song types B and C, and during the latter he nearly always jumped or bobbed and flapped his wings ([Figure 2](#)). When males sang song type D, the tail was usually wide and the legs and wings still. Some individual movements were associated with particular songs: step movements were characteristic of song A, whereas wing flaps, jumps, and bobs occurred with song C. However, characterization based on wing, tail, or leg movement alone was not enough to distinguish between the four song types ([Figure 2](#)), showing that males combined repertoires of movements to form characteristic gestures for each song type.

Males did not need to dance in order to produce song types sung in dance displays. During focal watches, we observed 12 adult males singing song types A–D without performing dance movements. Specifically, these males had their tails folded behind them, their legs were motionless, and they did not flap their wings. Nine of these males were also observed producing displays incorporating all dance movements. Thus, dance is an optional, voluntary addition to singing.

Male lyrebirds ordered their songs and associated gestures into a predictable sequence. Transition probabilities between

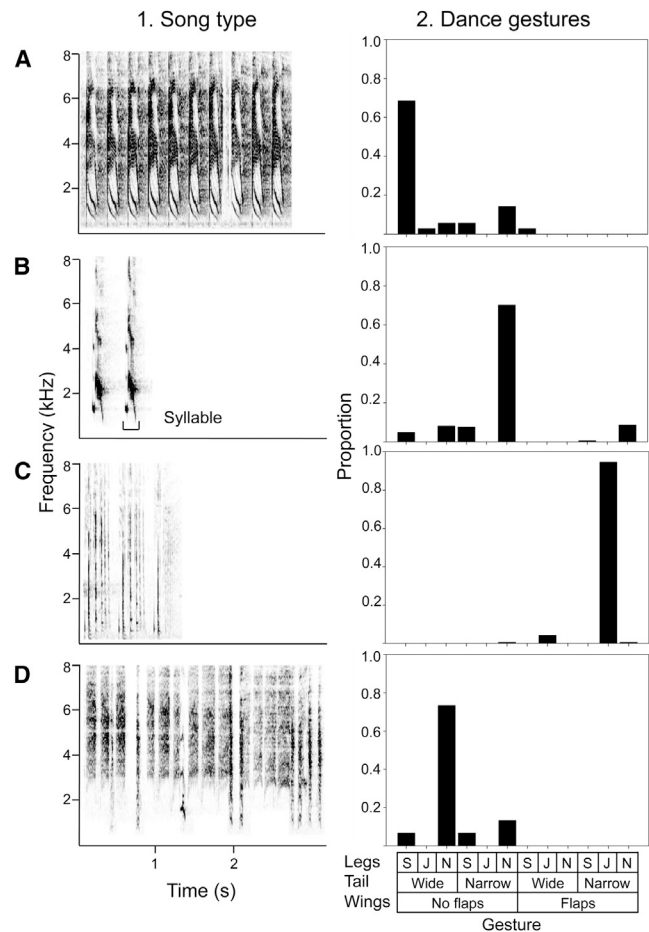


Figure 2. The Relationship between Song and Gesture in Lyrebird Dance Displays

Column 1: song types sung during dance displays by type (A–D). Sonograms of A, B, and C depict mean syllable number. Column 2: the proportion of gestures accompanying each song type. The factor “Gesture” is the combined score of three aspects of dance (x axis): leg movement (steps, “S”; jumps or deep bobs, “J”; or none, “N”); tail position (“Wide” or “Narrow”); and wing movement (“Flaps” or “No flaps”). Proportions were calculated from REML predictions generated from a log-linear model of a count of each combination of song type and gesture. Two-way interaction between song type and gesture: $F_{33, 517.0} = 2.32$, $p < 0.001$ (see also [Tables S1 and S2](#), [Figure S1](#), and [Movie S1](#)).

song types within the lyrebird displays revealed that birds always started with song type A, then typically alternated between song types B and C several times before repeating song type A and finishing with song type D ([Figure 3](#); see [Experimental Procedures](#) for details). The analysis confirmed that shorter song types B and C occurred frequently (46% and 41% of songs performed, respectively), with the longer types A and D used less often (9% and 3%, respectively). However, because of their long duration, types A and D formed a significant component of the display ([Table S2](#)).

Dance displays by male lyrebirds are tightly structured at multiple levels of signal organization and may be challenging to perform. First, sound and movement are themselves highly structured: syllables are structured into songs, postures and movements into gestures ([Figure 2](#)). At the next level of organization, types of gestures are coordinated with types of songs, creating four different multimodal display components

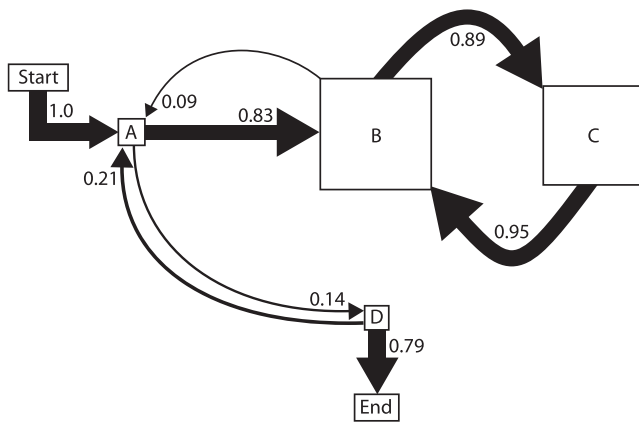


Figure 3. Relative Frequency of Occurrence and Sequential Relationship of Song Types during Dance Displays

Displays start with song type A and often end with song type D. Transition probabilities suggest the following typical sequence of song: from song type A, they alternate between B and C several times before repeating song type A and finishing with song type D. Song types B and C were performed at least four times more often than A and D song types, as indicated by box size (see also [Table S2](#) and [Movie S1](#)). Transition probabilities less than 0.05 are not shown.

([Figure 2](#)). Finally, each type of multimodal component is coordinated with the others, creating a predictable sequence ([Figure 3](#)). Dance gestures and song structures appear to be governed by separate mechanisms, since songs sometimes occur without the associated dance movements and song types are occasionally accompanied by gesture types other than the modal type ([Figure 2](#)). How males pair song types with dance gestures is a possible source of variation on which selection could act. These characteristics are consistent with a cognitively and physiologically demanding display that could be used by females to choose mates.

There are three wider implications of our study. First, the coordinated repertoires of acoustic and movement signals that are common in humans occur in at least one other animal, and this animal is capable of vocal learning. Whether the ontogeny of coordinated song and dance in lyrebirds involves learning is unclear, but it seems plausible that birds could learn song-dance coordination as an extension of the process of learning songs [24]. Second, our study illustrates how signal components expressed in different modalities can interact in complex ways [11, 12, 15, 16] and at multiple hierarchical levels of signal organization [36], emphasizing the importance of comprehensive analyses of signal structure. Finally, our results suggest that auditory-motor coordination itself is a potential target of selection. Clarifying the ultimate and proximate causes of coordinated repertoires of song and dance in humans and nonhumans alike requires detailed studies of species that perform these intriguing displays.

Experimental Procedures

Study Population and Recordings

We filmed dance displays during focal watches of individual male lyrebirds in Sherbrooke Forest (37°53', 145°21'), part of the Dandenong Ranges National Park in Australia. Most males in this population are habituated to humans, permitting recordings within 5–20 m. Recordings were made each year from 2007 to 2009 between June 10 and August 20, the peak egg-laying period [33]. First, we filmed the full dance displays of 12 males (dance duration: \bar{x} = 49.3, SD = 29.4, range = 14–114 s). Six males were color

banded, two further males had distinctive markings, and the remaining four males were separated by 0.9–3.8 km. Since color-banded adult males defended the same territories in successive years, the risk of pseudoreplication is low. Male lyrebirds typically acquire full adult plumage between 7 and 9 years of age [33]. All the males we recorded had mature, adult tail feathers, except one color-banded 6-year-old that obtained adult plumage the year following our recording. Second, we observed and audio recorded a different but overlapping sample of 12 adult males singing sequences of song types A–D without dancing. We filmed three such displays. Nine of these males were also observed or filmed performing full dance displays. Third, we audio recorded 18 adult males singing sequences of song containing song types other than A–D. All recordings were collected under permits from the Australian National University Animal Experimentation Ethics Committee and the Victorian Department of Sustainability and Environment.

Males were video and audio recorded using camcorders or digital cameras in video mode. Displays were recorded using a Canon PowerShot S2 IS, a Canon camcorder MD335, a Sony DCR-TRV330E, a Canon camcorder MV850i, a Canon PowerShot A550, and a Panasonic Lumix DMC-FZ5. Additional audio recordings recorded simultaneously with video recordings were made using a Sennheiser ME66 shotgun microphone and a Marantz PMD670 digital recorder sampling wave files at 44.1 kHz and 16 bits.

Audio-visual Analysis

Within the video recordings with the best visibility, we identified dance sequences, which we defined as a series of display-like motions performed by males with their tails fully inverted. In contrast with utilitarian movements such as walking and flying, display motions included steps, jumps or bobs, and a distinctive wing flap. Males only performed this series of display motions while producing a sequence of the song types A–D. While singing sequences of song containing other song types, males never performed this series of movements (216 sequences from 18 males). Since maximal dance displays included four different song types, we excluded from our sample incomplete displays with fewer song types.

To investigate the relationship between song and dance, we first identified songs before scoring movements. We classified songs into types by visual inspection of sonograms created using Syrinx 2.6h (J. Burt; <http://www.syrinxpc.com>) or Adobe Soundbooth CS3 1.0 and identified the start and endpoint of each song type. We then scored the leg movement, wing movement, and tail position for the duration of each song type using Adobe Soundbooth, which depicts both audio and video tracks. Cursors in the audio track show progress of the video. When slow motion was required to score movements, we first measured the duration of each song in Adobe Soundbooth and then used VLC Media Player 1.0.5 to play the time period of interest in slow motion. All movement terms were mutually exclusive within a movement character (legs, wings, or tail), except the tail, which could change position during the course of a song. If this occurred, the score recorded was the position of the tail for the majority of the song. Scores of the three movement characters were then combined into a 12-level factor, “gesture” ([Figure 2](#)). We excluded from our analysis five songs from five birds where wing movements were obscured from view.

Statistical Analysis

The relationship between song type and dance gesture was assessed using a log-linear approach [37], where the observed number of each possible combination of song type and gesture was regressed against the saturated model. A log-linear model was used because it makes no assumptions about causal relationships between the modeled categorical variables [37], and we had no grounds for considering song type to be dependent on gesture or vice versa. While we analyzed one dance display from each bird, males repeated each song type a variable number of times. Accordingly, the generalized linear mixed model was fitted with the identity of the dancing bird as the random term, and effects were estimated using restricted maximum likelihood (REML) ([Table S1](#)). We used GenStat 13.2 (VSN International, 2010).

We quantified serial dependencies of song types during displays by calculating transition probabilities. After identifying the temporal sequence of display components for each of 12 males, we calculated the transition probabilities between song types and associated measures of uncertainty using the software UNCERT [38]. Three measures of uncertainty (U) were calculated, based on Shannon’s equation for entropy [39, 40]. Briefly, U_0 takes into account the relative frequency of each song type, and U_1 considers the serial correlation between adjacent components in the sequence and is based on the matrix of transitional frequencies.

Uncertainty analysis of the transition probabilities between song types within displays revealed a large drop from U_0 (1.52) to U_1 (0.48), indicating unequal use of song [38]. Transition probabilities between song types revealed a clear sequential order (Figure 3). As there was no further drop in uncertainty when considering ordered pairs (U_2 : 0.49), we conclude that the preceding song type predicts the next with high accuracy and transitions can be considered semi-Markovian [40].

Supplemental Information

Supplemental Information includes one figure, two tables, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.05.018>.

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