Report

Experimental Evidence for Synchronization to a Musical Beat in a Nonhuman Animal

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Summary

The tendency to move in rhythmic synchrony with a musical beat (e.g., via head bobbing, foot tapping, or dance) is a human universal [1] yet is not commonly observed in other species [2]. Does this ability reflect a brain specialization for music cognition, or does it build on neural circuitry that ordinarily serves other functions? According to the "vocal learning and rhythmic synchronization" hypothesis [3], entrainment to a musical beat relies on the neural circuitry for complex vocal learning, an ability that requires a tight link between auditory and motor circuits in the brain [4, 5]. This hypothesis predicts that only vocal learning species (such as humans and some birds, cetaceans, and pinnipeds, but not nonhuman primates) are capable of synchronizing movements to a musical beat. Here we report experimental evidence for synchronization to a beat in a sulphur-crested cockatoo (*Cacatua galerita eleonora*). By manipulating the tempo of a musical excerpt across a wide range, we show that the animal spontaneously adjusts the tempo of its rhythmic movements to stay synchronized with the beat. These findings indicate that synchronization to a musical beat is not uniquely human and suggest that animal models can provide insights into the neurobiology and evolution of human music [6].

Results and Discussion

Synchronization of movement to a musical beat develops spontaneously in humans [7, 8] yet is not commonly observed in other species, including domesticated animals (such as dogs) that have lived with humans and their music for thousands of years [2]. Musical beat perception and synchronization (BPS) has several distinguishing features compared to rhythmic entrainment in other species (e.g., the rhythmic chorusing of certain katydids and frogs [9, 10]). For example, BPS involves a periodic motor response to complex sound sequences (not just pulse trains), can adjust to a broad range

of tempi, and is crossmodal, with sound eliciting periodic movement that is not necessarily aimed at sound production [11]. BPS is thus an unusual form of rhythmic entrainment and is the focus of a growing body of behavioral, neural, and computational research [e.g., 12–16].

The spontaneous development and apparent species specificity of BPS make it reminiscent of how aspects of language develop. Yet BPS does not appear to be a by-product of our linguistic abilities: ordinary speech does not employ regularly timed beats or elicit periodic movements from listeners [3, 17]. Might BPS be a biological specialization for music, reflecting natural selection for musical abilities in our species [18, 19]? Or is it a consequence of brain circuitry that evolved for other reasons [20]? According to the "vocal learning and rhythmic synchronization" hypothesis [3], BPS relies on the brain circuitry for complex vocal learning because (1) BPS resembles vocal learning in that it involves special links between the auditory and motor systems [4, 14] and (2) the neural substrates of vocal learning and BPS appear to overlap in the brain (e.g., in the basal ganglia and supplementary motor areas) [5, 12, 21]. This hypothesis predicts that only vocal learning species (such as parrots, dolphins, and seals) are capable of BPS and that vocal nonlearners (e.g., dogs, cats, and nonhuman primates) are not capable of BPS.

Motivated by this hypothesis, the current study investigated BPS in a sulphur-crested cockatoo (*Cacatua galerita eleonora*) named Snowball (Figure 1). Snowball came to our attention via a YouTube video in which he moves rhythmically (including head bobs and foot steps) in response to a pop song. Remarkably, the movements appeared well synchronized to the musical beat, providing the first indication that BPS might not be a uniquely human ability. However, two important issues remained unresolved. First, with home videos it is not possible to rule out imitation of human movement, which is of particular concern with parrots because they have the unusual ability to mimic nonverbal human movements [22]. Second, it was not clear whether Snowball could synchronize to music across a broad range of tempi (a key feature of BPS). To address these issues, we report here an experimental study involving suppression of human movement and manipulation of the musical tempo.

We used a 78 s excerpt of a song familiar to Snowball ("Everybody," by the Backstreet Boys; tempo = 108.7 beats per minute [bpm]) manipulated to create versions at 11 different tempi without shifting the pitch of the song: original and ±2.5%, ±5%, ±10%, ±15%, and ±20%. These versions were presented in each of four sessions. Rhythmic movements were coded from video, focusing on the timing of head bobs (see Supplemental Data). The time of each bob was compared to the time of the nearest auditory beat and assigned a relative phase (e.g., a head bob coinciding with an auditory beat was assigned a phase angle of 0, a bob 25% of the beat period ahead of a beat was assigned a phase angle of $-90°$, a bob 25% of the beat period after a beat was assigned a phase angle of $90°$, etc.). Because visual inspection of the videos suggested that there were periods of synchrony ("synchronized bouts") interspersed with periods where Snowball was dancing but was not synchronized to the music, we used

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Figure 1. Snowball

Snowball, a male sulphur-crested cockatoo (*Cacatua galerita eleonora*) investigated in the current study.

Figure 2. Circular Histogram of Head Bob Phases Relative to the Beat

Phase angles for all head bobs in synchronized bouts (n = 544). 0° indicates head bobs coincident with the musical beat. Positive angles indicate bobs that occur after the beat, whereas negative angles indicate bobs that occur before the beat. The average phase angle of bobs is 3.94° (indicated by the arrow) and is not significantly different from 0.

a windowed analysis to determine the location and extent of synchronized bouts in each trial. A synchronized bout (henceforth simply "bout") was defined as at least two adjacent overlapping windows of eight consecutive head bobs, with each window exhibiting synchronization to the beat via the phase-sensitive Rayleigh test with a criterion of $p < 0.05$ (equation 4.15 in [23]; this test requires that head bobs match the musical tempo and be aligned in time with musical beats). Because windows were overlapped by four beats, a bout consisted of a minimum of 12 successive head bobs. For each trial with bouts, the number of head bobs that were part of bouts was recorded.

Only trials in which Snowball showed sustained dancing (number of head bobs $\geq$ 50% of the number of beats) were analyzed. There were 38 such trials, distributed across all 11 tempi, as shown in Table 1 (row 1). Bouts occurred in 22 (58%) of these trials, spanning 9 tempi ranging from 10% slower to 20% faster than the original tempo (i.e., 97.8 to 130.4 bpm; Table 1, row 2). As is evident from Table 1, no bouts occurred at the slowest two tempi, and most bouts occurred at tempi faster than the song's original tempo.

The 22 trials with synchronization had 101 head bobs on average (SD 19). Within these 22 trials, a total of 33 bouts were observed. The median bout length was 16 head bobs and ranged from 12 to 36 consecutive bobs synchronized to the beat. Figure 2 shows a histogram of head bob phase angles relative to the beat (0 phase) during bouts. The mean angle was 3.9° and was not significantly different from 0 (t = 1.6, p = 0.11, degrees of freedom = 543). Thus, on average, head bobs during bouts were closely aligned to auditory beats, which resembles the timing of human tapping to music [24].
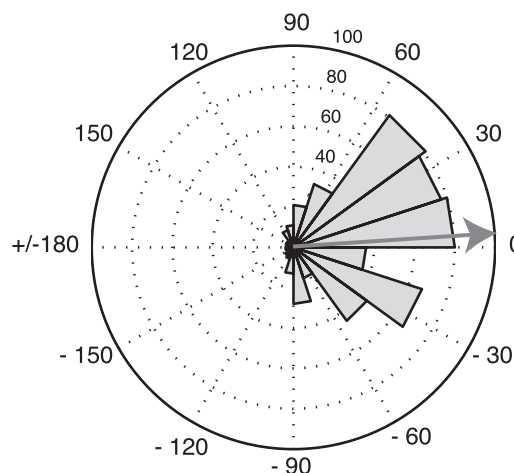
Two bouts are illustrated in Figure 3, which shows Snowball's dance tempo during a trial with musical tempo = 130.4 bpm (i.e., 20% faster than the song's original tempo). Bouts are indicated by boxes around the tempo time series. Across the 22 trials with synchronization, bouts accounted for 25% of the head bobs in each trial on average (range = 10%–51%). The figure illustrates that bouts were interspersed with periods in which Snowball was dancing more slowly or quickly than the beat. Snowball's pattern of occasional synchronization during periods of sustained dancing may resemble how young children (versus adults) synchronize to music [25].

This pattern of occasional synchronization naturally raises the question of whether Snowball simply dances rhythmically (and with variable tempo) in response to music, with periods of apparent synchronization occurring by chance. To test our data against this null hypothesis, we performed a permutation test in which each head bob time series was randomly paired with a beat time series from a trial at a different tempo. A Monte Carlo test involving 10,000 such simulated experiments revealed that Snowball's actual degree of synchrony is unlikely to have occurred by chance (p = 0.002; see Experimental Procedures).

It is notable that Snowball's movements during synchronization appear not to be simple copies of movements typically found in the natural repertoire of sulphur-crested cockatoos. For example, the male courtship display of sulphur-crested cockatoos is brief and involves rhythmic head bobs (not obviously synchronized to auditory cues), side-to-side figure-eight head movements, and "soft, chattering" vocalizations [26]. In

Table 1. Number of Experimental Trials in the Different Conditions

	−20%	−15%	−10%	−5%	−2.5%	0%	2.5%	5%	10%	15%	20%
Number of trials with sustained dancing	2	2	2	3	4	5	4	4	4	4	4
Number of trials with synchronized bouts	0	0	1	1	4	3	1	1	3	4	4

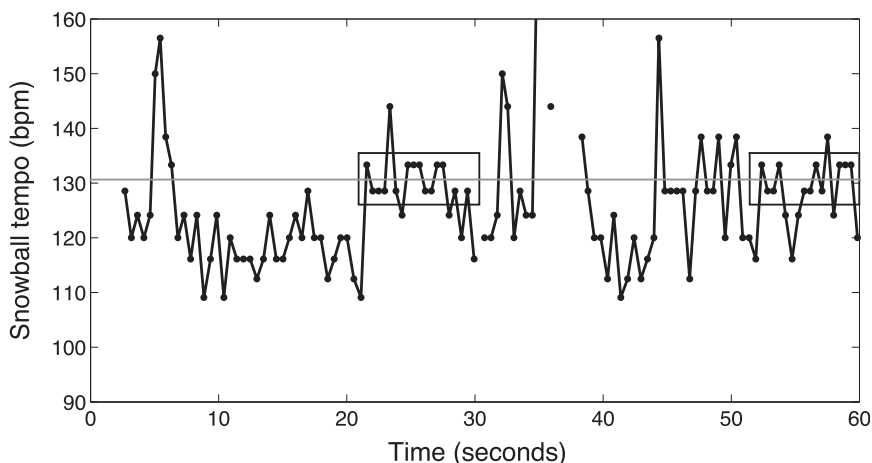Percentages indicate tempo change from original song.

Figure 3. Timing of Rhythmic Movements in One Trial

Snowball's instantaneous dance tempo during an experimental trial in which the musical tempo was 130.4 beats per minute (bpm) (gray horizontal line), i.e., 20% faster than the original song. (Instantaneous tempo was computed by dividing each time interval between successive head bobs into 60 s—e.g., an interval of 0.5 s becomes an instantaneous tempo of 120 bpm.) Black boxes indicate synchronized bouts, when head bobs were synchronized with the musical beat. At other times Snowball continued to dance, but not at the musical tempo.

our study, we observed a variety of rhythmic gestures in addition to head bobs (including swaying the head and trunk from side to side on every other beat), but we did not observe figure-eight head movements or courtship-like vocalizations.

A natural question about these results is whether they can be generalized to other parrots, or more broadly, to other vocal learning species. Schachner and colleagues (in this issue of *Current Biology* [27]) surveyed YouTube videos and found that all species which appeared to move in synchrony with a musical beat were vocal learners (n = 15, mostly parrots). Although these findings are consistent with the vocal learning hypothesis [3], there is a need for further experimental work involving other species. Studies of nonhuman primates (such as chimpanzees and macaques) are particularly important, in that they are the closest living relatives of humans yet lack complex vocal learning [28, 29] and should thus be incapable of BPS according to the vocal learning hypothesis. It would also be worth conducting experiments with species that engage in rhythmic chorusing, to test the alternative hypothesis that the origins of musical synchronization lie in chorusing behavior rather than in vocal learning [18]. More generally, future comparative work can help determine what neural abilities are necessary foundations for BPS. In this regard, it is important to note that vocal learning may be a necessary but not sufficient foundation. For example, BPS may require the neural circuitry for open-ended vocal learning (i.e., the ability to imitate novel sound patterns throughout life) as well the ability to imitate nonverbal movements, two evolutionarily rare traits shared by parrots and humans [11, 22].

The discovery of synchronization to music in a nonhuman animal shows that a fundamental aspect of music cognition is shared with other species and provides valuable clues about the neurological substrates of this aspect of music. The finding also suggests the utility of developing animal models of movement to music. Such models could have relevance to the study of human movement disorders (including Parkinson's disease), symptoms of which have been shown to be alleviated by moving with a musical beat [30, 31]. More generally, it appears that comparative studies of other species can be a powerful approach for gaining insight into the neurobiological and evolutionary foundations of our own musical abilities [6, 17, 32].

Experimental Procedures

Participant

Snowball is a 12-year-old male sulphur-crested cockatoo (*Cacatua galerita eleonora*) (family Cacatuidae), from the order Psittaciformes, a group of animals known for their vocal learning skills and for living in complex social groups [33, 34]. He was relinquished to author I.S. in August 2007. His previous owner (PO) indicated that Snowball liked to dance to music, and Snowball has since been observed dancing to a wide variety of songs. The PO acquired him at a bird show when Snowball was 6, and Snowball's experience with music prior to this is not known. The PO mentioned that soon after he acquired Snowball, he noticed Snowball bobbing his head to the music of the Backstreet Boys. (The PO felt that this was not done in imitation of human movement.) Subsequently, the PO and his daughter began dancing with Snowball using pronounced arm gestures, which may be the origin of Snowball's foot-lifting behavior while dancing. Snowball currently resides at Bird Lovers Only Rescue Service, where the experiments took place.

Stimuli

Stimuli are described in the main text. Audacity public domain software (version 1.2.5, "Change Tempo" effect) was used to create versions at different tempi. These were checked by ear to ensure that they were free of acoustic artifacts.

Procedures and Equipment

The study consisted of four video sessions conducted between January and May 2008. Two humans familiar to Snowball (his owners) were present in the room and recorded the video. A fifth session was recorded but was excluded because of distraction caused by the presence of a new person unfamiliar to Snowball.

During each session, Snowball was placed on the back of an armchair. A variety of tempi were presented, typically by starting with the original tempo and then moving between manipulated tempi in a step-like fashion, from slow to fast, with occasional repeated trials. Short pauses were given between trials. On each trial, Snowball was given verbal encouragement to dance, but humans did not dance and remained at least 5 feet away. (In sessions 1 and 2, author I.S. inadvertently bobbed her head to the beat in a subtle fashion. This was suppressed in sessions 3 and 4 and did not affect the results: during sessions 1 and 2, when I.S. bobbed her head slightly, 11 of 20 trials (55%) had bouts. During sessions 3 and 4, when I.S. suppressed rhythmic movement, 11 of 18 trials (61%) had bouts, indicating that imitation of human movement cues could not account for Snowball's synchronization to the beat. Hence, data from all sessions were combined for further analysis.) No training or food rewards were involved in this study: dancing began and ended spontaneously when the music was turned on and off. Sessions lasted about 30 min each and took place between 1 and 5 p.m.

Music was presented via Altec Lansing Series 5100 speakers connected to a personal computer. Videos were taken with a Panasonic Mini DV camera (NTSC format) mounted on a tripod, approximately 6 feet from Snowball. After each session, the video was transferred to computer for analysis.

Data Analysis

Videos were segmented into individual trials, and each segment was deinterlaced to obtain 60 frame-per-second time resolution. (Deinterlacing was not possible for session 2, which thus had 30 fps resolution.) Snowball's rhythmic movements were coded with the sound turned off and the coder unaware of which condition the trial represented. Although several different classes of rhythmic movements were observed, vertical head position was found to be the most reliable rhythmic gesture. To study the timing of head

bobs, the frame number was noted each time Snowball's head reached a locally minimal position in the vertical plane. (As a reliability check, a second coder independently recoded four trials: 94.7% of frame numbers were within 1/60th of a second of the original coder, and 99.6% were within 1/30th of a second).

Audio tracks were extracted for each trial, and beat times were determined with a beat tracking algorithm [35]. Rare periods when the beat track was judged inaccurate were excluded from analysis (only ~10 s at the end of one trial). As described in the main text, each head bob within each trial was assigned a phase angle relative to the closest auditory beat, and synchronized bouts were identified via a windowed analysis. Use of the phase-sensitive Rayleigh test ensured that our statistical test of synchrony was sensitive to both the period and the phase of rhythmic movements with respect to the musical beat.

Permutation Test

Because the experiment consisted of 38 trials across 11 different tempi (Table 1, row 1), we randomly re-paired the head bob time series and beat time series so that each head bob series was paired with a beat time series at a different tempo, with the constraint that all 11 tempi were represented in the permuted data. This created a simulated experiment of 38 trials, which was analyzed for synchrony in the same way that we analyzed the original data. Via this approach, we recorded the total number of bobs that were part of bouts in each trial, yielding 38 values (i.e., one per simulated trial). These numbers were summed to compute the total number of head bobs synchronized with the beat across the simulated experiment. A Monte Carlo test with 10,000 such simulated experiments resulted in a distribution of the number of head bobs synchronized with the beat in each of the simulated experiments. We compared this distribution to the total number of head bobs synchronized to the beat in our actual data (544) and computed the p value of our data as the proportion of simulated experiments that had the same or higher number of synchronized head bobs. This proportion was 0.002, indicating that our observed degree of synchrony is highly unlikely to arise by chance.

Supplemental Data

The Supplemental Data include one movie and can be found with this article online at http://www.cell.com/current-biology/supplemental/S0960-9822 (09)00890-2.

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