Avian and human movement to music
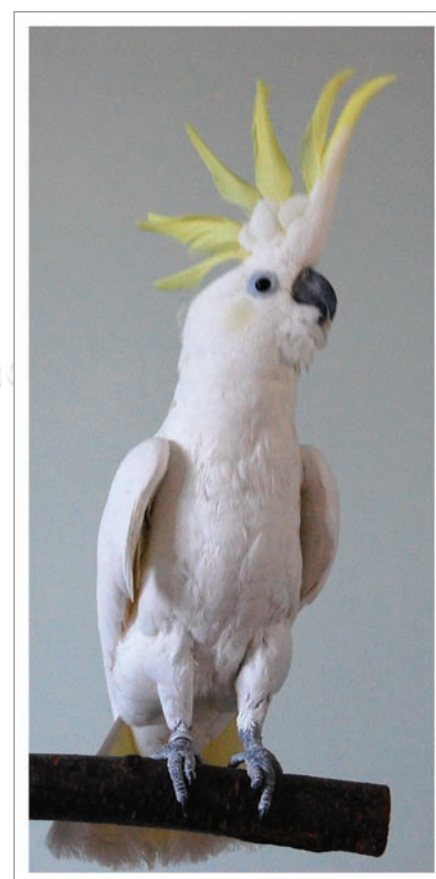## Two further parallels

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It has recently been demonstrated that a nonhuman animal (the medium sulphur-crested cockatoo *Cacatua galerita eleonora*) can entrain its rhythmic movements to the beat of human music across a wide range of tempi. Entrainment occurrs in "synchronized bouts", occasional stretches of synchrony embedded in longer sequences of rhythmic movement to music. Here we examine non-synchronized rhythmic movements made while dancing to music, and find strong evidence for a preferred tempo around 126 beats per minute [bpm]. The animal shows best synchronization to music when the musical tempo is near this preferred tempo. The tendency to dance to music at a preferred tempo, and to synchronize best when the music is near this tempo, parallels how young humans move to music. These findings support the idea that avian and human synchronization to music have similar neurobiological foundations.

Snowball, a cockatoo that dances to music.

All over the world, people move rhythmically in response to music with a regular beat. One notable feature of this response is the tendency to synchronize movements to the timing of perceived beats.[1] This ability involves the conjunction of two underlying abilities: musical beat perception (the ability to infer a regular pulse from a complex rhythmic/melodic pattern), and rhythmic motor production synchronized to the inferred beat. Musical beat perception and synchronization (BPS) is a complex form of biological entrainment that differs in several ways from other examples of synchrony in nature, such as the chorusing of certain frogs or insects.[2,3] Some theorists have speculated that BPS is uniquely human, reflecting an evolutionary adaptation for music cognition.[4] However, recent empirical research has documented BPS abilities in a number of vocal-learning species,[5,6] supporting the hypothesis that BPS is a consequence of the brain circuitry for complex vocal learning.[7]

At least one species, the medium sulphur-crested cockatoo *Cacatua galerita eleonora*, can entrain its rhythmic movements to the beat of human music across a wide range of
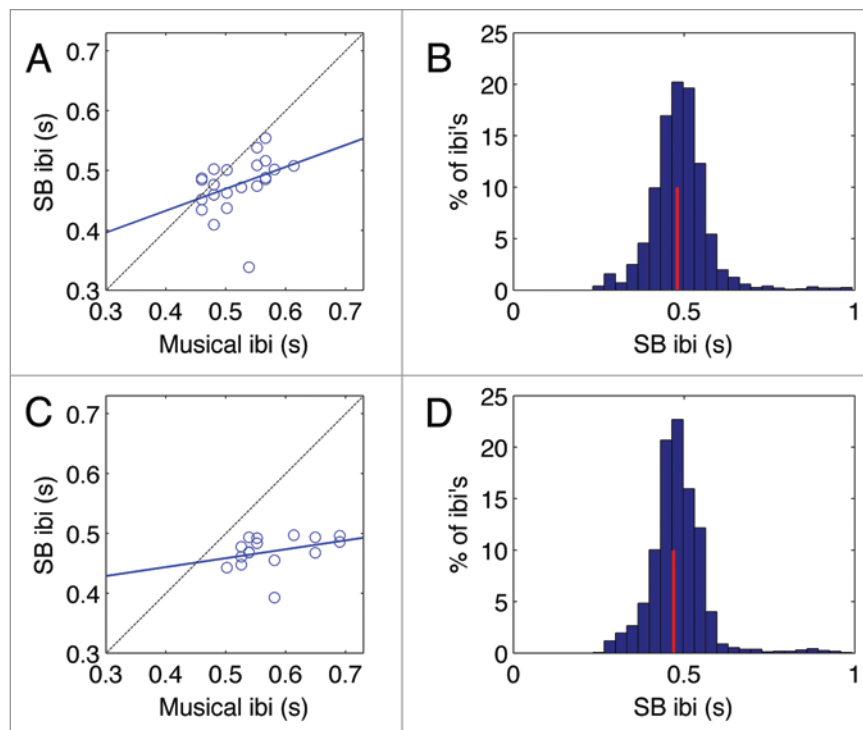
Figure 1. The rate of Snowball's inter-bob-intervals (SB ibi) for head bobs not entrained to the musical beat. (A) Mean SB ibi of non-entrained head bobs in the 22 trials with bouts, as a function of musical inter-beat-intervals (Musical ibi). The best fitting regression line is shown (thick solid, Y = 0.286 + 0.366 * X; if outlier point is excluded, Y = 0.262 + 0.427 * X), as well as the identity line (thin dashed). (B) Histogram of all non-entrained SB ibi's in trials with bouts (n = 1,529; mean value shown by red line). (C) SB ibi as a function of Music ibi in the 16 trials without bouts. The best fitting regression line is shown (thick solid, Y = 0.384 + 0.149 * X; if outlier point is excluded, Y = 0.387 + 0.153 * X), as well as the identity line (thin dashed). (D) Histogram of SB ibi in trials without bouts (n = 1,693; mean value shown by red line). In the scatterplots, tempo and musical inter-beat-interval are related by the following equation: Musical tempo [bpm] = 60/Musical ibi (s). In the histograms, bin width is 33 ms (equal to 1 video frame at 30 frames per second), and values >=1 s have been excluded, as these indicate pauses in dancing.

tempi.[5] This temporal flexibility provides an important parallel to human BPS, and raises the question of whether other parallels exist between avian and human movement to music. One might expect further parallels if similar brain mechanisms subserve movement to music in birds and humans. Here we provide evidence for two further parallels, based on data gathered during our experimental study of a *Cacatua galerita eleonora* named "Snowball".[5] In that study, Snowball entrained his head bobs to the beat of music at 9 different tempi spanning 98–130 beats per minute [bpm]. Entrainment occurred in "synchronized bouts" (henceforth, "bouts"), episodes of synchrony embedded in longer stretches of rhythmic movement to music. Notably, bouts accounted for a minority of head bobs made to music. Across the entire experiment, bouts occurred in a subset of trials (58%), and in these trials, accounted

for about 25% of the head bobs on average. In fact, across all head bobs measured in the study (n = 3,999), only 14% were part of bouts.

The current paper focuses on the remaining 86% of head bobs, and asks if these show any systematic timing patterns. In particular, do they show any evidence of a preferred tempo, a rate of rhythmic movement toward which Snowball naturally gravitates while dancing? This question is motivated by research on young children.[8] Specifically, a study of 2–4 year old children dancing rhythmically to music found strong evidence for a preferred movement tempo. In that study, the tempo of a musical excerpt was varied across 4 rates, spanning 113 to 169 bpm. Despite this variation, younger children (2–3 y) tended to dance at a tempo of about 155 bpm. Older children (3–4 y) tended to dance a bit more slowly, around 145 bpm,

and showed a slight (but statistically non-significant) tendency to adjust movement tempo according to musical tempo. Hence when young children dance rhythmically to music, they tend to move at a preferred tempo which is not very sensitive to the musical tempo. Does Snowball, like young children, also have a preferred tempo when he is moving rhythmically to music but not synchronized to the beat?

Evidence for Preferred Tempo

To address this question, we examined all head bobs in our study which were not part of synchronized bouts. **Figure 1A** shows Snowball's mean inter-bob-interval (mean Snowball ibi) for all non-entrained head bobs in each of the 22 trials with bouts. Mean Snowball ibi is plotted as a function of the musical inter-beat-interval (music ibi, i.e., the temporal interval between musical beats as computed from the musical tempo: see **Fig. 1** caption for the equation relating tempo and Music ibi). As evident from the figure, there is a tendency for these non-entrained head bobs to slow down as the music slows down in tempo (i.e., as Music ibi increases). However, the regression relating Snowball ibi to Music ibi is only marginally significant (p = 0.08, r^2 = 0.14). If the outlying data point with Snowball ibi <0.4 s is excluded, the regression becomes significant (p < 0.01), but still explains only a modest amount of variance (r^2 = 0.35, see **Fig. 1** caption for regression equations). In other words, the rate of non-entrained head bobs is only moderately sensitive to musical tempo. **Figure 1B** suggests this could be due to a tendency for the timing of these head bobs to be dominated by a preferred tempo. This figure presents a histogram of all non-entrained Snowball ibi durations across the 22 trials with bouts. The distribution has a single clear peak, near the mean value of 0.480 s, corresponding to a tempo of 125 bpm.

Figure 1C and D extend these analyses to the 16 trials without bouts. **Figure 1C** shows mean Snowball ibi values as a function of Music ibi values during these trials. Once again, the regression line relating Snowball ibi to Music ibi is not significant (p = 0.20, r^2 = 0.11). If the outlying data point with Snowball ibi <0.4 s is excluded, the regression becomes significant (p <

0.04), but explains only a modest amount of variance ($r^2 = 0.29$, see **Fig. 1** caption for regression equations). Thus again, the rate of non-entrained head bobs is not very sensitive to musical tempo. The histogram in **Figure 1D** again suggests that this is due to a strong preferred tempo. This histogram has a peak near its mean value of 0.469 s, corresponding to a tempo of 127.9 bpm.

The mean values of the distributions in panels 1B and D are significantly different (two-tailed t-test, $t = 3.6593$, $p < 0.001$), yet are numerically close (in terms of tempo, only ~3 bpm apart). Thus overall, the data in **Figure 1** suggest that non-entrained head bobs to music cluster around 0.475 s in duration (=2.1 Hz), corresponding to a preferred tempo of 126.3 bpm. It would be interesting to know if this preferred tempo corresponds to a rhythm in the natural behavior of cockatoos, e.g., the rate of head bobs used in courtship displays.[9] (When seeking data on rates of natural rhythmic movements in nonhuman animals, one important factor to keep in mind is that such rates can change with age,[10] just as with humans.)[11]

Relationship of Preferred Tempo to Synchronization

What is the relationship of Snowball's preferred tempo to his synchronization abilities? Once again this question is motivated by research on young children. When children are asked to tap to the beat of music or to an external timekeeper (such as a metronome), their synchronization is most accurate when the auditory beat is near their "spontaneous motor tempo", the rate at which they naturally tap in the absence of an auditory stimulus (Jones MR, McAuley JD, unpublished data).[12,13] While we did not collect data on spontaneous motor tempo for Snowball, we can examine the relationship between his synchronization performance and preferred tempo.

Figure 2A shows Snowball's total dance time during each of the 11 different conditions/tempi in our original study (collapsing across all trials at a given tempo). **Figure 2B** shows for each tempo the percent of dance time during which Snowball was synchronized to the beat (i.e., percent of tim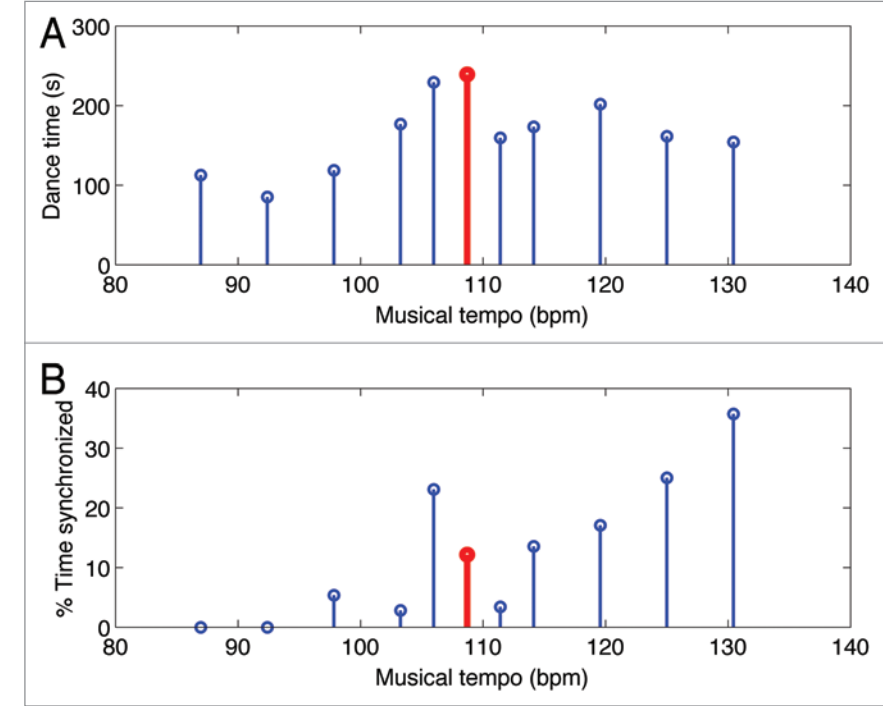e occupied by bouts). Using this latter measure as an index of synchronization performance, it is clear that synchronization is best at the two experimental tempi nearest Snowball's preferred tempo of 126.3 bpm.

This result is confirmed by a related analysis in **Table 1**, which shows the total number of head bobs measured at each tempo, and the percent of head bobs entrained to the beat at each tempo (i.e., percent of head bobs in bouts). Again, entrainment is best at the two tempi closest to Snowball's preferred tempo.

Notably, the two tempi with best synchronization are considerably faster than the song's original tempo of 108.7 bpm. Since the original version song was the most familiar to Snowball, these data suggest that preferred tempo overrides familiarity in terms of predicting synchronization performance.

Conclusions and Future Directions

The timing of avian rhythmic movement to music appears to have at least three components: (1) a strong preferred tempo, (2)

Figure 2. Snowball's synchronization performance at different tempi. (A) Total duration of dancing measured at each tempo (collapsed across all trials at a given tempo, and across entrained and non-entrained head bobs. Grand total dance time is 1,813 s, i.e., ~30 min.) (B) Percent of dance time at each tempo occupied by synchronized bouts, i.e., when head bobs were entrained to the musical beat. (Grand total synchronized time is 252.4 s, i.e., ~4 min) The thick red line at 108.7 bpm corresponds to the song's original tempo.

Table 1. Distribution of head bobs across trials at 11 different musical tempi

	Musical tempo [bpm]										
	87.0	**92.4**	**97.8**	**103.3**	**106.0**	**108.7**	**111.4**	**114.1**	**119.6**	**125.0**	**130.4**
Number of head bobs measured	243	184	244	406	460	518	383	397	455	358	351
% head bobs entrained to the beat	0	0	4.9	3.0	21.8	13.9	3.1	12.1	17.6	26.8	36.5

a modest tendency for this tempo to be modulated by musical tempo, and (3) occasional bouts of genuine synchronization to the musical beat, during which movements match the timing of beats in both period and phase. Patterns (1) and (2) are known from research on how young humans move to rhythmic music. It remains to be seen if pattern (3) is also characteristic of how young children move to music. If so, it may be possible to identify the human developmental stage to which avian dancing is most equivalent.

In light of the strong preferred tempo, which may represent a natural frequency of movement, a further question of interest is whether different types of rhythmic movements made while dancing to music have different preferred tempi (e.g., swaying the body from side to side on every other beat, foot lifting, etc.,) and, if so, whether these modes are differentially elicited by music at different tempi.

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