



This unedited manuscript has been submitted for publication in the Annals of the NYAS. This paper has not been copyedited.

Studying synchronization to a musical beat in nonhuman animals

| | |
|-------------------------------|---|
| Journal: | <i>Annals of the New York Academy of Sciences</i> |
| Manuscript ID: | annals-1453-008.R1 |
| Volume Title: | The Neurosciences and Music III: Disorders and Plasticity |
| Date Submitted by the Author: | 12-Feb-2009 |
| Complete List of Authors: | Patel, Aniruddh; The Neurosciences Institute, Theoretical Neurobiology Iversen, John; The Neurosciences Institute, Theoretical Neurobiology Bregman, Micah; UC San Diego, Cognitive Science Schulz, Irena; Bird Lovers Only Rescue Service, Inc., Research Dept. |
| Keywords: | rhythm, beat, synchronization, entrainment, nonhuman animals, birds, primates, music |
| | |



Patel, Iversen, Bregman & Schulz

1

Patel, A.D. *et al.*: Animal synchronization to music**Studying synchronization to a musical beat in nonhuman animals**Aniruddh D. Patel¹, John R. Iversen¹, Micah R. Bregman^{1,2} & Irena Schulz³¹The Neurosciences Institute²University of California, San Diego³Bird Lovers Only Rescue Service, Inc.

Corresponding author: Aniruddh D. Patel, The Neurosciences Institute, 10640 John Jay

Hopkins Dr., San Diego, CA 92121, USA. Tel: 858-626-2085, Fax: 858-626-2099.

apatel@nsi.edu

Keywords: Rhythm, beat, synchronization, entrainment, nonhuman animals, birds,
primates, musicIn press in *Annals of the New York Academy of Sciences*

February 12, 2009

Patel, Iversen, Bregman & Schulz

2

1
2
3 **Abstract:** The recent discovery of spontaneous synchronization to music in a nonhuman
4 animal (the sulphur-crested cockatoo *Cacatua galerita eleanora*) raises several questions.
5
6 How does this behavior differ from nonmusical synchronization abilities in other species,
7
8 such as synchronized frog calls or firefly flashes? What significance does the behavior
9
10 have for debates over the evolution of human music? What kinds of animals can
11
12 synchronize to musical rhythms, and what are the key methodological issues for research
13
14 in this area? This paper addresses these questions and proposes some refinements to the
15
16 “vocal learning and rhythmic synchronization hypothesis.”
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

INTRODUCTION

Music is often regarded as a uniquely human phenomenon.¹ Yet many components of music cognition may have deep roots in brain functions shared with other animals.² For example, the perception of certain pitch combinations as rough (e.g., two pitches separated by a semitone, such as C and C#) likely has its origins in auditory processing mechanisms shared with other species, as evidenced by research with nonhuman primates.³ Hence humans likely resemble other primates in hearing pitch roughness, though we may be the only primate that forms aesthetic preferences for consonant and dissonant musical intervals based on this percept.^{4,5,6}

The study of musically-relevant abilities in other species can address the evolutionary and neural foundations of human musical abilities. One such ability is beat perception and synchronization (BPS), defined as the ability to perceive a beat in music and synchronize bodily movement with it. BPS is a human universal: every known culture has some form of music with a periodic beat to which listeners synchronize their movements (e.g., in dance).^{7,8} This response to music is not commonly observed in other animals. Recently, there has been growing interest in finding out whether BPS is a uniquely human ability, possibly reflecting a biological adaptation for music-making.^{9,10,11}

Hence many researchers were intrigued by a 2007 video of a sulphur-crested cockatoo (*Cacatua galerita eleanora*) dancing to music. In this video, the bird (named “Snowball”) was apparently synchronizing his movements, including head bobs and foot steps, in clear relation to the musical beat. (The video can be seen by searching YouTube

Patel, Iversen, Bregman & Schulz

4

1
2
3 for “snowball dancing cockatoo”.) This was the first inkling to researchers that a
4
5 nonhuman animal could synchronize to music. Soon thereafter, we conducted a
6
7 controlled experiment with Snowball, involving suppression of human movement (to
8
9 avoid rhythmic cueing) and manipulation of musical tempo. We found that Snowball
10
11 exhibits genuine synchronization to a musical beat, and that he can synchronize at several
12
13 different musical tempi spanning a range from 106 to 130 beats per minute.¹² Due to the
14
15 popularity of Snowball’s dancing on the internet, many other pet owners have posted
16
17 videos of their parrots moving to music (in fact, the website BirdChannel.com recently
18
19 hosted the world’s first bird dance contest). Hence it appears that Snowball is not
20
21 unique,¹³ and that BPS is not the sole province of humans.
22
23
24
25
26

27 While Snowball demonstrates that humans and other animals are not separated by
28
29 a categorical divide when it comes to BPS, it should be noted that Snowball’s BPS ability
30
31 is not as well developed as that of a human adult. In particular, he shows a pattern of
32
33 “sporadic synchronization”. That is, even when Snowball danced rhythmically during an
34
35 entire experimental trial, there were limited periods when he showed genuine
36
37 synchronization to the beat. (He may resemble human children more than human adults
38
39 in this regard.)¹⁴ This is illustrated in Figure 1a, which shows the tempo of Snowball’s
40
41 rhythmic movements (head bobs) during one experimental trial (about 70 seconds, music
42
43 tempo = 106 BPM).
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

[Figure 1 here]

1
2
3 The inset box shows the time during which he showed a synchronized “bout” (a period of
4 sustained synchronization to the beat, see ref 12 for details). During this bout, his tempo
5 matched the music tempo and the timing of head bobs was very close to the timing of
6 musical beats (i.e., entrainment near zero phase, as seen in human movement to music).
7
8 As is clear from the figure, however, the synchronized bout accounts for only about 20%
9 of the entire trial. Across the trial Snowball shows substantial tempo drift. For example,
10 towards the end of the trial he drifted toward a tempo of about 130 BPM. (This was
11 frequently observed across trials, suggesting that he has a preferred tempo for rhythmic
12 movement, just as humans do.)¹⁵ As discussed in point 11 of the “Methodological
13 Issues” section of this paper below, statistical methods are needed to determine whether
14 the observed degree of synchrony is greater than one would expect by chance.
15
16
17
18
19
20
21
22
23
24
25
26
27
28

29 The details of our experimental study (first presented at *The Neurosciences and*
30 *Music III*, June 2008, Montreal) will appear in a forthcoming scientific article. Rather
31 than repeat those details here (some of which can be found in ref 12, available at
32 <http://www.nsi.edu/users/patel>, together with video examples), the current paper takes a
33 broader view and discusses four issues relevant to the study of BPS in other species. This
34 is a new topic in music cognition, involving (so far) studies of birds and bonobos.^{12,13,16}
35
36 First, what distinguishes musical BPS from synchronized rhythmic displays in other
37 species? Second, what significance does nonhuman BPS have for debates over the
38 evolutionary status of music? Third, how do current findings help refine the hypothesis
39 that BPS builds on the brain circuitry for complex vocal learning?¹⁷ Fourth, what are
40 some key methodological issues for research in this area? The following sections
41 consider these issues in turn.
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

BPS VERSUS SYNCHRONOUS ANIMAL DISPLAYS

At first glance, BPS may not seem that special. Many species are known to engage in rhythmic synchronized acoustic or visual displays. The synchronous flashing of certain firefly species is a well known example.^{18,19} Other examples include rhythmic chorusing in frogs and katydids.^{20,21} A closer examination of such displays, however, suggests that they differ from BPS in important ways (Table 1). First, BPS typically involves extracting a regular beat from a very complex signal (namely, music), rather than from simple pulse trains. Second, BPS involves substantial flexibility in movement tempo: humans adjust the rate of their rhythmic movements to synchronize to music across a wide range of tempi. Third, BPS is truly cross-modal, with an auditory stimulus driving the motor system in periodic behavior that it not (necessarily) aimed at sound production. To our knowledge, no natural animal displays have this combination of features. These differences between BPS and nonhuman animal displays argue against the view that synchronization to a musical beat is a minor variant of synchronization abilities of other species. Instead, BPS appears to be an unusual behavior in the animal kingdom, raising questions about its evolutionary origins and significance.

[Table 1 here]

THE EVOLUTIONARY SIGNIFICANCE OF BPS IN OTHER SPECIES

Patel, Iversen, Bregman & Schulz

7

1
2
3 There is currently an active debate whether human music is a product of biological
4 evolution, or an invention built on brain systems which evolved for other purposes.^{11,22,23}

5
6
7
8 BPS is important in this debate, because it is central to music cognition and is not an
9 obvious byproduct of other human cognitive abilities, such as language.¹⁵ Is BPS a
10 biological adaptation for music?^{24,25} This question can be addressed by comparative
11 research with other species. If other animals (whose brains have not been shaped by
12 natural selection for music) are capable of BPS, this would argue against the view that
13 BPS is an adaptation for music (see reference 17 for a fuller exposition of this argument).
14
15
16
17
18
19
20
21

22 In this light, the discovery of BPS in a sulphur-crested cockatoo is particularly
23 interesting. This species (native to the Australia/New Guinea region) is not known for
24 melodious vocalizations or for complex dancing in courtship displays. According to
25 Forshaw, the courtship display “is simple and brief. The male struts along a branch
26 towards the female. With crest raised he bobs his head up and down and swishes it from
27 side to side in a figure-eight movement, uttering soft, chattering notes all the while (p.
28 131).”²⁶ Of course, in species with complex, melodious songs²⁷ or elaborate courtship
29 dances,²⁸ one might argue that musically-relevant abilities have been shaped by natural
30 selection. In sulphur-crested cockatoos, however, such arguments seem unlikely to apply,
31 making it plausible that that BPS is a byproduct of some non-musically-relevant ability.
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

51 Before turning to that section, however, it is worth discussing the evolutionary
52 relationship between avian and human BPS. At one level, the relationship appears to be
53 one of convergence, i.e., the historically independent evolution of a trait in distinct
54
55
56
57
58
59
60

Patel, Iversen, Bregman & Schulz

8

1
2
3 lineages of organisms. However, if the vocal learning hypothesis is correct, and if vocal
4
5 learning circuitry in birds and humans has common neural foundations (as argued in
6
7 reference 29), then BPS in the two species could share underlying biological mechanisms.
8
9 In other words, BPS in birds and humans could be an instance of “deep homology”,³⁰
10
11 which would imply that neurobiological studies of BPS in birds could shed light on
12
13 mechanisms of BPS in humans. The practical significance of this possibility is discussed
14
15 in the final section of the paper.
16
17
18
19
20
21

22 **REFINEMENTS TO THE “VOCAL LEARNING AND RHYTHMIC** 23 24 **SYNCHRONIZATION HYPOTHESIS”** 25 26 27 28

29 Patel¹⁷ proposed that BPS builds on the brain circuitry for complex vocal learning, i.e.,
30
31 learning to produce complex acoustic communication signals based on imitation. This
32
33 “vocal learning and rhythmic synchronization” hypothesis was motivated by three
34
35 observations. First BPS involves a special auditory-motor interface in the nervous
36
37 system, as evidenced by the fact that people synchronize much more poorly to the beat of
38
39 complex visual vs. auditory rhythms matched in temporal structure.³¹ Vocal learning
40
41 creates a tight auditory-motor interface in the brain, since it involves integrating auditory
42
43 perception with rapid and complex vocal gestures. Second, vocal learning in birds
44
45 involves modifications to brain regions (such as the basal ganglia³⁴) which are also likely
46
47 to be involved in vocal learning in humans, based on comparative neuroanatomical
48
49 research.²⁹ Third, neuroimaging research suggests that some of these same regions are
50
51 involved in human beat perception in music (see reference 15 for details).³³
52
53
54
55
56
57
58
59
60

1
2
3 A testable prediction of the vocal learning hypothesis is that only vocal-learning
4 species are capable of BPS. (Notably, humans are unique among primates in having
5 complex vocal learning, an evolutionarily rare trait shared by only a few groups of
6 animals, including humans, parrots, songbirds, hummingbirds, dolphins, seals and some
7 whales.)^{34,35} Some provisional support for this hypothesis has been provided by
8 Schachner et al.,¹³ who surveyed numerous videos of animals moving to music (on
9 YouTube) and found that all species which appeared to move in synchrony with the
10 musical beat (n=28) were vocal learners. (This finding naturally calls for replication
11 using controlled experiments to rule out imitation of rhythmic movements by humans.)
12
13
14
15
16
17
18
19
20
21
22
23

24 As originally stated, the vocal learning hypothesis claimed that vocal learning is a
25 necessary foundation for BPS. However, vocal learning may not be the only necessary
26 foundation. Parrots share more than just vocal learning with humans. Table 2 lists some
27 traits shared by these species.
28
29
30
31
32
33
34
35

36 [Table 2 here]
37
38
39
40

41 At this point, it is not clear what traits in Table 2 might be necessary foundations for BPS.
42
43 The vocal learning hypothesis states that complex vocal learning is a necessary
44 foundation, and hence predicts that chimps and bonobos (who share only the third and
45 fourth traits in the table with humans) are incapable of BPS. However, it may be that
46 complex vocal learning is not enough, and that open-ended vocal learning (and its
47 concomitant brain substrates) is also necessary. Only comparative work with other
48 species can resolve this question. For example, starlings have open-ended vocal
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 learning,⁴⁰ and are thus a logical choice for testing an open-ended vocal learning
4
5 hypothesis for BPS. If Starlings are not capable of BPS, however, then it may be that
6
7 open-ended vocal learning **and** non-vocal movement imitation are necessary foundations
8
9 for BPS, a hypothesis that could be tested with dolphins (who share all traits in Table 2
10
11 with humans).
12
13

14
15 Stepping back, the fundamental question that needs to be addressed by
16
17 comparative research is “What kinds of brains are capable of BPS?”. If the mechanisms
18
19 of BPS are similar across different species, then such work can help identify the
20
21 evolutionary foundations of BPS in humans.
22
23

24 25 26 27 **STUDYING BPS IN OTHER SPECIES: ELEVEN METHODOLOGICAL ISSUES** 28

29
30
31 Since the study of nonhuman animal (henceforth, “animal”) synchronization to music is a
32
33 new research area, it is worth discussing a number of methodological issues relevant for
34
35 those planning to conduct (or evaluate) research in this area.
36
37

38 39 40 41 *1. What are the criteria for synchronization?* 42

43
44
45 BPS in human adults involves rhythmic movements (such as finger or foot taps) that
46
47 match the musical beat in both tempo and phase.⁴¹ These two criteria are conceptually
48
49 distinct. Tempo matching means that the period of movement matches the musical beat
50
51 period, without regard to relative phase between movements and beats (for example, taps
52
53 might be in antiphase with the beat, clustered around a time point midway between beats).
54
55
56
57
58
59
60

1
2
3 Phase matching means that rhythmic movements occur near the onset times of musical
4 beats (zero phase). Hence when testing for BPS it is important to specify whether one is
5 testing only for tempo matching, or for both tempo and phase matching. Different
6 statistical tests are required in the two cases. One test (based on circular statistics) which
7 is sensitive to both tempo and phase matching is the Rayleigh test for a specified mean
8 direction (see equation 4.15 on p. 69 of reference 42).
9
10
11
12
13
14
15
16
17
18
19

20 ***2. How complex is the stimulus?***

21
22
23
24 As noted previously, synchronization to pulse trains is seen in numerous species (e.g.,
25 fireflies and frogs). BPS, in contrast, typically involves extracting a regular beat from
26 signals rich in rhythmic and/or melodic complexity (e.g., real music). Hence
27 demonstration of animal synchronization with metronome-like stimuli, while interesting,
28 is not a strong demonstration of BPS (cf. Table 1).
29
30
31
32
33
34
35

36 Conversely, if an animal demonstrates BPS there is no guarantee that the same
37 animal would synchronize with metronome-like stimuli. While the ability to synchronize
38 to simple pulse trains is implied by BPS, such behavior may not be easy to elicit if the
39 pulse trains do not sustain the animal's interest or attention.
40
41
42
43
44
45
46
47

48 ***3. How flexible is the tempo of the animal's rhythmic movements?***

49
50
51
52
53 A key feature of BPS is tempo flexibility. Humans adjust the tempo of their rhythmic
54 movements (e.g., foot taps) to synchronize with music across a wide range of tempi.
55
56
57
58
59
60

Patel, Iversen, Bregman & Schulz

12

Hence if an animal synchronizes its movements to a musical beat, it is important to establish whether it can adjust its tempo to synchronize with music at different tempi.

The use of different tempi also rules out coincidental matches between the musical tempo and the animal's natural frequency of movement.

4. What modality is the response?

Very often, human BPS often involves movements which are not aimed at sound production. For example, head bobbing, finger tapping, and dancing are not usually aimed at making sound. Thus if an animal synchronizes movements to music, it is important to ask if this is only done in the context of making sound (e.g., striking a drum or some other musical instrument), or if it is a purely motor response. If synchronization is only accomplished while making sound, this could point to synchronization mechanisms based on joint action (e.g., "chorusing")²⁴, which may differ somewhat from mechanisms involved in silent rhythmic responses to sound.

5. How well were visual rhythmic cues controlled?

Humans tend to move to music, and can thus inadvertently give rhythmic cues to the beat to animals (e.g., via head bobs). This is a particular concern in studies of parrots and chimps/bonobos, who are capable of imitating non-vocal movements.³⁸ Studies which seek to demonstrate BPS in animals need to eliminate possible visual rhythmic cues from humans involved in the experiments. This can be done via verbal instructions to humans

1
2
3 (e.g., to avoid head bobbing). Even better is having video footage of any humans in the
4 room during experimental trials, so that human movements can be checked for possible
5 subtle rhythmic cues. The best control, of course, is to have no humans in the room. For
6 example, humans could be outside the room giving verbal encouragement over speakers,
7 but while listening to masking stimuli so that verbal cues are not in time with the music.
8 (The absence of a human in the room, however, may influence the animal's motivation to
9 dance.)
10
11
12
13
14
15
16
17
18
19
20
21

22 ***6. Can the animal synchronize to novel music?***

23
24
25
26
27 Humans easily synchronize to the beat of novel music. If an animals' synchronization to
28 music is strongly stimulus-bound (e.g., only observed to a particular piece of music), this
29 would point to an important difference between animal synchronization and human BPS.
30
31 Our experimental study of Snowball employed just one piece of music (presented at
32 several distinct tempi). We have informal observations of his dancing to a variety of
33 other pieces (without human movement cues), which suggests that his synchronization
34 abilities are not stimulus-bound, though formal analysis is needed to demonstrate this
35 point.
36
37
38
39
40
41
42
43
44
45
46
47

48 ***7. How much training was required?***

49
50
51
52
53 BPS emerges relatively spontaneously in humans. Children's early experiences in being
54 bounced rhythmically to music,⁴³ observing others moving to the beat of music, and
55
56
57
58
59
60

Patel, Iversen, Bregman & Schulz

14

1
2
3 being socially rewarded for their own dancing may play a role in the development of BPS,
4
5 but it is clear that human BPS develops without elaborate, explicit instruction (unlike, say,
6
7 reading and writing). Thus in studying BPS in animals, it is important to document how
8
9 the behavior emerged. What role did modeling and reward play? Was an extensive
10
11 training period required, or did it emerge more spontaneously? In this regard, it should
12
13 be noted that if an animal does not demonstrate spontaneous BPS, this may reflect a lack
14
15 of interest or attention rather than a lack of ability. Studies which aim to discover whether
16
17 an animal is capable of BPS need to take motivational factors into account.
18
19
20
21

22 We know relatively little about the development of Snowball's dancing abilities.
23
24 His previous owner acquired him at a bird show when Snowball was 6, and mentioned
25
26 that soon thereafter he noticed Snowball bobbing his head to rock music (the owner felt
27
28 that this was not done in imitation of human movement). Subsequently, the owner and
29
30 his children began to encourage Snowball's dancing, partly by making rhythmic arm
31
32 gestures to the beat of the music. Snowball quickly developed his own rhythmic foot-
33
34 lifting behavior, perhaps in imitation of the human arm gestures. Hence from the age of 6
35
36 onward, his dancing behavior was socially reinforced but was not a target of deliberate
37
38 training (e.g, using food rewards).
39
40
41
42
43
44
45

46 ***8. Is the synchronization mutual or one-way?***

47
48
49

50 In recent research on bonobo synchronization to music, an interactive approach was used
51
52 in which human and bonobo played rhythmic chords on separate keyboards at the same
53
54 time, usually out of view of each other.¹⁶ During periods when both participants played
55
56
57
58
59
60

1
2
3 at stable tempi the degree of synchrony between human and bonobo was quantified. In
4
5 this “mutual synchrony” approach, an important question concerns to what extent such
6
7 synchrony reflects the human adapting to the animal’s timing, rather than vice-versa.
8
9 This is a particularly salient issue because humans have been shown to adjust the phase
10
11 of their rhythmic tapping in response to changes in the timing of an external pacing
12
13 stimulus, without their own awareness.⁴⁴ Hence when studying mutual synchronization
14
15 between human and animal, statistical methods are needed to tease apart the degree to
16
17 which entrainment reflects human (rather than animal) synchronization. Notably, human
18
19 BPS need not be interactive: humans are quite capable of synchronizing to music in a
20
21 “one-way” fashion in which the human responds to the music but not vice versa (e.g.,
22
23 when dancing to recorded music). Hence an important question for animal BPS studies is
24
25 whether the animal being studied is capable of one-way synchronization.
26
27
28
29
30
31

32 Of course, this is not to say that the role of interaction and social cues should be
33
34 neglected in research on animal BPS. On the contrary, there are good reasons to study
35
36 these issues. For example, it has recently been demonstrated that young children are
37
38 better at synchronizing to a steady beat in a social vs. nonsocial context.⁴⁵ This naturally
39
40 raises the question of whether the same is true for animals. This can be addressed, for
41
42 example, by measuring whether an animal synchronizes with music better when moving
43
44 jointly with a human than when moving alone.
45
46
47
48
49
50

51 ***9. What is the relationship to the animal’s natural display behavior?***
52
53
54
55
56
57
58
59
60

1
2
3 Many animals make rhythmic movements as part of ritualized displays. Chimps perform
4
5 brief bouts of drumming on the buttresses of trees,⁴⁶ and a number of bird species
6
7 perform elaborate “dances” as part of displays aimed at conspecifics.²⁸ Hence when
8
9 studying animal BPS, a question of interest concerns the relationship of the observed
10
11 rhythmic movements to natural display movements. Specifically, does BPS involve
12
13 adapting an existing display behavior, or does it represent a novel movement sequence
14
15 not seen in the animal’s natural display repertoire? If an animal exhibits BPS using a
16
17 movement adapted from a natural display (and is incapable of learning to synchronize
18
19 using other types of movements), this would indicate a lower degree of flexibility than
20
21 human BPS, since humans can synchronize to music using a variety of movements and
22
23 body parts (e.g., head bobbing, foot tapping, side-to-side swaying, etc.).
24
25
26
27
28
29
30
31

32 ***10. Are there hierarchical levels of rhythmic movement?***

33
34
35
36 Much music has a hierarchical rhythmic structure, whereby there are not only regular
37
38 beats, but also regular patterns of accentuation among beats which create a metrical
39
40 hierarchy.⁴⁷ For example, in a march every second beat is accented. Human movements
41
42 associated with BPS shows evidence of sensitivity to such structure.³¹ If an animal
43
44 exhibits BPS, it is of interest to know if the rhythmic movements mark only one level of
45
46 the metrical hierarchy, or if there is evidence for sensitivity to multiple levels.
47
48
49

50
51 Snowball’s dancing is notable in this regard because he sometimes moves his
52
53 head from side to side on every other beat, while simultaneously bobbing his head with
54
55 each beat (note that these side-to-side movements are distinct from the figure-eight head
56
57
58
59
60

1
2
3 movements which are part of courtship displays). This suggests sensitivity to the
4
5 hierarchical rhythmic structure of beats in music, though further work is needed to
6
7 determine whether the side-to-side movements have any systematic relationship to the
8
9 metrical structure (e.g., if they tend to mark out beats 1 and 3 in each measure of a 4/4
10
11 time song, as these are the stronger beats in the measure).
12
13

14 15 16 17 18 *11. Could it have happened by chance?* 19

20
21
22 A key issue for animal studies of BPS is whether the observed synchronization is merely
23
24 a coincidence. This question is particularly important when synchronization to music is
25
26 transient, as in our study of Snowball (cf. Figure 1a). Statistical methods are needed to
27
28 estimate the probability that occasional synchronized episodes could have happened by
29
30 chance. That is, one must consider the null hypothesis that the animal moves
31
32 rhythmically in response to music, and that due to natural variability in movement tempo
33
34 there are periods when (by pure chance) the movements have a consistent relationship to
35
36 the beat. Our methods for dealing with this problem are discussed in detail in our
37
38 forthcoming scientific article on Snowball. For the moment, we discuss one seemingly
39
40 intuitive way of dealing with the problem.
41
42
43
44

45
46 This is the approach of scrambling the order of the temporal intervals between
47
48 rhythmic gestures (e.g., head bobs) within a trial, and then recomputing synchronization
49
50 measures. If this is done repeatedly (e.g., 1,000 times), one can compute the probability
51
52 of observing the actual degree of synchronization (e.g., in the case of Figure 1a, how
53
54
55
56
57
58
59
60

1
2
3 often does one observe a synchronized bout lasting 20% or more of the trial?). At first
4
5 glance, this Monte Carlo approach seems attractive for its conceptual simplicity.
6
7

8 Figures 1b-c, however, indicate why this approach is unsatisfactory. Figure 1b
9
10 shows the inter-bob-intervals corresponding to the tempo curve in Figure 1a (that is,
11
12 Figure 1b re-represents the data in Figure 1a in a more conventional way for rhythm
13
14 studies, namely as time intervals between successive rhythmic gestures). Randomly
15
16 scrambling these time intervals and converting them back to a tempo curve produces the
17
18 time series in Figure 1c. As can be seen, the resulting curve has a very different
19
20 structure from the curve in Figure 1a. Specifically, the original curve shows fast local
21
22 tempo fluctuations superimposed on a slower pattern of tempo drift. The curve produced
23
24 from scrambled data, in contrast, lacks the slow tempo drift and is thus not representative
25
26 of how the animal actually moves. Hence doing synchronization tests on scrambled data
27
28 is not a fair test of the null hypothesis mentioned above.
29
30
31
32
33

34 Stepping back from these details, the important point is that to test the null
35
36 hypothesis of no true synchronization to music, one must use data that statistically
37
38 resembles the movement pattern produced by the animal under study. Using simulated
39
40 data that is unlike actual animal movement patterns (e.g., Figure 1c) is not adequate for
41
42 testing the null hypothesis of no true synchronization to a musical beat.
43
44
45
46
47

48 **BROADER SIGNIFICANCE**

49
50
51
52

53 As the study of animal synchronization to music gets underway, it is worth asking what
54
55 broader significance such research has for human concerns. Apart from addressing
56
57
58
59
60

1
2
3 debates over the evolution of music (as outlined in this paper), such research has potential
4
5 practical significance. This is because BPS has a powerful impact on the human motor
6
7 system, as documented by music therapy researchers. For example, some patients with
8
9 Parkinson's disease can become "unfrozen" and able to walk when they synchronize their
10
11 movements with a musical beat.^{48,49} The mechanisms behind this effect are in need of
12
13 further investigation.
14
15

16
17 Other species have simpler brains than we do. If it can be shown that nonhuman
18
19 animals move to music in much the same way that humans do, and if this movement is
20
21 based on similar brain mechanisms as in humans, this would open the way to
22
23 comparative neural studies of the biological foundations of BPS. That is, having an
24
25 animal model of BPS would give scientists a new approach to studying synchronization
26
27 to music and its power to alleviate human movement disorders.
28
29
30
31
32
33

34 **ACKNOWLEDGMENTS**

35
36
37
38 We thank Tecumseh Fitch, Sebastian Kirschner, Bruno Repp, Katie Overy, and Guiliano
39
40 Avanzini for insightful comments on this paper, and Simon Conway Morris and Michael
41
42 Greenfield for helpful discussions. Supported by Neurosciences Research Foundation as
43
44 part of its program on music and the brain at The Neurosciences Institute, where ADP is
45
46 the Esther J. Burnham Senior Fellow.
47
48
49
50

51 **REFERENCES**

Patel, Iversen, Bregman & Schulz

20

- 1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
1. Hauser, M. D. & J. McDermott. 2003. The evolution of the music faculty: A comparative perspective. *Nat. Neurosci.* 6: 663–668.
2. Fitch, W. T. 2006. The biology and evolution of music: A comparative perspective. *Cognition* 100: 173–215.
3. Fishman, Y.I, D.H. Reser, J.C. Arezzo & M. Steinschneider. 2000. Complex tone processing in primary auditory cortex of the awake monkey. I. Neural ensemble correlates of roughness. *J. Acoust. Soc. Am.* 108: 235-246.
4. McDermott, J., & M. Hauser. 2004. Are consonant intervals music to their ears? Spontaneous acoustic preferences in a nonhuman primate. *Cognition* 94: B11–B21.
5. Trainor, L. J., C.D. Tsang & V.W.H. Cheung, V. H. W. 2002. Preference for consonance in 2-month-old infants. *Music Percept.* 20: 185–192.
6. Vassilakis, P. 2005. Auditory roughness as means of musical expression. *Selected Reports in Ethnomusicology* 12: 119–144.
7. Nettl, B. 2000. An ethnomusicologist contemplates universals in musical sound and musical culture. *In The Origins of Music.* N. L. Wallin, B. Merker & S. Brown, Eds.: 463–472. MIT Press. Cambridge, MA.

Patel, Iversen, Bregman & Schulz

21

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

8. McNeill, W.H. 1995. Keeping Together in Time: Dance and Drill in Human History. Harvard Univ. Press. Cambridge, MA.

9. Fitch, W.T. In press. The biology and evolution of rhythm: Unraveling a paradox. *In* Language and Music as Cognitive Systems. P. Rebuschat et al., Eds. Oxford Univ. Press. Oxford.

10. Cross, I. & G.E. Woodruff. In press. Music as a communicative medium. *In* R. Botha & C. Knight, Eds. The Prehistory of Language. Oxford Univ. Press. Oxford.

11. Patel, A.D. 2008. Music, Language, and the Brain. Oxford Univ. Press. New York.

12. Patel, A.D., J.R. Iversen, M.R. Bregman, I. Schulz & C. Schulz. 2008. Investigating the human-specificity of synchronization to music. *In* Proceedings of the 10th International Conference on Music Perception & Cognition (ICMPC10). K. Miyazaki et al., Eds.: 100-104. Causal Productions. Adelaide.

13. Schachner, A., T.F. Brady, I. Pepperberg & M. Hauser. 2008. Spontaneous entrainment to auditory rhythms in vocal-learning bird species. Presented at The Neurosciences and Music III. Montreal, Canada, June 26.

14. Eerola, T., G. Luck & P. Toiviainen. 2006. An investigation of pre-schoolers' corporeal synchronization with music. *In* Proceedings of the 9th International Conference

Patel, Iversen, Bregman & Schulz

22

on Music Perception & Cognition (ICMPC9). M. Baroni, A. R. Addessi, R. Caterina & M. Costa, Eds.: 472-476. ICMPC and ESCOM. Bologna, Italy.

15. McAuley, J. D., M. R. Jones, S. Holub, H. M. Johnston, & N. S. Miller. 2006. The time of our lives: Lifespan development of timing and event tracking. *Journal of Experimental Psychology: General* 135: 348-367.

16. Large, E.W., M.J. Velasco & P.M. Gray. 2008. Rhythmic analysis of musical interactions between bonobo and human. Presented at 10th International Conference on Music Perception & Cognition (ICMPC10). Sapporo, Japan, August 26.

17. Patel, A.D. 2006. Musical rhythm, linguistic rhythm, and human evolution. *Music Percept.* 24: 99-104.

18. Buck, J. 1988. Synchronous rhythmic flashing in fireflies. II. *Quarterly Review of Biology* 63: 265-289.

19. Strogatz, S. 2003. *Sync: The Emerging Science of Spontaneous Order*. Hyperion. New York.

20. Gerhardt, H. C. & F. Huber. 2002. *Acoustic Communication in Insects and Anurans*. University of Chicago Press. Chicago.

Patel, Iversen, Bregman & Schulz

23

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

21. Greenfield, M.D. & J. Schul. 2008. Mechanisms and evolution of synchronous chorusing: Emergent properties and adaptive functions in *Neoconocephalus* katydids (Orthoptera: Tettigoniidae). *J. Comp. Psychol.* 122: 289–297.

22. Wallin, N. L., B. Merker & S. Brown, Eds. 2000. *The Origins of Music*. MIT Press. Cambridge, MA.

23. Pinker, S. 1997. *How the Mind Works*. Allen Lane. London.

24. Merker, B. 2000. Synchronous chorusing and human origins. *In The Origins of Music*. N. L. Wallin, B. Merker & S. Brown, Eds.: 315-327. MIT Press. Cambridge, MA.

25. Bispham, J. 2006. Rhythm in music: What is it? Who has it? And why? *Music Percept.* 24: 125-134.

26. Forshaw, J.M. 1978. *Parrots of the World*. T. F. H. Publications. Neptune, N. J.

27. Kroodsma, D. 2005. *The Singing Life of Birds : The Art and Science of Listening to Birdsong*. Houghton Mifflin. New York.

28. Armstrong, E.A. 1965. *Bird Display and Behavior*. Dover Publications. New York.

Patel, Iversen, Bregman & Schulz

24

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

29. Jarvis, E. D. (2004). Learned birdsong and the neurobiology of human language.

Annals of the New York Academy of Sciences 1016: 749–777.

30. Shubin, N., C. Tabin & S. B. Carroll. 1997. Fossils, genes and the evolution of animal limbs. *Nature* 388: 639-648.

31. Patel, A.D., J.R. Iversen, Y. Chen & B.H. Repp. 2005. The influence of metricality and modality on synchronization with a beat. *Experimental Brain Research* 163: 226-238.

32. Doupe, A. J., D. J. Perkel, A. Reiner & E.A. Stern. (2005). Birdbrains could teach basal ganglia research a new song. *Trends in Neurosciences* 28: 353–363.

33. Grahn, J. A. & M. Brett. 2007. Rhythm and beat perception in motor areas of the brain. *Journal of Cognitive Neuroscience* 19: 893–906.

34. Janik, V.M., & P. B. Slater. 1997. Vocal learning in mammals. *Advances in the Study of Behavior* 26: 59-99.

35. Fitch, W. T. 2000. The evolution of speech: A comparative review. *Trends in Cognitive Sciences* 4: 258-267.

36. Egnor, S. E. R. & M.D. Hauser. 2004. A paradox in the evolution of primate vocal learning. *Trends in Neurosciences* 27: 649–654.

- 1
2
3
4
5
6 37. Nottebohm, F. 1975. A zoologists's view of some language phenomena with
7
8 particular emphasis on vocal learning. *In* Foundations of language development : a
9
10 multidisciplinary approach, Vol. 1. E. H. Lenneberg & E. Lenneberg, Eds.: 61-103.
11
12 Academic Press. New York.
13
14
15
16
17
18 38. Moore, B.R. 1992. Avian movement imitation and a new form of mimicry: Tracing
19
20 the evolution of a complex form of learning. *Behaviour* 122: 231-263.
21
22
23
24
25 39. Emery, N.J. 2006. Cognitive ornithology: The evolution of avian intelligence. *Philos.*
26
27 *Trans. R. Soc. Lond. B.* 361: 23–43
28
29
30
31
32 40. Schmidt, I. 1995. Song sharing reflects the social organization in a captive group of
33
34 European starlings (*Sturnus vulgaris*). *Journal of Comparative Psychology* 109: 222–241.
35
36
37
38
39 41. Toiviainen, P., & J.S. Snyder. 2003. Tapping to Bach: Resonance-based modeling of
40
41 pulse. *Music Perception* 21: 43–80.
42
43
44
45
46 42. Fisher, N. I. 1983. *Statistical Analysis of Circular Data*. Cambridge University Press.
47
48 Cambridge.
49
50
51
52
53 43. Phillips-Silver, J. & L.J. Trainor. 2005. Feeling the beat in music: Movement
54
55 influences rhythm perception in infants. *Science* 308: 1430.
56
57
58
59
60

- 1
2
3
4
5
6 44. Repp, B. H. & P.E. Keller. 2005. Adaptation to tempo changes in sensorimotor
7
8 synchronization: Effects of intention, attention, and awareness. Quarterly Journal of
9
10 Experimental Psychology A 57: 499–521.
11
12
13
14
15 45. Kirschner, S. & M. Tomasello. In press. Joint drumming: Social context facilitates
16
17 synchronization in preschool children. J. Exp. Child Psychol.
18
19
20
21
22 46. Arcadi, A. C., D. Robert & C. Boesch. 1998. Buttress drumming by wild
23
24 chimpanzees: Temporal patterning, phrase integration into loud calls, and preliminary
25
26 evidence for individual distinctiveness. Primates 39: 503–516.
27
28
29
30
31
32 47. Lerdahl, F., & R. Jackendoff. 1983. A Generative Theory of Tonal Music. MIT Press.
33
34 Cambridge, MA.
35
36
37
38
39 48. Thaut, M. 2005. Rhythm, Music, and the Brain: Scientific Foundations and Clinical
40
41 Applications. Routledge. London.
42
43
44
45
46 49. Sacks, O. 2007. Musicophilia. Knopf. New York.
47
48
49
50
51
52
53
54
55
56
57
58
59
60

FIGURE CAPTION

Figure 1. Time series illustrating real (a,b) and time-scrambled (c) measurements of the timing of Snowball's rhythmic movements during one experimental trial in which the musical tempo was 106 beats per minute (BPM). Temporal measurement of rhythmic movements was based on head bobs (see reference 12 for details). Panel (a) shows Snowball's instantaneous dance tempo in BPM, while panel (b) shows the same data converted into temporal intervals between head bobs (musical tempo in all graphs is indicated by the thin grey horizontal line). In panels (a) and (b) the inset shaded box indicates a synchronized bout. Panel (c) shows a tempo curve generated by randomly scrambling the time points in panel (a). Note the lack of slow drift in (c), compared to (a).

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

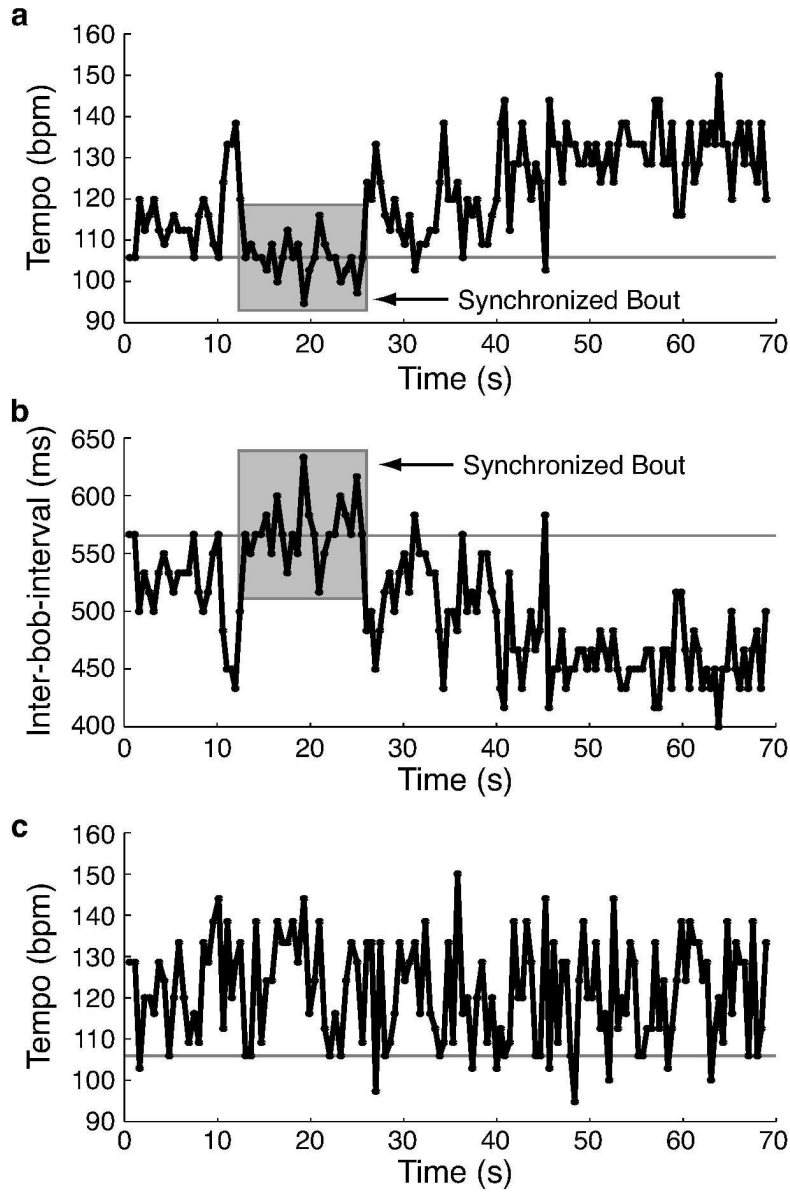
TABLES

Table 1: General features of pulse-based synchronization vs. BPS (beat perception and synchronization)

| | Pulse-based synchronization | BPS (Beat perception and synchronization) |
|--|---|---|
| Stimulus complexity | Low Metronome-like pulse trains | High Rhythmically and / or melodically complex signals |
| Tempo flexibility | Narrow Limited tempo range of rhythmic actions | Wide Broad tempo range of rhythmic actions |
| Response modality (compared to input) | Same e.g., flashing in response to rhythmic flashes | Different e.g., silent rhythmic movement in response to sound |

Table 2: Traits shared by parrots and humans

| Trait | Comment |
|---------------------------------|---|
| Complex vocal learning | A rare ability in the animal kingdom, ³⁵ and unique to humans among primates. ³⁶ |
| Open-ended vocal learning | The ability to acquire complex new sound patterns throughout life. Some songbirds can also do this (e.g., Starlings), but many cannot. ^{27,37} |
| Non-vocal movement imitation | Convincing evidence for this ability is rare in other species, and has been provided for parrots, chimps, and dolphins. ³⁸ |
| Living in complex social groups | A trait that may have consequences for brain size and organization. ³⁹ |



103x159mm (600 x 600 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60