

## The origins of human and avian auditory-motor entrainment

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## Abstract

Recent findings suggest that the capacity to entrain, or move in time with an auditory pulse, may have evolved as a byproduct of our capacity for vocal imitation rather than being selected for directly. However, recent work in social psychology has shown that synchronization of movement may promote prosocial behavior. This has been used to argue that entrainment, which increases the likelihood of synchrony, is adaptive and was subject to direct natural selection. In this chapter, I review the evidence that entrainment emerged as a byproduct of vocal imitation, and argue that this account is not in conflict with suggestions that synchrony may be adaptive. In particular, I propose a distinction between the capacity to entrain, an ability shared with avian species; and the innate motivation and tendency to entrain, which is present in humans but which avian species may lack. In line with this distinction, I propose that human entrainment may have evolved in at least two stages: First, the capacity to entrain arose as a byproduct of selection for vocal mimicry; secondly, the motivation to engage in entrained behavior was selected for directly, thus increasing levels of synchrony and prosocial behavior in the population.

Dance is a universal human behavior, appearing in cultures around the world (Nettl, 1983). Dance is also ancient: Depictions of dance in cave art date back at least 9,000 years (Chakravarty and Bednarik, 1997), and musical instruments such as bone flutes can be dated back to at least 40,000 years (Conard et al., 2009). Altogether, the data strongly suggest that dance is not merely a recent cultural invention, but an innate and fundamental part of the human behavioral repertoire.

If our capacity for dance is innate, this raises the question of how the human capacity for dance evolved. This question is complex, since dance is not a monolithic capacity: it involves a large set of highly distributed cognitive mechanisms, each of which may have independent evolutionary origins (Brown et al., 2006). As such, it is necessary to investigate the origins of each component of dance separately.

In our work, we have focused on one core component of dance: the capacity for auditory-motor entrainment (henceforth entrainment). Humans around the world can entrain, or align their motor actions with an external auditory pulse (colloquially, ‘move to a beat’) (Clayton et al., 2005). We not only have this capacity, but widely express it: humans often choose to or spontaneously begin to entrain to rhythmic and periodic sounds. When more than one person hears the same stimuli, this tendency to entrain often leads to synchrony, in which more than one person moves in the same way at the same time.

In the current chapter, we address two key questions: Firstly, why *can* we entrain? How did our capacity for keeping a beat emerge? We will discuss recent data suggesting that this capacity may have emerged as a byproduct of selection for another capacity, namely vocal imitation. Secondly, why do we *tend* to entrain? I will propose that after

the necessarily mechanisms for entrainment were in place, subsequent selection may have favored those individuals with a tendency and motivation to entrain, due to the adaptive consequences of synchronization.

### **The evolution of the capacity for entrainment**

How did the human capacity for entrainment evolve? In recent work, my colleagues and I turned to cross-species comparative methods to address this question (Schachner et al., 2009). Our initial question was: Does any other species of animal engage in human-like auditory-motor entrainment?

Many species engage in synchronized behavior, or other behavior with interdependent timing, such as synchronous chorusing (e.g. Klump and Gerhardt, 1992) the claw-waving display of crabs (Backwell et al., 1998), synchronized flashing displays in fireflies (Buck, 1988), and trained synchronization to specific stimuli in rhesus macaques (Zarco et al., 2009). However, all of the aforementioned behaviors differ from human auditory-motor entrainment behavior in critical ways (detailed below). These different behavioral signatures suggest that these behaviors do not depend on analogous neural mechanisms to those used in human entrainment. Because we were interested in the evolution of the particular type of neural mechanism used for human auditory-motor entrainment, these more distantly related behaviors were not of immediate interest in the current work.

In contrast, if we find behavior in other species that features the specific behavioral signatures of human entrainment, this would suggest that both species' entrainment behaviors rely on a similar type of cognitive mechanism. Evidence of

analogous mechanisms in species closely related to humans would suggest that this capacity was inherited from a common ancestor. Conversely, evidence of analogous mechanisms in phylogenetically distant species would suggest a process of convergent evolution, in which similar evolutionary pressures led similar mechanisms to evolve independently in two lineages.

### **Characteristics of human entrainment**

Many of the features of entrainment serve to distinguish the human capacity for entrainment from the synchronized displays of other animals. These features serve as the defining characteristics of human auditory-motor entrainment.

Firstly, entrainment requires temporal prediction, not simple reaction to auditory stimuli. For example, when tapping in time with a metronome, human subjects tap slightly *before* the onset of each auditory stimulus (Aschersleben, 2002). Thus, during entrainment we form a cognitive representation of the time intervals between beats, and use this representation to predict the onset time of each subsequent beat (Repp, 2005).

Secondly, entrainment involves real-time monitoring of auditory input, and constant error correction of movements to match. Even if an individual begins moving to a beat accurately, without constant error correction the accumulation of motor and cognitive error would quickly lead movements to drift away from the beat (Repp, 2005). This constant monitoring also enables rapid adjustment to new tempos as auditory stimuli increase or decrease in speed.

Third, human entrainment easily generalizes to new auditory stimuli. We may entrain not only to stimuli that we have heard before, but to any stimulus in which we

perceive a clear periodicity within the appropriate range of speeds.

Human auditory-motor entrainment is a truly cross-modal capacity, requiring the translation of auditory input to motor output, and monitoring that output for error by constantly comparing it to the auditory input. It is not accomplished by relying on auditory output, since we are able to entrain entirely silent motor actions (Repp, 2005).

Furthermore, human auditory-motor entrainment is highly flexible and robust. Both males and females display accurate entrainment, and we can entrain many body parts across a wide range of tempos. However, accuracy steeply drops off at slow tempos below ~33 beats per minute. When tapping along to a metronome at this speed, subjects' taps no longer slightly precede beats but occur after the auditory stimulus, suggesting an inability to perform accurate temporal prediction at slow tempos (Engström et al., 1996; Mates et al., 1994; Miyake et al., 2004). In addition, entrainment is more accurate for auditory stimuli than for visual stimuli (e.g. Patel et al., 2005), suggesting the involvement of a modality-specific mechanism.

### **The vocal mimicry hypothesis**

Crucially, the capacity to entrain to auditory stimuli is not seen in other primate species, even in great apes (Wallin et al., 2000). This suggests that our capacity for entrainment is a recent evolutionary development, emerging after our ancestry diverged from that of chimpanzees approximately 6 million years ago (Kumar et al., 2005). If this capacity does not exist in other primates, how did it evolve in our species?

Recently, Patel has proposed that entrainment may have evolved as the byproduct of selection for another capacity, namely vocal mimicry or vocal imitation (Patel, 2006;

2008). According to this hypothesis, selection for vocal mimicry led to a strong coupling between auditory and motor representations. This auditory-motor linkage was also necessary for entrainment, and was later co-opted to allow for entrainment as well.

If selection for vocal mimicry results in the necessarily neural machinery for entrainment, then in the case that vocal mimicry never evolved in a particular species, that species should not have the mechanisms needed to entrain. Thus, Patel's hypothesis makes a strong prediction: The capacity for entrainment should only exist in vocal mimicking species, and never in vocal non-mimicking species.

In recent work, we aimed to answer two questions: firstly, is the capacity for entrainment uniquely human? Previously, entrainment was widely believed to be uniquely human (e.g. Zatorre et al., 2007; Wallin et al., 2000; Brown et al., 2006; Clayton et al., 2005; Thaut, 2003; Bispham, 2006; McNeill, 2005). However, work had not yet focused on vocal mimicking animals, which were predicted to entrain by Patel's vocal mimicry hypothesis. Secondly, we aimed to test this vocal mimicry hypothesis, asking: do we only find evidence of entrainment in vocal mimicking animals, and never in species that cannot imitate sound?

We defined vocal mimicry broadly, as any species that learns vocalizations from an external auditory model.<sup>1</sup> By this definition, vocal mimics are still a small group, including humans, three clades of bird (hummingbird, parrot and songbird; Doupe and Kuhl, 1999); two lineages of marine mammal (cetaceans and pinnipeds; Janik and Slater, 1999; Rawls et al., 1985), elephants (Poole et al., 2005), and some bats (Boughman,

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<sup>1</sup> This ability is also termed 'vocal learning' in other literature; however the term 'vocal learning' is also used to refer to a larger category of abilities unrelated to imitation, such as the ability to learn produce innate vocalizations in novel contexts (e.g. Janik and Slater, 2000), and as such was avoided here.

1998).

### **Spontaneous entrainment in non-human species**

To test for entrainment, we first performed two case studies on an African Grey parrot (Alex) as well as a Sulphur-Crested Eleanora cockatoo (Snowball). In these studies, we simply recorded and analyzed the birds' spontaneous behavior in response to recorded music. However, we also took two steps necessary to make these sessions well-controlled experiments: Firstly, we eliminated visual cues, such as human movement, to ensure that the birds were responding to the auditory stimuli, not simply using visual input. Secondly, we included novel auditory stimuli. Using novel stimuli (created by the author using music sequencing software) meant that the birds would have to generalize any entrainment behavior to novel sounds. This ensured that any response was not due to simple behavioral shaping, or training to respond to particular sounds with particular movements. By generalizing their entrainment to new stimuli, the birds would have to perform a behavior analogous to human entrainment.

When we played the birds these stimuli, we saw a surprising response: At the very first hearing, Alex bobbed his head seemingly in time to the beat. This same phenomenon was seen in Snowball, who not only bobbed his head but also lifted his feet, again seemingly in time with the musical beat.

Were the birds actually entrained to the musical beat, more so than we would expect by chance? Or were our minds simply finding patterns in what is truly randomness? To analyze the data, we first performed a frame-by-frame manual coding of the birds' head location. This gave us accurate, continuous data on the birds' movements

over the course of the video. Where discrete data was needed, the points at which the birds stopped moving (due to changing direction at the top and bottom of their movement cycle) were used as the beat locations. Then, we collected tapping data from humans: Subjects entrained to the same stimuli as the birds, and the timing of their taps was recorded. This data gave us an idea of the beat locations, as well as the amount of error acceptably present in human entrainment. We then examined the extent to which the birds' and humans' beats aligned in frequency and phase. Using multiple convergent analyses allowed us to characterize the data in a detailed manner, and allowed for convergent evidence of entrainment from multiple aspects of the movement signal.

In our frequency analysis, we first asked: Does the bird maintain a consistent frequency over time, or seem to be moving at a range of frequencies, as we might expect by chance? To address this, we first took a Fourier transform of the movement signal, giving us the magnitude or amount of each frequency present in the signal. If the bird is moving at one frequency more than the others, we should see a peak in the Fourier transform at that frequency. Then the question becomes: is the bird consistent enough that it is highly unlikely to have happened by chance? To address this question, we performed a Monte Carlo simulation, simulating what the data would look like if the bird were simply moving at a range of random frequencies. We simulated 5,000 null-hypothesis datasets of this type, and then asked: How likely is it that a peak as high as the peak we see in the real data would occur under the null hypothesis? This allowed us to determine a threshold for significance, such that when the peak height was higher than that threshold the bird was so consistent that it was very highly unlikely to be due to chance ( $p < .05$ ).

Moving at a consistent frequency only matters if the bird is also moving at the *correct* frequency. To determine whether the birds' frequency matched that of the musical beat, we compared the peak location (which is the birds' modal frequency) to the distribution of human modal tapping frequencies, and counted anything  $<2$  SD from the human mean as a match.

Next we performed phase analyses. In the case of a person tapping to a beat, *phase* refers to the temporal distance between a tap and the nearest musical beat. The word phase is used because beat-based data are inherently circular. Imagine a few beats visually, with time going from left to right. If one is trying to tap to the beat, there are multiple temporal locations that are equally accurate: tapping in time with the first beat, and tapping in time with the second beat, for instance. The time in between these beats is less accurate, as a function of the temporal distance from whichever beat is closest. Thus, the most inaccurate time to tap is right in between two beats, which is maximally far from both the first and the second correct time point. Thus, as a person's taps move away from the first beat, the taps become more and more inaccurate only until they pass the midpoint between the beats. At this point, the tap locations once again become more accurate as they begin approaching the second beat. This data is thus well represented as mapped onto a circle, where zero degrees is the beat location and 180 degrees is the midpoint in between two beats. The timing of each tap relative to the beat can be mapped onto a point on this circle. Because of the circular structure of the data, circular statistics serve as the appropriate methods to analyze alignment of phase, and determine whether this alignment was accurate enough to have been unlikely to occur by chance.

Our first phase analysis asked whether the bird maintained a consistent phase

relationship with the musical beat, or if the bird slowly slipped out-of-time with the beat over the course of a series of movements. We would expect such slipping in the case that the bird was moving at approximately the right frequency, but was not really entrained. We commonly experience this phenomenon while driving: when we turn on music, we at times have the perception that the windshield wipers are moving in time with the musical beat. However, since the wipers are not at precisely the correct frequency, and are not correcting their speed to match subtle tempo changes in the song, the wipers slowly slip farther and farther away from the beat until we no longer perceive them as aligned. If the birds gradually slip out of phase in this way, this would suggest that they are not actually entrained, but that the matching frequency of movement happened by chance.

Conversely, if the birds retain a consistent phase-relationship with the beat over a long period of time, this would serve as very strong evidence of entrainment. Consistent phase is highly unlikely to be maintained without intentional entrainment and error-correction, because of the cognitive and motor error intrinsic to the process (Repp, 2005). Without error correction we would quickly slip out of time as this error accumulated. Thus, maintaining consistent phase over time strongly supports the case for entrainment.

To determine consistency of phase, we performed a Rayleigh test for consistency of phase angle (Fisher, 1983). This analysis takes into account the amount of data and length of videos in calculating how likely the data would be to occur by chance. Thus if a bird was highly aligned, but our dataset contained only 10 seconds of periodic movement in that trial, the Rayleigh test was even more stringent in its determination of significance, taking the limitation of dataset length into account (Fisher, 1983).

The second analysis went further, asking if the birds were not only maintaining a

consistent phase but were actually phase-matched, or synchronized with the beat. For this we performed a second type of Rayleigh test, using a specified mean direction of zero (Fisher, 1983). This test detects the presence of consistency and synchrony together, and thus identified trials where the birds' movements aligned with the beats themselves, instead of consistently occurring just after or just before each beat.

Across all four of these analyses, we found robust evidence of entrainment in both of our case study subjects. Subject 1 showed evidence of phase-matched entrainment across all four analyses in two out of six trials, and non-phase-matched entrainment in another two of the six. Subject 2 showed robust evidence of phase-matched entrainment across all four analyses in three out of four trials. Notably, this subject demonstrated entrainment across a wide range of tempos, changing speed in order to match the music at tempos ranging from 108 to 132 beats per minute. In addition to performing a head-bobbing movement, Subject 2 also seemed to lift his feet in time with the music—complete analysis of this movement showed that the foot movement was also entrained (Schachner et al., 2009). The case studies thus showed strong evidence of entrainment in non-human animals. In addition, convergent data from Patel and colleagues documented that when a song was manipulated to change its tempo, Snowball changed speeds to maintain alignment (Patel et al., 2009), further strengthening the case for entrainment.

Multiple aspects of the birds' entrainment behavior paralleled human auditory-motor entrainment. For instance, avian entrainment does not seem to occur reflexively; the birds do not obligatorily move every time a song plays, or continue to entrain for the entire duration of the song. Thus, the behavior does not seem to be a low-level obligatory response but instead appears volitionally controlled. In addition, the birds are able to

entrain across a range of tempos, generalize the response to novel stimuli, and entrain the movement of multiple body parts. All of these qualities suggest that avian entrainment may rely on similar cognitive mechanisms to human entrainment.

### **Testing the vocal mimicry hypothesis**

Both of the case study subjects were proficient vocal mimics. Thus, the finding that these birds are able to entrain is consistent with the vocal mimicry hypothesis. However, in order to truly test this idea, we must show not only that entrainment appears in vocal mimicking species, but also that the capacity never appears in non-mimicking species. To support this negative claim, we need a vast comparative dataset, containing data from non-mimics as well as vocal mimics. These data should be varied enough to find any evidence of entrainment, should it exist; thus it must include examples of non-mimics from many species. In addition, we must have data from multiple animals within each species, so as to account for a large range of experiences.

To find such a dataset, we turned to YouTube.com, a vast public video database consisting of millions of user-contributed videos. We asked: do we find evidence of entrainment in vocal mimicking species, but never in vocal non-mimics? To answer this question, we conducted a series of systematic searches of the database using animal terms selected to represent species across the taxonomic tree, and added the word "dancing" to each animal search term.

While this dataset does contain some biases, such as users posting only the best videos, there is no possibility of systematic bias with regard to our question of interest, the difference between vocal mimicking and non-mimicking species, as the people

posting videos were unaware of the hypotheses driving this work. In addition, vocal non-mimicking animals are better represented in the database than vocal mimics by approximately 2:1 (Schachner et al., 2009), increasing our relative chances of finding entrainment in this group should it exist. For these reasons, the YouTube database provides a useful and appropriate test case for the vocal mimicry hypothesis.

We performed a total of 161 searches, finding 3879 unique videos, 1019 of which contained a non-human animal. We analyzed these videos for evidence of entrainment using the same motion-tracking and statistical methods used for the case studies and detailed above. In the final dataset, vocal mimics and vocal non-mimics were approximately equally represented; however, evidence of entrainment was found only for vocal mimicking species. In particular, evidence of entrainment was found in 33 vocal mimicking animals and zero vocal non-mimics, a result highly unlikely to happen by chance (Schachner et al., 2009). Overall, we found evidence of entrainment in 14 species of parrot, as well as in Asian elephants.<sup>2</sup>

To our knowledge, none of the species found to entrain are known to naturally entrain to sound in the wild. Auditory-motor entrainment does not seem to be part of the natural behavioral repertoire of parrot species. This detail can inform our understanding of the evolution of avian entrainment: If the capacity is truly not expressed in natural behavior, there is no potential for this behavior itself to increase or decrease fitness.

Effectively, the behavior does not exist, and as such cannot be selected for (or against) by

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<sup>2</sup> Data from Asian elephants did show evidence of entrainment in terms of the extent of the elephants' alignment with the beat; however, this data in particular calls for further replication due to the circumstances under which it was recorded. While parrot owners reported spontaneous entrainment by the birds, the elephants' movements appear to be staged performances by professional trainers. Thus, further work should test elephant entrainment in a controlled environment.

natural selection. Thus it must have arisen as a byproduct of selection for another cognitive capacity. Coupled with evidence that only vocal mimicking species entrain, this lends support to the idea that avian entrainment emerged as a byproduct of selection for vocal mimicry.

Humans are only distantly related to parrots, and many more closely related species do not entrain. As such it is extremely unlikely that humans and parrots inherited the capacity for entrainment from their last common ancestor. A pattern of convergent evolution is more likely, in which similar evolutionary pressures led to the development of similar genetic and neural mechanisms in the two lineages. While it is thus possible that human and avian entrainment emerged in different ways, the close parallels between the features of the behavior suggest similar evolutionary origins. Hence, these data make it plausible that human entrainment as well as avian entrainment may have emerged as a byproduct of selection for vocal mimicry.

To return to the first of the two questions originally posed in this chapter: Why can we entrain? These data give us a potential answer: Natural selection for vocal imitation may have given us the cognitive machinery needed for entrainment.

### **Why do we tend to dance?**

How did human entrainment emerge? While selection for vocal mimicry may have given us the prerequisite machinery, we still must account for another phenomenon: The universal human motivation to engage in entrained behavior. We not only *can* move to a beat, but we actually *do* move to a beat. Entrained movement is omnipresent in human culture; in contrast, entrainment seems not to be a part of avian species' natural

behavioral repertoire. How do we account for this difference?

One potential explanation rests on the idea that the tendency to entrain may have been directly selected for in subsequent evolution, for the following reason: If people tend to entrain to sounds they hear, and people tend to hear the same thing when they are in nearby locations, this will lead to synchronized movement. If synchrony is adaptive in some way, then the tendency or motivation to entrain should be directly selected for. Thus, if we start out with a population in which people differ in their capacity to entrain or in their tendency to express the behavior, selection will favor those who are motivated and tend to entrain, as those people will experience the most synchrony.

Why might synchrony be adaptive? There are theoretical reasons to suspect that synchrony may increase social bonding and cooperative behavior, and recent experimental work has supported this idea. For instance, synchronized marching is widely used to train the armed forces. In today's military, marching exercises are valued not for their direct use in combat, but for their ability to promote camaraderie and cooperation among the troops (McNeill, 1995).

In addition, work on imitation has shown that subtly mimicking a person's posture, movements or mannerisms (a widespread phenomenon termed behavioral mimicry or behavioral matching) leads to increased liking, empathy and cooperation (e.g. Chartrand and Bargh, 1999; Ashton-James et al., 2007). Since synchrony can be construed as mimicry without a delay, it seems plausible that synchrony might promote cooperation through the same mechanism as behavioral mimicry (Hove and Risen, 2009). In particular, perceiving another's movements as parallel to your own may increase the similarity between one's representation of oneself and that of another (Iacoboni, 2005).

Since we cooperate most with similar others, this increase in self-other representational overlap would likely result in prosocial behavioral effects (Galinsky et al., 2005).

Recent experimental evidence has supported the idea that synchrony promotes prosocial behavior. A recent paper purported to show that synchrony increased cooperation in economic games, such as the public goods task (Wiltermuth and Heath, 2009); however, there is some question as to the replicability of this data (Schachner and Garvin, 2010). More recent papers have been more carefully controlled, and have also found convergent evidence that synchrony increases prosociality (e.g. Hove and Risen, 2009). Our ongoing work has also supported a role for synchrony itself in promoting prosocial behavior, above and beyond the effects of playing music together (Schachner & Garvin, in preparation). Based on this evidence, it seems likely that synchrony does lead to prosociality and increased cooperation.

How can this literature fit together with comparative evidence suggesting that the entrainment capacity emerged as a byproduct? These literatures are not necessarily in conflict. Entrainment is a complex capacity, which depends on many neural mechanisms and evolved in a complex process over a long period of time. The evolution of human entrainment may have occurred in two steps: First, selection for mimicry gave us the cognitive machinery needed to entrain. Second, once we had this prerequisite cognitive machinery, the tendency or motivation to entrain was adaptive; people who tended to express this behavior more often experienced more synchrony and thus formed more cooperative relationships. Thus, the tendency or motivation to engage in entrainment behavior was directly selected for during human evolution. By this hypothesis, entrainment is widely expressed in human behavior but remains latent in avian behavior

because our species has experienced direct selection for synchrony, while avian species have not experienced this type of selection.

There are two reasons why avian species might not have experienced selection for the tendency to entrain. Firstly, it is possible that entrainment evolved in these species very recently in evolutionary time, and while synchrony is adaptive in these species as well, avian species have not yet had sufficient time for selection for the tendency to entrain to have an effect. Secondly, it is possible that synchronized movement simply does not confer an adaptive advantage in parrot species. This hypothesis seems plausible, since the cooperative effects of synchrony and mimicry are thought to rest on high-level abstract representations of self and other (Hove and Risen, 2009). These abstract social representations may be fundamentally different in parrot species as compared to our own.

This second possibility makes a testable prediction: After engaging in synchronized movement with other individuals, parrots should not become more cooperative or prosocial, even if they are capable of entrainment. Conversely, non-human primates who are incapable of entrainment may nonetheless become more prosocial after engaging in synchronized movement. If this complex prediction were supported, this may suggest the existence of two stages of the evolution of the human capacity for entrainment: A first stage, in which the capacity for entrainment emerged as a byproduct; and a second stage in which the tendency to engage in entrained behavior proved adaptive, and was selected for directly. This theoretical proposal thus would account not only for our ability to move to a beat, but for the widespread human propensity to groove, tap, bop or bounce in time with music and with other individuals.

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