

Auditory-motor entrainment in vocal mimicking species

Additional ontogenetic and phylogenetic factors

Adena Schachner

Department of Psychology; Harvard University; Cambridge, MA USA

We have recently found robust evidence of motor entrainment to auditory stimuli in multiple species of non-human animal, all of which were capable of vocal mimicry. In contrast, the ability remained markedly absent in many closely related species incapable of vocal mimicry. This suggests that vocal mimicry may be a necessary precondition for entrainment. However, within the vocal mimicking species, entrainment appeared non-randomly, suggesting that other components besides vocal mimicry play a role in the capacity and tendency to entrain. Here we discuss potential additional factors involved in entrainment. New survey data show that both male and female parrots are able to entrain, and that the entrainment capacity appears throughout the lifespan. We suggest routes for future study of entrainment, including both developmental studies in species known to entrain and further work to detect entrainment in species not well represented in our dataset. These studies may shed light on additional factors necessary for entrainment in addition to vocal mimicry.

to be a uniquely human capacity.⁴⁻⁸ However, we have recently found strong evidence of auditory-motor entrainment (henceforth 'entrainment') in non-human species, particularly parrot species.^{9,10} In addition, by systematically searching and analyzing material from a large public video database (YouTube.com), we found that while there was extensive evidence of entrainment in animals capable of vocal mimicry, the ability remained markedly absent in many closely related species incapable of vocal mimicry.⁹ This finding lends support to the theory that the capacity for entrainment emerged as a byproduct of selection for vocal mimicry.¹¹ By this hypothesis, vocal mimicry would be a necessary precondition for entrainment. Our data suggest that, in line with the predictions of this hypothesis, only vocal mimicking animals are able to entrain.

However, entrainment appeared non-randomly even within the vocal mimicking species in our dataset. Known vocal mimics include humans, three avian clades (songbirds, parrots and hummingbirds), two marine mammal clades (cetaceans and pinnipeds), elephants and some bats.⁹ We found robust evidence of entrainment in multiple parrot species, and some evidence of entrainment in elephant species; however we saw no evidence of entrainment in other vocal mimicking animals. This pattern suggests that while vocal mimicry may be *necessary* for entrainment, it is not *sufficient*. What factors other than vocal mimicry determine an animals' capacity for entrainment? To determine which capacities could potentially be needed, we examine the types of abilities shared by the species known to entrain (humans and

Key words: entrainment, sensorimotor synchronization, vocal mimicry, vocal learning, evolution, avian cognition

Submitted: 03/02/10

Accepted: 03/02/10

Previously published online:
www.landesbioscience.com/journals/cib/article/11708

Correspondence to: Adena Schachner;
 Email: amschach@fas.harvard.edu

Addendum to: Schachner A, Brady TF, Pepperberg I, Hauser M. Spontaneous motor entrainment to music in multiple vocal-mimicking species. *Curr Biol* 2009; 19:831-6. PMID: 19409786; doi:10.1016/j.cub.2009.03.061.

Dance is a universal human behavior, appearing in all modern-day cultures.¹ Dance is also ancient: cave art depictions of dance date back at least 9,000 years,² and musical instruments date back to at least 35,000 years.³ Thus, dance appears to be a fundamental part of modern human behavior.

Auditory-motor entrainment, the ability to align motor actions with an external auditory beat, is a crucial component of dance, and has been commonly assumed

parrots), particularly the subset of abilities not shared by a wide range of other vocal mimicking species that do not entrain. We next discuss the availability of videos from different species in our dataset, and how this affects the likelihood of entrainment being observed in these species. Finally, we discuss new data on differences within parrots that may be important for entrainment.

Differences between Species

Parrots are able to imitate non-vocal movements as well as vocalizations.^{12,13} This ability may be crucial for entrainment. While experimental studies have shown that motor imitation is not necessary for each episode of avian entrainment, it is possible that imitation plays a role in initially encouraging the individual to engage in entrained movement to music. Some initial role for motor imitation remains plausible, since the individual parrots known to entrain have all had extensive experience with humans and therefore may have observed entrainment to music prior to themselves engaging in entrainment.

Parrots also imitate a wide range of sounds, including other species' vocalizations and environmental sounds. This contrasts with many songbird species, which only imitate sounds produced by conspecifics.¹⁴ It may be that only the true mimics, which imitate the sounds of other species, can entrain. In addition, both parrots' and humans' vocal mimicry abilities do not fade in adulthood like those of many songbirds, but are retained throughout the lifespan.¹⁴ This type of open-ended vocal mimicry may also be necessary for entrainment to occur.

Complex social cognition has also been hypothesized to form a necessary prerequisite for entrainment, in conjunction with vocal mimicry.¹³ While there has been little experimental work on parrot social cognition, there is reason to suspect advanced social cognitive abilities in parrot species.¹⁵ Many species exhibit complex social behavior, forming large individualized social networks and maintaining close long-term attachments to other individuals.¹⁶ High social intelligence has been reported in African Grey parrots,¹⁷

and parrot species overall show larger relative brain size and telencephalic volume than non-passerine bird species and similar relative brain size to primates.¹⁸ It is thus possible that some aspect of advanced social cognition, in conjunction with vocal mimicry, enables entrainment.

Data Availability

If a complex social system is indeed relevant to entrainment, this suggests that other vocal mimics with complex social systems should also be able to entrain. This set of species includes some passerine birds, such as corvids,¹⁵ as well as dolphins.¹⁹ However, we did not find evidence of entrainment in these species in our dataset. This is at least partly due to the low availability of videos of these species in the database, which is a crucial factor in our ability to make inferences about entrainment from the YouTube dataset.

In particular, while vocal mimics and vocal non-mimics were equally represented in our dataset, each individual species within these groups was not equally represented. This is an important point, since the power of the dataset to make negative conclusions for individual species depends on the baseline availability of videos of that species in the database. For instance, there are far fewer videos of wild animal species than there are of domesticated animal species in the YouTube database. In addition, since wild species are rarely exposed to human music, videos of these animals with periodic sound are very rare. For an animal to entrain to an auditory stimulus, there must be periodic auditory stimuli available. For these reasons, the YouTube database does not contain sufficient data to make strong negative conclusions about most individual wild species. This includes many vocal mimicking species such as starlings and lyrebirds, which appear with a low base-rate in the database.

Dolphins also fall into this category. We found no evidence of dolphin entrainment in our analyses, but this does not yet serve as strong negative evidence, since dolphins are not well represented in the database. More experimental work is called for in this species, particularly since they would be predicted to entrain if both advanced

social cognition and vocal mimicry are needed for entrainment.

Elephants are also not well represented on YouTube; however, we did find videos of elephants in which the animals appear to be entrained. However, while parrot owners reported spontaneous entrainment by the birds, the elephants' entrained movements appear to be staged performances by professional trainers. Thus, while the animals in the videos appear entrained, our data from Asian elephants calls for further replication. Further work should test elephant entrainment in controlled circumstances.

In contrast to these species, dogs are extremely well represented in the database, and are often recorded in the presence of period sounds and music. However, we still found no evidence of entrainment in dogs. Due to the large amount of data available, in the case of dogs our dataset strongly supports a negative result in terms of entrainment ability.

We also found no evidence of entrainment in non-human apes. These species are also only moderately represented in our dataset.^{9,20} However, observations from other experiments are consistent with the idea that non-human primates may truly be incapable of entrainment. In the past century, questions about linguistic development have led multiple scientists to adopt apes and raise them as human children. In these studies, apes were raised as like to a human infant as possible, and sometimes alongside a similarly-aged human child.²¹⁻²⁴ It is likely that these infant apes were exposed to music and movement to music, as these are a typical part of human life, particularly in infancy.²⁵ However, to the authors' knowledge, these studies did not report entrained movement to music by these human-reared apes. In contrast, parrots kept in human environments do entrain to music.⁹ This additional negative evidence for primates is consistent with our result, and suggests that non-human primates may indeed lack the capacity for entrainment.

Individual Differences

In addition to differences between species, we also see differences within species. Most individuals of particular parrot species do

not show evidence of entrainment, even when multiple individuals of that species entrain. This suggests that individual experience and ontogeny play a role in determining an animal's ability or tendency to entrain. The nature of these individual experiences is as of yet unknown. Since only domestic parrots have been seen to entrain thus far, it is possible that prior observation of other individuals engaging in entrainment may be necessary to motivate and initiate entrained motor behavior, as discussed above.

An additional question is whether these experiences must occur at specific points in development, during a sensitive period for entrainment. If so, and if the particular experiences involve the observation of humans, then birds wild-caught in adulthood would not learn to entrain. Alternatively, it may be that the relevant experience is effective regardless of age. If this is the case, then a non-entraining individual (of a species where other individuals are known to entrain) could learn to entrain at any age by exposure to the relevant experience. Future developmental research in parrot species should shed light on the type and timing of individual experience necessary for entrainment.

Lack of Gender Specificity

One of the hallmarks of human entrainment is its lack of gender specificity: male and female humans seem equally skilled at accurately moving to a beat, as extensive research on the topic has not noted gender differences.²⁶ This contrasts with the strict gender-specificity of certain types of synchronized motor behaviors previously studied in other species (e.g., the claw-waving behavior of crabs or synchronized flashing of lightning bugs). This gender specificity forms one reason to believe that these phenomena depend on cognitive mechanisms very different from the ones humans use for entrainment.^{13,27} If avian entrainment is also gender-specific, this would point to a possibly substantial difference between the cognitive mechanisms used in avian and human entrainment.

Both of the subjects explored in published case studies were male, and at the time of our previous publication we did not know the gender of animals from our

database analysis. Thus, previous work has been unable to address the question of gender-specificity.^{9,10} However, we have recently begun to survey the owners of animals from the online dataset for the animals' demographic information. Of the nine owners who responded, eight had determined the gender of their parrot via reliable methods (e.g., DNA testing). Of these eight parrots, fully half (four) were female. In addition, the survey showed a wide array of ages among entrained parrots, ranging from two to thirty-three years. Thus, in parrot species the capacity for entrainment is not confined to male individuals only, nor is it confined only to young ages. Parrot entrainment resembles the human entrainment capacity in that it appears in both males and females and is retained throughout the lifespan.

Previous data has shown that avian and human entrainment have strikingly similar phenomenology: parrots as well as humans match the frequency and phase of their movements to the musical beat, changing to match multiple tempos, and flexibly using different body parts and types of movement to entrain. Also, both parrots and humans appear to have volitional control over whether they engage in entrained movements; these movements are not a reflexive, obligatory response to music.^{9,10} Now, we may add the gender and age invariance to this list of common features. Overall, these common behavioral signatures strongly suggest that human and avian entrainment rely on highly similar cognitive mechanism, each of which arose independently through convergent evolution. This is consistent with recent literature on the neural mechanisms for vocal mimicry, showing that the structure of neural mechanisms underlying vocal mimicry is highly constrained, as the mechanisms used remain highly similar across multiple clades of vocal learners, in spite of seemingly independent evolutionary origins.^{28,29}

Conclusions

While only vocal mimicking animals have been shown to entrain, not every vocal mimicking animal shows evidence of entrainment. This suggests that additional factors may potentially be needed

for entrainment in conjunction with vocal mimicry. In the current paper, we have found that both male and female parrots can entrain, and that the capacity seems to be retained throughout the lifespan, thus ruling out age and sex as preconditions for avian entrainment, and adding a further parallel of avian and human entrainment. The nature of additional capacities needed for entrainment is yet unknown, and the number of viable hypotheses remains extremely large. We suggest two main routes for future research. Firstly, further work to detect entrainment in species not well represented in our dataset may inform debates on species-general capacities needed for entrainment. For example, if advanced social cognition and vocal imitation are the only needed components, species such as dolphins and corvids should be able to entrain.

However, even when some individuals of a particular species can entrain, many others will not exhibit this behavior. Thus, a negative result in a small set of individuals may not be representative of the capacity of the species, but reflect the lack of entrainment-relevant experience by the tested group. Therefore, to most effectively detect the capacity for entrainment in a species, we should first develop a better understanding of the ontogeny of entrainment behavior in each individual animal. Developmental work in parrot species known to entrain can shed light on the types of individual experiences needed for entrainment to emerge. Once we have some understanding of the ontogenetic factors involved in entrainment, these factors can be used to develop more effective and informative tests for entrainment in other species, and ultimately to understand the causal mechanisms determining an animal's capacity or lack of capacity for entrainment.

Acknowledgements

The author would like to thank Timothy Brady for comments on the manuscript.

References

1. Nettl B. The study of ethnomusicology: Twenty-nine issues and concepts. University of Illinois Press. Urbana 1983.
2. Chakravarty KK, Bednarik RG. Indian Rock Art and Its Global Context. New Motilal Banarsidass Publishers. Delhi, India 1997.

3. Conard NJ, Malina M, Munzel SC. New flutes document the earliest musical tradition in southwestern Germany. *Nature* 2009; 460:737-40.
4. Zatorre RJ, Chen JL, Penhune VB. When the brain plays music: auditory-motor interactions in music perception and production. *Nature Rev Neurosci* 2007; 8:547-58.
5. Wallin NL, Merker B, Brown S. *The Origins of Music*. MIT Press. Cambridge 2000.
6. Brown S, Martinez MJ, Parsons LM. The neural basis of human dance. *Cereb Cortex* 2006; 16:1157-67.
7. Clayton M, Sager R, Will U. In time with the music: the concept of entrainment and its significance for ethnomusicology. *ESEM Counterpoint* 2005; 1:3-75.
8. McNeill W. *Keeping Together in Time: Dance and Drill in Human History*. Harvard Univ Press. Cambridge 1995.
9. Schachner A, Brady TF, Pepperberg I, Hauser M. Spontaneous motor entrainment to music in multiple vocal-mimicking species. *Curr Biol* 2009; 19:831-6.
10. Patel AD, Iversen JR, Bregman MR, Schulz I. Experimental evidence for synchronization to a musical beat in a nonhuman animal. *Curr Biol* 2009; 19:827-30.
11. Patel AD. *Music, Language and the Brain*. Oxford Univ Press. New York 2008.
12. Moore BR. Avian movement imitation and a new form of mimicry: tracing the evolution of a complex form of learning. *Behaviour* 1992; 122:231-63.
13. Patel AD, Iversen JR, Bregman MR, Schulz I. Studying synchronization to a musical beat in nonhuman animals. *Ann NY Acad Sci* 2009; 1169:459-69.
14. Kroodsma D. *The Singing Life of Birds: The Art and Science of Listening to Birdsong*. Houghton Mifflin. New York 2005.
15. Emery NJ. Cognitive ornithology: the evolution of avian intelligence. *Philos Trans R Soc Lond B* 2006; 361:23-43.
16. Emery NJ. Are corvids 'feathered apes'? Cognitive evolution in crows, jays, rooks and jackdaws. In: Watanabe S, ed. *Comparative analysis of minds*. Keio University Press. Japan 2004; 181-213.
17. Pepperberg IM. *The Alex Studies*. Harvard University Press. Cambridge MA 1999.
18. Iwaniuk AN, Dean KM, Nelson JE. Interspecific allometry of the brain and brain regions in parrots (Psittaciformes): comparisons with other birds and primates. *Brain Behav Evol* 2005; 65:40-59.
19. Wells RS. Dolphin social complexity: Lessons from long-term study and life history. In de Waal FBM, Tyack PL, (eds), *Animal social complexity: Intelligence, culture and individualized societies*. Harvard University Press. Cambridge 2003; 32-56.
20. Fitch WT. Biology of music: another one bites the dust. *Curr Biol* 2009; 19:403-4.
21. Kellogg WN, Kellogg LA. *The Ape and The Child: A Comparative Study of the Environmental Influence Upon Early Behavior*. Hafner Publishing Co., New York 1933.
22. Hayes C. *The Ape in Our House*. Harper. New York 1951.
23. Terrace HS. *Nim. Knopf*. New York 1979.
24. Gardner RA, Gardner BT, Van Cantfort TE. *Teaching sign language to chimpanzees*. State University of New York Press. Albany 1989.
25. Trehub SE, Hannon EE, Schachner A. Perspectives on music and affect in the early years. In: Juslin PN, Sloboda JA, (eds), *Handbook of music and emotion: Theory, research, applications*. Oxford University Press. New York 2010.
26. Repp BH. Sensorimotor synchronization: a review of the tapping literature. *Psychon Bull Rev* 2005; 12:969-92.
27. Patel AD, Iversen JR, Chen Y, Repp BH. The influence of metricality and modality on synchronization with a beat. *Exp Brain Res* 2005; 163:226-38.
28. Feenders G, Liedvogel M, Rivas M, Zapka M, Horita H, Hara E, et al. Molecular mapping of movement-associated areas in the avian brain: a motor theory for vocal learning origin. *PLoS ONE* 2008; 3:1768.
29. Jarvis ED. Learned birdsong and the neurobiology of human language. *Ann NY Acad Sci* 2004; 1016:749-77.

©2010 Landes Bioscience.
Do not distribute.