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The evolutionary biology of dance without frills

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Recently psychologists have taken up the question of whether dance is reliant on unique human adaptations, or whether it is rooted in neural and cognitive mechanisms shared with other species [1,2]. In its full cultural complexity, human dance clearly has no direct analog in animal behavior. Most definitions of dance include the consistent production of movement sequences timed to an external rhythm. While not sufficient for dance, modes of auditory-motor timing, such as synchronization and entrainment, are experimentally tractable constructs that may be analyzed and compared between species. In an effort to assess the evolutionary precursors to entrainment and social features of human dance, Laland and colleagues [2] have suggested that dance may be an incidental byproduct of adaptations supporting vocal or motor imitation — referred to here as the ‘imitation and sequencing’ hypothesis. In support of this hypothesis, Laland and colleagues rely on four convergent lines of evidence drawn from behavioral and neurobiological research on dance behavior in humans and rhythmic behavior in other animals. Here, we propose a less cognitive, more parsimonious account for the evolution of dance. Our ‘timing and interaction’ hypothesis suggests that dance is scaffolded off of broadly conserved timing mechanisms allowing both cooperative and antagonistic social coordination.

Below, we briefly address supporting arguments for the imitation and sequencing hypothesis (Figure 1A). First, as Laland and colleagues [2] note, motor imitation plays a role in the transmission of human dance. However, imitation is a general process supporting social learning in a vast array of human behaviors, including sport, visual art, and language. Second, humans moving to music show increased activation in brain regions implicated in imitation,

including frontal operculum and the ‘mirror system’. Laland and colleagues [2] suggest this could be indicative of a relationship between imitation and dance. However, frontal operculum and mirror system activation is not selective for imitation, and there are many tenable alternative hypotheses to explain their activation during rhythm tasks. Third, Laland and colleagues [2] cite a comparative hypothesis attempting to link vocal imitation and ability to move in time to external rhythm predictively and flexibly [3]. However, this hypothesis is heavily debated [4–7] and focuses on capability of synchronizing movement with music, for which there are few comparative data. While early evidence of at least intermittent synchronization to music was found in a cockatoo and other vocally imitative species [4], newer findings have shown strong predictive and flexible entrainment (based on auditory cues alone) in a much less vocally flexible species, the California sea lion [8]. Our preliminary Bayesian meta-analysis of comparative experiments does not support a strong link between synchronization and vocal learning but suggests that results from some crucial species might (Supplemental information). Fourth, Laland and colleagues [2] draw on an emerging literature on the role of behavioral synchrony in social affiliation to suggest that cooperation is both cause and consequence of entrainment. However, comparative biology shows entrainment is reached by competition and other forms of social interaction aside from cooperation [5]; further, cooperation can lead to a broad range of interdependent behaviors aside from entrainment [9].

While imitation clearly aids in the social and cultural transmission of human dance, a propensity for joint rhythmic behavior may be rooted in a more widely conserved biological faculty for rhythm and social interaction. In our timing and interaction hypothesis (Figure 1A), we propose that species-general timing mechanisms support purposeful, socially motivated coordination with conspecifics, resulting in diverse patterns of co-timing [10]. At the same time, individual timing behavior may be evolutionarily shaped by social dynamics of interdependent timing, subject to pressures for e.g. sexual selection and kin recognition [5]. In humans, these interdependently timed behaviors may

be shared and shaped by cultural transmission and flexibly integrated with music [1], leading to the range of human dance behavior. We believe this hypothesis to be consistent with growing evidence for broad distribution of auditory motor entrainment behavior across species, as well as with the wealth of data on co-timing and social coordination in almost all animal clades [5,7,9,10]. Our framework advances a number of testable hypotheses that can be directly compared with those of the imitation and sequencing hypothesis (Figure 1D).

If human dance is rooted in widely shared mechanisms of co-timing, dance may be further illuminated by broadly comparative studies. Zoologists should continue the growing trend of describing temporal interdependencies, focusing on movement, vision and possibly cross-modal interactive displays in animal communication (Figure 1B,C). In the acoustic domain, researchers are increasingly recognizing the importance of different modes of group vocalization timing, such as antisynchrony [9]. Empirical research into motor timing might follow suit, adopting a ‘movement chorusing’ approach, focusing on interdependence of movements rather than solo entrainment capacities [5]. Importantly, testing groups in addition to individuals might elicit temporal behaviors otherwise unattainable in isolated testing. Diverse coordination modes (e.g. antisynchrony, hemiola) and timing mechanisms (e.g. reactive, anticipatory) can be mapped to group movement in non-human animals and to dancing patterns in humans, and mathematically modeled as interdependent temporal sequences to categorize the diversity of these behaviors [5,10]. Models may be further enriched by integrating neural measures of brain function in subcortical regions known to play a role in movement timing and oscillatory firing patterns in cortex [10].

The empirical study of the neural and cognitive underpinnings of dance is in its infancy: hypotheses advanced now may shape the field for years to come. Restrictive hypotheses attempting to delineate restricted neurocognitive adaptations associated with rhythmic or dance behavior [2,3] can be productive. However, they must be weighed against, and when possible empirically pitted

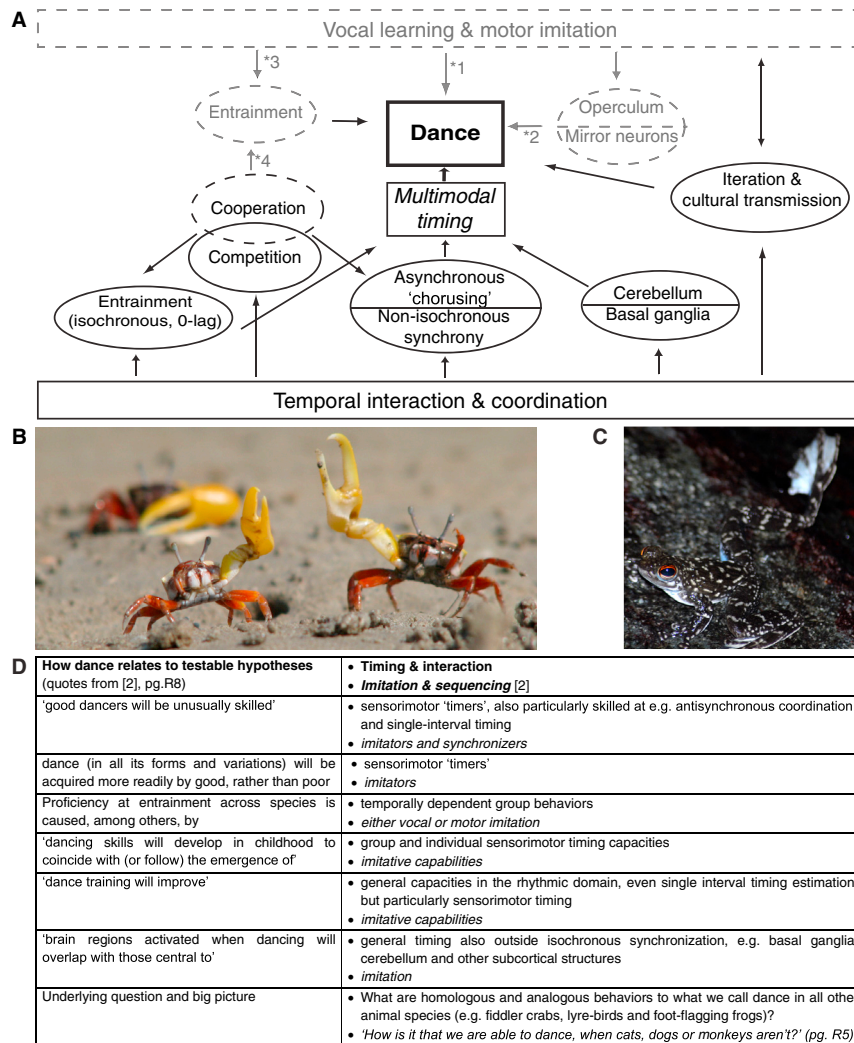


Figure 1. Theoretical frameworks and key model species for the evolution of dance.

(A) Laland *et al.*'s top-down model (broken lines, top) and our bottom-up model (unbroken lines, bottom) for the evolution of dance. Ideas from Laland *et al.* shaded in gray are not incorporated in our model because: (1) imitation is only one of many psychological variables affecting dance; (2) operculum and mirror neurons have many functions beyond imitation; (3) the 'vocal learning hypothesis' needs more empirical data to be supported or refuted (Supplemental information); (4) cooperation is neither necessary nor sufficient for entrainment. The core of our framework is represented by temporal interaction and coordination, giving rise not only to 0-lag, isochronous synchrony but also to a range of non-isochronous and non-synchronous movements [9]. This array of temporal interdependence is achieved by competition, coordination, and many other sorts of timed social interaction [5]. Mechanistically, subcortical structures may be more relevant to the comparative study of the evolution of dance than cortical areas [10]. Finally, iteration and cultural transmission produce much of the complexity and diversity of human behaviors. These forces could apply to dance as well, leading to refinement and transmission of behaviors emerging from broadly conserved mechanisms for timing and social coordination. (B) Dance-like group display of fiddler crabs, *Uca annulipes*. (C) Multimodal timed signaling in foot-flagging frogs, *Stauroids latopalermatus*. Research on all other species showing timed group movements or crossmodally timed signaling can unveil the evolutionary underpinnings of human dance. (Photos: P. Backwell, T. Detto, M. Böckle). (D) Dance capacities (left) as predicted by our hypothesis (right, first bullet) and [2] (second bullet, in italics). Hypotheses are not mutually exclusive: conserved mechanisms for timing, as in our hypothesis, could explain the rhythmic fundamentals of dance, while restricted mechanisms for imitation might support other features of human dance, e.g. cultural transmission of complex sequences. The hypotheses also provide some discordant predictions across species and tasks. Some species, not fully capable of vocal production learning, are predicted to entrain because of their natural chorusing or isochronous behavior: gibbons, chimpanzees, marmosets, California sea lions, Cape fur seals, and wolves. Entrainment in wrens and bats would support both hypotheses; in harbor seals it would confute ours and support the alternative.

against (Figure 1D), more biologically inclusive hypotheses. Given the incredibly diverse array of species that practice co-timed behaviors [5,7], it is premature to restrict comparative inquiry into the roots of dance to the relatively sparse species practicing imitation.

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures and two tables can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.07.076>.

AUTHOR CONTRIBUTIONS

Conceptualization, investigation and writing: A.R and P.C.

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REFERENCES

1. Fitch, W.T. (2016). Dance, music, meter and groove: a forgotten partnership. *Front. Hum. Neurosci.* 10, 1–7.
2. Laland, K., Wilkins, C., and Clayton, N. (2016). The evolution of dance. *Curr. Biol.* 26, R5–R9.
3. Patel, A.D. (2006). Musical rhythm, linguistic rhythm, and human evolution. *Music Percep.* 24, 99–104.
4. Iversen, J.R. (2016). In the beginning was the beat: Evolutionary origins of musical rhythm in humans. In *The Cambridge Companion to Percussion*, R. Hartenberger, ed. (Cambridge University Press).
5. Ravignani, A., Bowling, D.L., and Fitch, W.T. (2014). Chorusing, synchrony and the evolutionary functions of rhythm. *Front. Psychol.* 5, 1118.
6. Large, E.W., and Gray, P.M. (2015). Spontaneous tempo and rhythmic entrainment in a bonobo (*Parapaniscus*). *J. Comp. Psychol.* 129, 317–328.
7. Wilson, M., and Cook, P.F. (2016). Rhythmic entrainment: Why humans want to, fireflies can't help it, pet birds try, and sea lions have to be bribed. *Psychon. Bull. Rev.* 1–13.
8. Cook, P., Rouse, A., Wilson, M., and Reichmuth, C.J. (2013). A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. *J. Comp. Psychol.* 127, 1–16.
9. Ravignani, A. (2015). Evolving perceptual biases for antisynchrony: a form of temporal coordination beyond synchrony. *Front. Neurosci.* 9, 1–6.
10. Meck, W.H., and Ivry, R.B. (2016). Editorial overview: Time in perception and action. *Curr. Opin. Behav. Sci.* 8, vi–x.

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