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Recycling rules: In ecological cycles, one species' waste is another's valuable resource. Our civilisation has yet to learn to operate in such circular patterns rather than in a linear flow from (overexploited) resource to (polluting) waste. (Photo Kay-africa/Wikimedia Commons.)

take a decade at least before he could watch a fully grown Siberian elephant trample the tundra.

Meanwhile in Siberia, Sergey Zimov, director of the Northeast Science Station in Cherskii in the Russian Republic of Sakha, has set up a Pleistocene Park to study the ecosystem services of megafauna and is trying to re-establish a Pleistocene-style population of large beasts. The project has already reintroduced or encouraged the expansion of a number of large animal species, including reindeer, moose, wild horses, musk-oxen, and predators such as wolves, bears, lynxes, wolverines and foxes, on a current area of around 160 square kilometres.

Zimov has already discussed the possible mammoth project with Church. His observations so far suggest that bringing back a mammoth-like proboscidean would not only enrich the landscape but also help to lock in the permafrost that stores large quantities of methane. This is because the large-footed heavyweights have a unique way of compacting the snow and the ground which helps to stabilise the tundra environment.

Thus, in Siberia, as in the oceans, large mammals can help to achieve what our own species blatantly fails to do — recycle nutrients and stabilise the climate.

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Essay

The evolution of dance

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Evidence from multiple sources reveals a surprising link between imitation and dance. As in the classical correspondence problem central to imitation research, dance requires mapping across sensory modalities and the integration of visual and auditory inputs with motor outputs. Recent research in comparative psychology supports this association, in that entrainment to a musical beat is almost exclusively observed in animals capable of vocal or motor imitation. Dance has representational properties that rely on the dancers' ability to imitate particular people, animals or events, as well as the audience's ability to recognize these correspondences. Imitation also plays a central role in learning to dance and the acquisition of the long sequences of choreographed movements are dependent on social learning. These and other lines of evidence suggest that dancing may only be possible for humans because its performance exploits existing neural circuitry employed in imitation.

Dance is observed in all human societies. People readily move their bodies to rhythm or music, frequently coordinating their motion with others. The apparent effortlessness and ubiquity of human dance, however, belies the complexity of the act. How is it that we are able to dance, when cats, dogs or monkeys aren't? The scientific answer to this question reveals a surprising connection between dance and imitation.

Dancing requires the performer to match their actions to music, or to time their movements to fit the rhythm — sometimes an internal rhythm, such as the heartbeat. This demands a correspondence between the auditory inputs that the dancer hears and the motor outputs they produce. Likewise, competent couple or group dancing requires individuals to coordinate their actions, and in the process matching, reversing or complementing each other. This too calls for a correspondence between visual inputs and motor outputs. Convergent lines of evidence suggest that people solve these challenges by harnessing the same neural architecture as deployed in imitation (Figure 1).

Like dance, imitation requires an observer to learn through watching another individual perform the motor pattern, but the observer does not receive any direct reinforcement, and consequently the performer must map across different sensory modalities to produce a corresponding output. For instance, when an individual learns through observation to ride a bicycle, they must connect the sight of someone else pedalling with the utterly different sensory experience of themselves riding. Even today, there is little consensus as to how this 'correspondence problem' is solved [1]. Some researchers believe that imitation is mediated by special-purpose neural structures, while others maintain that imitation can be explained by general learning and motor control mechanisms [1]. Imitative proficiency may have been favoured by selection for cognitive proficiencies that built upon and enhanced general learning mechanisms to promote social learning. For example, the tendency to produce and attend to 'motherese' may be adaptations that enhance the social learning of language learning [2,3]. This debate has been stimulated by the discovery of mirror neurons — cells, or bundles of cells, that fire when the subject observes and executes a given action [4]. It remains to be established whether mirror neurons evolved to allow imitation or for some more general function, or even whether mirror neurons are best regarded as cause or consequence of observational learning proficiency [1,5]. However, solving the correspondence problem unquestionably requires links, in the form of networks of neurons, connecting the visual or auditory sensory regions of the brain with the motor cortex. It equally requires neural mechanisms that allow the learning

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Figure 1. Degas' *The Rehearsal*.
This painting by Edgar Degas not only depicts a ballet rehearsal but also illustrates the roles of imitation and synchrony (Image: The Yorck Project, Wikimedia Commons.).

of sequences of action units, and that 'recognize' the correspondence between oneself's and another's performance of each action unit [5,6].

Contemporary theories suggest that, while the potential for imitation is inborn in humans, competence is only realized with appropriate lifetime experience [1,5,6]. Early experiences, such as being rocked and sung to as a baby, help infants to form neural connections that link sound, movement and rhythm. Numerous activities later in life, such as playing a musical instrument, strengthen these networks. The relentless motivation to copy the actions of parents and older siblings seen in young children may initially serve a social function, such as to strengthen social bonds [7], but it also trains the 'mirroring' neural circuitry of the mind, leaving the child better placed later in life to integrate across sensory modalities. Theoretical work suggests that the experience of synchronous action forges links between the perception of self and others performing the same act [5,6]. Whether it is because past natural selection has tuned human brains specifically for imitation, because humans construct developmental environments that promote imitative proficiency, or both, there can be no doubt that, compared to other animals, humans are exceptional imitators. It may be no coincidence that a recent PET scan analysis of the neural basis of dance found that foot movement to music excited regions of neural circuitry (e.g. the right frontal operculum) previously associated with imitation [8]. Dancing may only be possible because its performance exploits the neural circuitry employed in imitation. Such reasoning applies equally where individuals dance alone; unlike much human behavior, dancing inherently seems to require a brain capable of solving the correspondence problem.

Comparative evidence is remarkably consistent with this hypothesis. A number of animals have been described as dancers, including snakes, bees, birds, bears, elephants and chimpanzees. However, whether animals can truly be said to dance remains a contentious issue, which depends at least in part on how dance is defined. In contrast, the more specific question of whether animals can move their bodies in time to music or rhythm has been extensively investigated, with clear and positive conclusions. Strikingly, virtually all of those animals that pass this test are known to be highly proficient imitators, frequently in both vocal and motor domains (Box 1) [9,10].

Dance often tells a story, and this representational quality provides another link with imitation. For instance, in the astronomical dances of ancient Egypt, priests and priestesses, accompanied by harps and pipes, mimed significant events in the story of a god or imitated cosmic patterns, such as the rhythm of night and day [11]. Africa, Asia, Australasia and Europe all possess long-standing traditions for masked dances, in which the performers portray the character associated with the mask and enact religious stories [11]. Native Americans have many animal dances, such as the Buffalo dance, which was thought to lure buffalo herds close to the village, and the eagle dance, which is a tribute to these revered birds [11]. This tradition continues to the present. In 2009, Rambert (formerly the Rambert Dance Company), a world leader in contemporary dance, marked the bicentenary of Charles Darwin's birth and 150th anniversary of his seminal work On the Origin of Species by collaborating with one of us (N.C.) to produce Comedy of Change (Figure 2), which evoked animal behaviour on stage with spellbinding accuracy. In all such instances, the creation and performance of the dance requires an ability on the part of the dancer to imitate the movements and sounds of particular people, animals, or events. Such dances re-introduce the correspondence problem, as the dancer, choreographer and audience must be able to connect the dancers' movements to the target phenomenon they represent.

The most transparent connection between dance and imitation, however, will be apparent to anyone who has ever taken or observed a dance lesson: dance sequences are typically learned through imitation. From beginner ballet classes for infants to professional dance companies, the learning of a dance routine invariably begins with a demonstration of the steps from an instructor or choreographer, which the dancers then set out to imitate. It is no coincidence that dance rehearsal studios around the world almost always have large mirrors along one wall.

These allow the learner rapidly to flit between observing the movements of the instructor or choreographer and observing their own performance. This not only allows them to see the correspondence — or lack of it — between the target behaviour and what they are doing, but also allows them to connect the proprioceptive and kinesthetic feedback they are getting from their muscles and joints to visual feedback on their performance, allowing error correction and accelerating the learning process.

In professional dance companies, prospective new members of the company are given challenging auditions in which they are evaluated for their ability to pick up new dance routines with alacrity — an essential skill for a dancer. Dancing is not just about body control, posture, grace and power, but also demands its own kind of intelligence. Central to whether or not a trainee dancer makes the grade is how good they are at imitating. A professional dancer at Rambert once told us that she had recently taken up sailing, and her instructor was flabbergasted at how quickly she had picked up the techniques involved. What the instructor failed to appreciate was that dancers earn their living by imitation.

Imitation is not the only cognitive faculty that is necessary for dance learning. Also important is sequence learning, particularly in choreographed dances, which require the learning of a long, and often complex, sequence of actions. Even improvised dances such as the Argentine tango require the leader to plan a sequence of movements that provide the basis for the exquisite conversation between leader and follower, allowing them to move as a ‘four-legged animal with two beating hearts’. Once again, scientific evidence connects this sequence learning ability to social learning. Recent theoretical work suggests that long strings of actions are very difficult to learn asocially, but that social learning substantially increases the chances that individuals will acquire the appropriate sequence [12]. Our ancestors were predisposed to be highly competent manipulators of strings of behavioural elements because many of their tool-manufacturing and tool-using skills, extractive foraging methods, and food-processing techniques required them to carry out precise sequences of actions, in the right order. These sequence-learning capabilities are clearly exploited in learning dance.

Box 1. Animal dancers.

This ability to move in rhythmic synchrony with a musical beat, for instance, by nodding our head or tapping our feet — a universal characteristic of humans — is actually very rarely observed in other species [10]. The most prominent explanation for why this should be, known as the ‘vocal learning and rhythmic synchronization’ hypothesis [9], suggests that entrainment to a musical beat relies on the neural circuitry for complex vocal learning, an ability that requires a tight link between auditory and motor circuits in the brain [22,23]. This hypothesis predicts that only species of animals capable of vocal imitation — such as humans, parrots and songbirds, cetaceans, and pinnipeds, but not nonhuman primates and not those birds that do not learn their songs — will be capable of synchronizing movements to music.

Consistent with this hypothesis, the internet is teeming with videos of birds, mostly parrots, moving to music, but compelling footage of other animals doing so is rare. Some of these ‘dancing’ birds have acquired celebrity status — the best known being Snowball (Figure 3), a sulphur-crested cockatoo (*Cacatua galerita eleonora*), whose performances on YouTube have ‘gone viral’. Experiments manipulating the tempo of a musical excerpt across a wide range have conclusively demonstrated that Snowball spontaneously adjusts the tempo of his movements to stay synchronized with the beat [24].

Thus far, evidence for spontaneous motor entrainment to music has been reported in at least nine species of birds, including several types of parrot, and the Asian elephant, all of whom are vocal imitators [9,10,24–26], and several of which show motor imitation [27]. Entrainment has also been shown in a chimpanzee [10], a renowned motor imitator [16]. The sole exception to this association is the California sea lion [10,16], which is not known to exhibit vocal learning. However, the fact that related species, including several seals and the walrus, show vocal learning [16] raises the possibility that this capability, or a relevant precursor, may yet be demonstrated. Lyrebirds have not been subject to entrainment experiments, but males — famous for their ability to imitate virtually any sounds, including dog barks, chainsaws and car alarms — match subsets of songs from their extensive vocal repertoire with tail, wing and leg movements to devise ‘dance’ choreography [25].

Clearly, there is more to human dance than entrainment to music, and coordination with others’ movements would seemingly draw on the neural circuitry that underlies motor, rather than vocal, imitation. However, a recent analysis of the avian brain suggested that vocal learning evolved through exploitation of pre-existing motor pathways [23], implying that vocal and motor imitation are reliant on similar circuitry. The animal data provide compelling support for a causal link between the capabilities for imitation and dance. Whether this is because imitation is necessary for entrainment, or merely facilitates it through reinforcing relevant neural circuitry, remains to be established.

Dancing also requires precise and controlled body movements, and recent studies of brain evolution suggest that this control evolved with increased brain size. Mammalian brains change in internal organization as they get larger, becoming more modular and asymmetrical [13]. With increasing size, larger brain regions typically become better connected and start to exert control over the rest of the brain [14]. This occurs because developing axons often compete for access to target sites and this competition is generally won by those axons that collectively fire the target cells, giving large brain regions a competitive advantage. The net result is an increase in the ability of the larger brain regions to influence other regions.

The dominant structure in the human brain is the neocortex, which accounts for approximately 80% of its volume, more than in any other animal [13]. In the primate lineage to humans, the neocortex has become larger over evolutionary time, and has exerted increasing control over the motor neurons of the spinal cord and brain stem, leading to increased manual dexterity, and more precise control of the limbs [13]. The cerebellum, the second largest region of the human brain, also plays an important role in motor control, and has enlarged during recent human evolution [15]. This motor control is what allows humans to dance easily and spontaneously, and in such precise ways. Recent comparative work suggests that large primate brains may have coevolved with social learning capabilities [16].

Dance is often pleasurable, generating a feeling of release, arousal and excitement. Why should dance induce a positive mood? Part of the explanation may be the release of endorphins that accompanies exercise, and of neurohormones, such as oxytocin, with increased arousal

Figure 2. Rambert dancers.
The Comedy of Change, a choreographic work created by Mark Baldwin for Rambert dancers. (Photo: © Hugo Glendening.)

and social behaviour [17]. Another factor is the thrill of courtship in dancing with someone attractive, or for the observer, the voyeurism associated with observing lithe, athletic and appealing young bodies move with grace and beauty. Yet, people enjoy dancing with individuals to whom they are not sexually attracted and when the physical demands are too modest to lead to an endorphin rush. Of particular interest here is social dance, for instance, dancing with a partner, or in a group, especially where the dancing is coordinated and synchronised, as for instance, ceilidh or river dance. Such dance often appears to lead to a sense of bonding, or shared pleasure, and can induce positive emotions in an audience [17]. While some properties of dance that make people feel socially close are very general, such as sharing attention and goals with others [18], others may be dance-specific, such as the externalization through music making of predictable rhythms, which helps people to synchronize their movements [17]. An empirical link between synchronous activity and social bonding is now well-established [17].

Here, an intriguing relationship between imitation and cooperation may be relevant. Recent psychological research has found that imitation enhances social interaction and induces positive moods, even when the imitated individual is unaware of being copied and the imitator does so unintentionally [19,20]. The relationship between imitation and cooperation is bidirectional: being imitated makes individuals more cooperative, whilst being in a cooperative frame of mind makes one more likely to imitate others [19]. These bidirectional causal relationships may function to maintain cooperation, collective action and information sharing between members of a social group [19]. If positive rewards to synchronous behaviour have been favoured by selection to facilitate cooperation, then that might explain why dancing in a synchronous manner would induce warm feelings. The same imitative neural networks in our brains, which link sight, sound and rhythm, and thereby allow us to dance to music, are also almost certainly what explains our tendency to tap or clap to music, and the pleasure that experience affords.

Dancing probably originated as an exaptation, rather than an adaptation: that is, as a character that was fashioned by natural selection for a different role — a byproduct of imitative proficiency. Whether dancing ability was subsequently directly favored by natural or sexual selection remains unclear, although that is certainly a possibility. However, historical data suggest that dance initially functioned as an ethnic marker that promoted within-group identity and alliances, and only relatively recently took on roles in the communication of religious and historical knowledge and sexual display [11].

If the above reasoning is correct, and dance is genuinely reliant on imitative capabilities, then a series of empirically tractable predictions follow. These include that good dancers will be unusually skilled imitators and synchronizers; good imitators will acquire dance more readily than poor imitators; animals that exhibit either vocal or motor imitation will be particularly proficient at entrainment; dancing skills will develop in childhood to coincide with (or follow) the emergence of imitative capabilities; dance training will improve imitative capabilities, and brain regions activated when dancing will overlap with those central to

Figure 3. Snowball, the dancing cockatoo.
Snowball can be seen to move with astonishing rhythmicity, head banging and kicking his feet in perfect time to Queen's *Another One Bites The Dust* (see https://www.youtube.com/watch?v=cJOZp2ZftCw). (Photo: Irena Schultz, Bird Lovers Only.)

imitation. Some provisional support for these hypotheses has already been presented, but there are clearly opportunities to test these hypotheses more rigorously. There are also likely to be implications for understanding some of the properties of music, as music and dance seemingly originated together [11], and some aspects of musical rhythm, such as syncopation, can only be fully understood as features that originated in a dancing context [21].

Curiously, in common parlance, the term imitation often has a derogatory quality, being associated with mindless and uninspired action, and contrasted with innovation. Historically the arts have placed value on creative and avant guard movements that push against established convention, and the inspiration for much dance innovation, as it has been for innovation more generally, has been precisely a reaction against 'mere imitation'. For instance, modern dance pioneers such as Isadora Duncan and Martha Graham positioned themselves against the stylized dance strictures exemplified in classical ballet. Only now, in the light of scientific evidence, can we appreciate how smart copying is, and how vital imitation and other forms of social learning are to dance.

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REFERENCES

1. Brass, M., and Heyes, C. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? Trends Cogn. Sci. *9*, 489–495.
2. Csibra, G., and Gergely, G. (2006). Processes of Change in Brain and Cognitive Development. Munakata, Y., and Johnson, M.H. (Eds). Oxford University Press, pp. 249–274.
3. Fitch, W.T. (2010). The Evolution of Language. Cambridge University Press.
4. Rizzolatti, G., Fogassi, L., and Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. *2*, 661–670.
5. Laland, K.N., and Bateson, P.P.G. (2001). The mechanisms of imitation. Cybernet. Sys. *32*, 195–224.
6. Heyes, C., and Ray, E. (2004). Spatial S-R compatibility effects in an intentional imitation task. Psych. Bulletin Rev. *11*, 703–708.
7. Carpenter, M. (2006). Instrumental, social and shared goals and intentions in imitation. In Imitation and the Social Mind: Autism and Typical Development. S.J., Rogers, and J.H.G., Williams. (Eds). (New York: Guilford Press) pp. 48–70.
8. Brown, S., Martinez, M.J., and Parsons, L.M. (2006). The neural basis of human dance. Cereb. Cortex. *16*, 1157–1167.
9. Patel, A.D. (2006). Musical rhythm, linguistic rhythm, and human evolution. Music Percept. *24*, 99–104.
10. Fitch, W.T. (2013). Rhythmic cognition in humans and animals: distinguishing meter and pulse perception. Frontiers Syst. Neurosci. *7*, 1–16.
11. Clarke, M., and Crisp. C. (1983). The History of Dance, 5th Edition (Crown Publishers: New York).
12. Whalen, A., Cownden, D., and Laland, K.N. (2015). The learning of action sequences through social transmission. Anim. Cogn. http://dx.doi.org/10.1007/s10071-015-0877-x.
13. Striedter, G.F. (2005). Principles of Brain Evolution (Sunderland, MA: Sinauer).
14. Deacon, T.W. (1997). The Symbolic Species: The Coevolution of Language and the Brain (New York: Norton.)
15. Barton, R.A. (2012). Embodied cognitive evolution and the cerebellum. Phil. Trans. R. Soc. Lond. Ser. B *367*, 2097–2107.
16. Reader, S.M., and Laland, K.N. (2002). Social intelligence, innovation, and enhanced brain size in primates. Proc. Natl. Acad. Sci. USA *99*, 4436–4441.
17. Tarr, B., Launay, J., and Dunbar, R.I.M. (2014). Music and social bonding: 'self-other' merging and neurohormonal mechanisms. Front. Psychol. http://dx.doi.org/10.3389/fpsyg.2014.01096.
18. Tomasello, M., Carpenter, M., Call, J., Behne, T., and Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. Behav. Brain Sci. *28*, 675–691; discussion 691–735.
19. Heyes, C.M. (2012). What can imitation do for cooperation? In Signalling, Commitment & Cooperation, B. Calcott, R. Joyce, and K. Sterelny, (Eds) (MIT Press).
20. van Baaren, R., *et al*. (2009). Where is the love? The social aspects of mimicry. Phil. Trans. R. Soc. B. *3641528*, 2381–2389.
21. Fitch, W.T. (Submitted). Dance, music, meter and groove: a forgotten partnership. Front. Hum. Neurosci.
22. Jarvis, E.D. (2004). Learned birdsong and the neurobiology of human language. Ann. NY Acad. Sci. *1016*, 749–777.
23. Feenders, G., Liedvogel, M., Rivas, M., Zapka, M., Horita, H., Hara, E., Wada, K., Mouritsen, H., and Jarvis, E.D. (2008). Molecular mapping of movement-associated areas in the avian brain: a motor theory for vocal learning origin. PLoS One *3*, e1768.
24. Patel, A.D., Iversen, J.R., Bregman, M.R., and Schulz, I. (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. Curr. Biol. *19*, 827–830.
25. Dalziell, A.H., Peters, R.A., Cockburn, A., Dorland, A.D., Maisey, A.C. and Magrath, R.D., (2013). Dance choreography is coordinated with song repertoire in a complex avian display. Curr. Biol. *23*, 1132–1135.
26. Schachner, A., Brady, T.F., Pepperberg, I.M., and Hauser, M.D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. Curr. Biol. *19*, 831–836.
27. Hoppitt, W., and Laland, K.N. (2013). Social Learning. An Introduction of Mechanisms, Methods, and Models (Princeton University Press).

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Book review

It's the principle of the thing

Charles F. Stevens

Principles of Neural Design
Peter Sterling and Simon Laughlin
(MIT Press, Cambridge, MA; 2015)
ISBN: 9780262028707

Principles of Neural Design, written by Peter Sterling and Simon Laughlin, is what I believe to be the first book whose goal is to identify neurobiological design principles and to use them to understand brain structure and function. Although the principles identified are brain-specific, they are usually motivated and explained by considering analogous principles used by engineers. And one of the great joys of the book is seeing how various aspects of neurobiology are illuminated by a detailed application of these principles.

I think I have detected a steady increase of interest — over the last two or three decades — in using theory to learn about the brain (indeed, about all biology), but most of this interest has expressed itself in modeling specific brain phenomena using artificial neural networks and in tool-making (software for sorting spikes, for example). A few papers have set as their goal the identification of principles that go across brain areas and species, but these papers have generally discovered 'small' principles with somewhat narrow applicability. What is unique about the Sterling and Laughlin book is the authors' interest in identifying general principles that apply to virtually all brains and species. Surely, discovering the fundamental general principles of neurobiology should be the ultimate goal of theory.

Towards this goal, the book is organized around ten principles: compute with chemistry, compute directly with analog primitives, combine analog and pulsatile (spike) processing, sparsify, send only what information is needed for a particular job, use the lowest acceptable rate to transmit information (save resources), minimize wire, make neural components irreducibly small,

