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The Evolution of Dance

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

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

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

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[Figure 1: Edgar Degas. The rehearsal]

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59 Like dance, imitation requires the performer to map across different
60 sensory modalities to produce a corresponding output. For instance, when an
61 individual learns through observation to ride a bicycle, they must connect the
62 sight of someone else peddling the bike, with the utterly different sensory
63 experience that they encounter when they themselves perform these actions.
64 Even today, there is little consensus as to how this 'correspondence problem' is
65 solved (see 1 for a recent review). Some researchers believe that imitation is
66 mediated by special-purpose neural structures, whilst others maintain that
67 imitation can be explained by general learning and motor control mechanisms
68 (1). Imitative proficiency may have been favoured by selection for cognitive
69 proficiencies that built upon and enhanced general learning mechanisms to
70 promote social learning, as for instance, appears to have occurred with the
71 evolution of motherese in language learning, or pedagogical cueing in
72 instrumental learning (2,3). This debate has been stimulated by the discovery of
73 mirror neurons - cells, or bundles of cells, that fire when the subject observes
74 and executes a given action (4). It remains to be established whether mirror
75 neurons evolved to allow imitation or for some more general function, or even
76 whether mirror neurons are best regarded as cause or consequence of
77 observational learning proficiency (1,5). However, solving the correspondence
78 problem unquestionably requires links, in the form of networks of neurons,
79 connecting the visual or auditory sensory regions of the brain with the motor
80 cortex. It equally requires neural mechanisms that allow the learning of
81 sequences of action units, and that 'recognize' the correspondence between the
82 self's and another's performance of each action unit (5,6).

83 Contemporary theories suggest that while the potential for imitation is
84 inborn in humans, competence is only realized with appropriate lifetime
85 experience (1,5,6). Early experiences, such as being rocked and sung to as a baby,
86 help infants to form neural connections that link sound, movement and rhythm,
87 whilst numerous activities engaged in later in life, such as playing a musical
88 instrument, strengthen such networks. The relentless motivation to copy the
89 actions of parents and older siblings, which we all witness in our young children,
90 may initially serve a social function, such as to strengthen social bonds (7), but it
91 undoubtedly also trains the 'mirroring' neural circuitry of the mind, leaving the

92 child better placed later in life to integrate across sensory modalities. Theoretical
93 work suggests that the experience of synchronous action forges links between
94 the perception of self and others performing the same act (5,6). Whether it is
95 because past natural selection has tuned human brains specifically for imitation,
96 because humans construct developmental environments in a way that promotes
97 imitative proficiency, or both, there can be no doubt that, compared to other
98 animals, humans are exceptional imitators. It may be no coincidence that a
99 recent PET scan analysis of the neural basis of dance found that foot movement
100 to music excited regions of neural circuitry (e.g. the right frontal operculum)
101 previously associated with imitation (8). Dancing may only be possible for
102 humans because its performance exploits the neural circuitry employed in
103 imitation.

104 Comparative evidence is remarkably consistent with this hypothesis. A
105 number of animals have been described as dancers, including snakes, bees, birds,
106 bears, elephants, and chimpanzees. However, whether animals can truly be said
107 to dance remains a contentious issue, which depends at least in part on how
108 dance is defined. In contrast, the more specific question of whether animals can
109 move their bodies in time to music or rhythm has been extensively investigated
110 by researchers, with clear and positive conclusions. Strikingly, virtually all of
111 those animals that pass this test are known to be highly proficient imitators
112 (9,10; see **Box 1**).

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[Box 1: Animal dancers]

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116 Dance often tells a story, and this representational quality provides
117 another link with imitation. For instance, in the astronomical dances of ancient
118 Egypt, priests and priestesses, accompanied by harps and pipes, performed
119 stately movements that mimed significant events in the story of a god, or
120 imitated cosmic patterns, such as the rhythm of night and day (17). Africa, Asia,
121 Australasia and Europe all possess long-standing traditions for masked dances,
122 in which the performers assume the role of the character associated with the
123 mask and enact religious stories (17). America in the 1920s was obsessed with a
124 cult of animal dances, including the 'Grizzly bear', 'Turkey trot' and 'Bunny hop',

125 which requires the dancer to imitate animal movements. This tradition continues
126 right through to the present. For instance, in 2009, the Rambert Dance Company,
127 a world leader in contemporary dance, marked the bicentenary of Charles
128 Darwin's birth and 150th anniversary of his seminal work *On the Origin of Species*
129 by collaborating one of us (NC) to produce *Comedy of Change*, which evoked
130 animal behaviour on stage with spellbinding accuracy. In all such instances, the
131 creation and performance of the dance requires an ability on the part of the
132 dancer to imitate the movements and sounds of particular people, animals,
133 machines, or worldly events. Such dances re-introduce the correspondence
134 problem, since the dancer, choreographer and audience must be able to connect
135 the dancers' movements to the target phenomenon that they represent.
136



137
138 **[Figure 3. Dancers from the Rambert Dance Company in Comedy of Change]**
139

140 The most transparent connection between dance and imitation, however,
141 will be readily apparent to anyone who has ever taken or observed a dance
142 lesson: dance sequences are typically learned through imitation. From beginner
143 ballet classes for infants to professional dance companies, the learning of a dance

144 routine invariably begins with a demonstration of the steps from an instructor or
145 choreographer, which the dancers then set out to imitate. It is no coincidence
146 that dance rehearsal studios around the world almost always have large mirrors
147 along one wall. These allow the learner rapidly to flit between observing the
148 movements of the instructor or choreographer and observing their own
149 performance. This not only allows them to see the correspondence - or lack of it
150 - between the target behaviour and what they are doing, but also allows them to
151 connect the proprioceptive and kinesthetic feedback they are getting from their
152 muscles and joints to visual feedback on their performance, allowing error
153 correction and accelerating the learning process.

154 In professional dance companies, prospective new members of the
155 company are given challenging auditions in which they evaluated for their ability
156 to pick up new dance routines with alacrity - an essential skill for a dancer.
157 Dancing is not just about body control, posture, grace and power, but also
158 demands its own kind of intelligence. A key element in whether or not a trainee
159 dancer makes the grade essentially comes down to how good they are at
160 imitating. A professional dancer at Rambert¹ once told us that she had recently
161 taken up sailing, and her instructor was flabbergasted at how quickly she had
162 picked up the techniques involved. What the instructor failed to appreciate was
163 that dancers earn their living by imitation.

164 That is not to suggest that imitation is the only cognitive faculty that is
165 necessary for dance learning. Also important is sequence learning, particularly in
166 choreographed dances, which require the learning of a long, and often complex,
167 sequence of actions. Even improvised dances such as the Argentine tango require
168 the leader to plan a sequence of movements that provide the basis for the
169 exquisite conversation between leader and follower, allowing them to move as a
170 'four-legged animal with two beating hearts'. Once again, scientific evidence
171 connects this sequence learning ability to social learning. Recent theoretical
172 work suggests that long strings of actions are very difficult to learn asocially, but
173 that social learning substantially increases the chances that individuals will
174 acquire the appropriate sequence (18). Hominins may be predisposed to be
175 highly competent manipulators of strings of behavioural elements because many

¹ Formerly Ballet Rambert until 1966 and then Rambert Dance Company until 2013

176 of their tool-manufacturing and tool-using skills, extractive foraging methods,
177 and food-processing techniques required them to carry out precise sequences of
178 actions, in the right order. These sequence-learning capabilities are clearly
179 exploited in learning dance.

180 Dancing also requires remarkably precise and controlled body
181 movements, and recent studies of brain evolution suggest that this control
182 evolved with increased brain size. Mammalian brains change in internal
183 organization as they get larger, becoming more modular and asymmetrical with
184 size (19). With increasing size, larger brain regions typically become better
185 connected and start to exert control over the rest of the brain (20). This occurs
186 because developing axons often compete with one another for access to target
187 sites and this competition is generally won by those axons that collectively fire
188 the target cells, giving large brain regions a competitive advantage. The net
189 result is an increase in the ability of the larger brain regions to influence other
190 regions.

191 The dominant structure in the human brain is the neocortex, which
192 accounts for approximately 80% of the human brain by volume, more than in
193 any other animal (19). In the primate lineage to humans, the neocortex has got
194 larger over evolutionary time, and has exerted increasing control over the motor
195 neurons of the spinal chord and brain stem, leading to increased manual
196 dexterity, and more precise control of the limbs (19). The cerebellum, the second
197 largest region of the human brain, also plays an important role in motor control,
198 and has enlarged during recent human evolution (21). This motor control is
199 what allows humans to dance easily and spontaneously, and in such precise
200 ways.

201 Dance is often pleasurable, generating a feeling of release, arousal and
202 excitement. Why should dance induce a positive mood? Part of the explanation
203 may be the release of endorphins that accompanies any form of exercise, and of
204 neurohormones, like oxytocin, with increased arousal and social behaviour (22).
205 Another factor is the thrill of courtship in dancing with someone attractive, or for
206 the observer, the voyeurism associated with observing lithe, athletic and
207 appealing young bodies move with grace and beauty. Yet people enjoy dancing
208 with individuals to whom we are not sexually attracted and when the physical

209 demands are too modest to lead to an endorphin rush. Of particular interest here
210 is social dance, for instance, dancing with a partner, or in a group, especially
211 where the dancing is coordinated and synchronised, as for instance, *ceilidh* or
212 *river dance*. Such dance often appears to lead to a sense of bonding, or shared
213 pleasure, and can induce positive emotions in an audience (22). While some
214 properties of dance that make people feel social close are very general, such as
215 sharing attention and goals with others (23), others may be dance-specific, such
216 as the externalization through music making of predictable rhythms, which helps
217 people to synchronize their movements (22). An empirical link between
218 synchronous activity and social bonding is now well-established (22).

219 Here an intriguing relationship between imitation and cooperation may
220 be relevant. Recent psychological research has found that imitation enhances
221 social interaction and induces positive moods, even when the imitated individual
222 is unaware of being copied and the imitator does so unintentionally (24,25). The
223 relationship between imitation and cooperation is bidirectional: being imitated
224 makes individuals more cooperative, whilst being in a cooperative frame of mind
225 makes one more likely to imitate others (24). These bidirectional causal
226 relationships may function to maintain cooperation, collective action and
227 information sharing between members of a social in-group (24). If positive
228 rewards to synchronous behaviour have been favoured by selection to facilitate
229 cooperation, then that might explain why dancing in a synchronous manner
230 would induce warm feelings. The same imitative neural networks in our brains,
231 which link sight, sound and rhythm, and thereby allow us to dance to music, are
232 also almost certainly what explains our tendency to tap or clap to music, and the
233 pleasure that experience affords.

234 Dancing probably originated as an exaptation, rather than an adaptation:
235 that is, as a character that was fashioned by natural selection for a different role -
236 a byproduct of imitative proficiency. Whether dancing ability was subsequently
237 directly favored by natural or sexual selection remains unclear, although that is
238 certainly a possibility. However, historical data suggest that dance initially
239 functioned as an ethnic marker that promoted within-group identity and
240 alliances, and only relatively recently took on roles in the communication of
241 religious and historical knowledge and sexual display (17).

242 If the above reasoning is correct, and dance is genuinely reliant on
243 imitative capabilities, then a series of empirically tractable predictions follow.
244 These include that (i) good dancers ought to be unusually skilled imitators and
245 synchronizers; (ii) good imitators ought to acquire dance more readily than poor
246 imitators; (iii) those animals that exhibit either vocal or motor imitation will be
247 those that show entrainment; (iv) dancing skills will develop in childhood to
248 coincide with (or follow) the emergence of imitative capabilities; and (v) those
249 brain regions activated when dancing will overlap with those central to
250 imitation. Some provisional support for these hypotheses has already been
251 presented, but there are clearly opportunities to test these hypotheses more
252 rigorously. There are also likely to be implications for understanding some of the
253 properties of music, as music and dance seemingly originated together (17), and
254 some aspects of musical rhythm, such as syncopation, can only be fully
255 understood as features that originated in a dancing context (26).

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

266

267 **Box 1: Animal dancers**

268 This ability to move in rhythmic synchrony with a musical beat, for instance, by
269 nodding our head or tapping our feet - a universal characteristic of humans - is
270 actually very rarely observed in other species (10). The most compelling
271 explanation for why this should be, known as the 'vocal learning and rhythmic
272 synchronization' hypothesis (9), suggests that entrainment to a musical beat
273 relies on the neural circuitry for complex vocal learning, an ability that requires a
274 tight link between auditory and motor circuits in the brain (11,12). This

275 hypothesis predicts that only species of animals capable of vocal imitation - such
276 as humans, parrots and songbirds, cetaceans, and pinnipeds, but not nonhuman
277 primates and not those birds that do not learn their songs - will capable of
278 synchronizing movements to music.

279 Consistent with this hypothesis, the internet is teeming with videos of
280 birds, mostly parrots, moving to music, but compelling footage of other animals
281 doing so is rare. Some of these 'dancing' birds have acquired celebrity status - the
282 best known being Snowball a sulphur-crested cockatoo (*Cacatua galerita*
283 *eleonora*), whose performances on YouTube have 'gone viral'². Experiments
284 manipulating the tempo of a musical excerpt across a wide range have
285 conclusively demonstrated that Snowball spontaneously adjusts the tempo of his
286 movements to stay synchronized with the beat (13).

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[Figure 2. Snowball – the dancing cockatoo]

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291 Another compelling experimental demonstration is found in lyrebirds, the
292 males of which will often match subsets of songs from their extensive vocal
293 repertoire with different combinations of tail, wing and leg movements to form
294 predictable 'gestures', and thereby devise their own choreography (14).

² 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>).

295 Lyrebirds are famous for their ability, unmatched in the animal kingdom, to
296 imitate just about any sounds, including dog barks, chainsaws and car alarms.
297 Thus far, evidence for spontaneous motor entrainment to music has been
298 reported in at least nine species of birds, including several types of parrot, and
299 the Asian elephant, all of whom are renowned vocal imitators (9,13-15). The sole
300 exception is the California sea lion (16), but this species is situated in a clade of
301 animals all of which have been shown to be capable of vocal learning.

302 Clearly, there is more to human dance than entrainment to music, and
303 coordination with others' movements would seemingly draw on the neural
304 circuitry that underlies motor, rather than vocal, imitation. However, a recent
305 analysis of the avian brain suggested that vocal learning evolved through
306 exploitation of pre-existing motor pathways (12), implying that vocal and motor
307 imitation are reliant on similar circuitry. The animal data provides convincing
308 support for a causal link between the capabilities for imitation and dance.

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