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Primer

Imitation

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Since antiquity, the term ‘imitation’ has been used promiscuously in biology and everyday life. Anything that makes some individuals look or act like others has been called imitation, from the evolutionary process that makes edible butterflies look like their inedible cousins (better known as Batesian mimicry), to the rag-bag of psychological processes that make people wear similar clothes, eat in the same restaurants, and use the same gestures for communication.

The first complaints about promiscuity came from the British ethologist Conwy Lloyd Morgan in 1900 and triggered a cascade of purification; attempts to fix the term imitation with a clear, specific, scientific meaning. In a succession of jargon-generating taxonomies, ‘true imitation’ was distinguished from pretenders such as ‘local enhancement’, ‘stimulus enhancement’, ‘matched dependent behaviour’, ‘observational conditioning’, ‘emulation’, ‘mimicry’, ‘response facilitation’, ‘contextual imitation’ and ‘object movement re-enactment’.

The good news is that the purification is almost complete. A few biologists and psychologists still use the term imitation in the broad everyday sense, as a synonym for ‘social learning’, referring to all the many ways in which the behaviour of an individual can come to resemble the behaviour of others through social interaction. But most now use imitation in a narrow sense (Figure 1, top) to refer to one type of social learning in which observation of another agent, M (for model), causes the behaviour of the observer, O, to become topographically similar — alike in ‘form’ — to the behaviour of M. In other words, as a result of observation of M by O, parts of O’s body move in a similar way, relative to one another, as the parts of M’s body.

In this primer I will explain why animal behaviour specialists, behavioural ecologists, cognitive neuroscientists, cultural evolutionists, and primatologists have settled on this narrow definition — what they find especially interesting about the copying of body movement topography — and discuss the most controversial outstanding questions. Is imitation a sign of cognitive sophistication (Figure 1, bottom left)? What does it contribute to cumulative cultural evolution (Figure 1, bottom right)? Are we *Homo imitans*, creatures who genetically inherit a prodigious capacity for imitation? But first a basic question: how can we tell whether behavioural similarity is due to imitation?

Detecting imitation

Imagine two baboons sitting side-by-side. One baboon, M, reaches out and picks up a stick using a power grip; she contacts the stick with the flat of her hand and lifts it by curling all four fingers around the stick towards her palm. The other baboon, O, seems to watch M and, a few minutes later, also picks up a stick. Did O imitate M? The answer has nothing to do with the object of O’s action, for example, whether he grabbed the same or a similar stick. The answer depends on *how* O lifted the stick. If O used a precision grip, contacting the stick only with the tips of his fingers and thumb, it is very unlikely he was imitating because the topography of O’s action was different from the topography of M’s action: their fingers moved in a different way relative to each other and to the rest of the actor’s hand. If O, like M, used a power grip, it is possible that he was imitating. We would, however, need to watch the two baboons for much longer to find out whether there was a causal relationship between O’s observation of M’s power grip and O’s performance of a power grip; to be sure that O did not use the same grip as M by chance, or because a power grip is the only practical way of grasping the sticks available to these baboons. We would

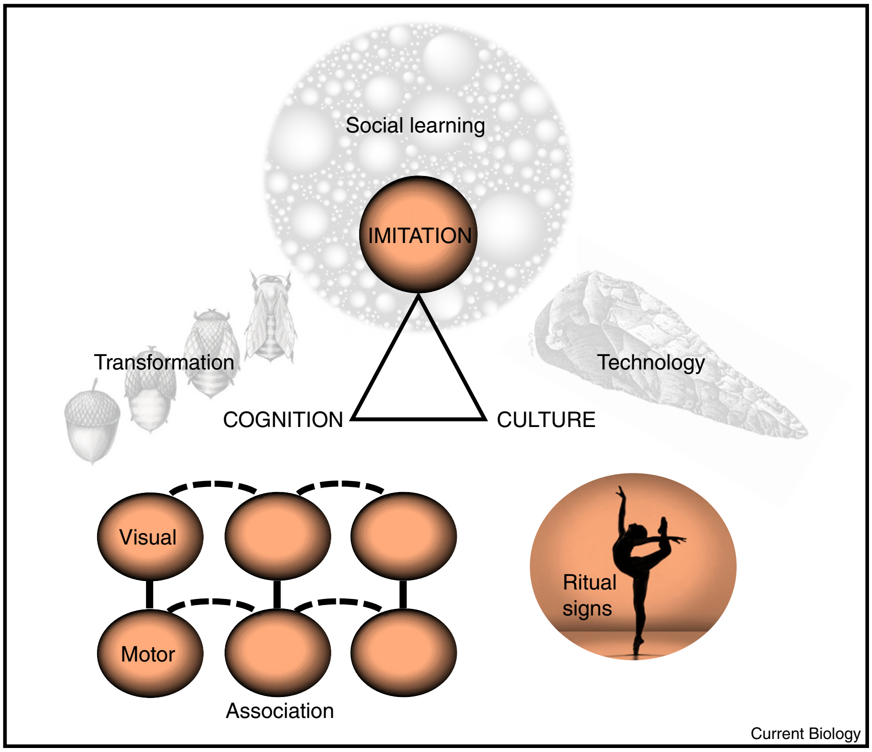

Figure 1. Developments in research on imitation.
Definition (top): once equated with social learning, imitation is now understood to be just one type of social learning in which an observer copies the ‘form’ or topography of a model’s body movements; that is, how parts of the body move relative to one another. Cognition (left side): it has long been assumed that imitation requires the cognitive system to know that the model’s and observer’s actions are similar from a third-party perspective; that it must be able to transform a sensory representation of the model’s body movements into a motor representation controlling the observer’s action. In contrast, the ‘gadget’ or ‘associative sequence learning’ theory suggests that imitation is achieved via association rather than transformation. Culture (right side): recent research suggests that imitation has contributed to human evolution primarily by enabling the cultural inheritance of group-specific rituals and communicative gestures, rather than technology, and that the cognitive capacity to imitate is itself a product of cultural evolution.

need to check, over many episodes of grasping, whether O is more likely to use a power grip than a precision grip when he has recently seen M using a power grip, and vice versa when he has recently seen M using a precision grip.

In the laboratory, where many members of the same species, or children of the same age, are tested for imitation in each experiment, this kind of check is known as a 'two-action test' or 'cross-target procedure'. It is the gold standard method of detecting imitation. In another method, known as the 'ghost control', one group of observers see a model perform an action on an object — for example, lift a stick using a power grip — whereas a control group observes the effects of the model's body movements without seeing the body movements themselves. They see a stick rising into the air as if held by an invisible spectre. Ghost controls are useful but not as powerful as two-action tests. If observers use a power grip after seeing a power grip, but not after seeing ghostly movement of a stick, it could be because the presence or activity of a model made the observers more interested in the stick. The observers' use of the same movement topography as the model could still be a coincidence.

Experiments using two-action tests and ghost controls have produced credible reports of imitation in chimpanzees reared from birth by humans (described by Michael Tomasello as 'enculturated' chimpanzees) and following 'Do-as-I-do' training, pioneered by Deborah Custance. In this kind of training, animals are rewarded, on presentation of a distinctive sound, for reproducing successive approximations to the action performed by a model. All reports of imitation without explicit training in mother-reared chimpanzees and other nonhuman apes are highly controversial. Well-known claims that Japanese macaques imitate wheat-cleaning and potato-washing, dating from the 1950s, are now considered misleading because they drew on the broad sense of imitation, equating it with social learning. Following the work of Bennett Galef and others, few, if any, biologists now believe that Japanese macaques learn to clean wheat and potatoes by copying the topography of body movements. Beyond primates, there is compelling evidence of imitation in domesticated dogs and in several bird species, including two African Grey parrots (Okíchoro and Alex), budgerigars, pigeons, and Japanese quail. The parrots had close relationships with the humans who studied them, Bruce Moore and Irene Pepperberg, and the dogs had close relationships with their owners. Like the chimpanzees that have tested positive for imitation, they were enculturated.

Many of the studies involving dogs and birds have demonstrated effector matching, use of the same appendage as a model. For example, if the model uses her head to displace an obstacle or activate a light, the observer is more likely to use his head than his hand or foot to produce the same outcome. Effector matching counts as imitation because the observer copies the way that one part of the body (for example the head) moves relative to the rest of the body (the trunk and appendages), but it is a minimal case. Copying the topography of body movement is distinct from copying the topography of object movement, sometimes called 'emulation', but each comes in degrees; neither imitation nor emulation has a fixed level of fidelity. When a ballet dancer copies the fine details of an arabesque, or an impressionist copies the facial gestures of a politician, they are harvesting and deploying much more information about body movement than an animal who imitates use of the head rather than the foot.

There is a consensus that, compared with other animals, adult humans are outstanding imitators. In the words of Andrew Meltzoff, we are *Homo imitans*. But there have been very few attempts to quantify human imitative skill, or to document how it varies across individuals and cultures. Reports that imitation is impaired in people with autism have been challenged by research showing that, when attention to modelled movements is controlled, autistic individuals are as likely, or even more likely, as other people to imitate hand movements and facial gestures. Research applying transcranial magnetic stimulation to healthy human adults indicates that the inferior frontal gyrus plays a key role in mediating imitation. Studies of patients with brain damage indicate that the left inferior and superior parietal lobules and postcentral gyrus are also likely to be involved. Mirror neurons, cells that discharge when an action is observed and also when the same action is executed, have been found in these areas, and in corresponding areas of the monkey brain.

It has taken more than 100 years, sometimes with bitter controversy, and much hard labour to find a crisp definition of imitation and reliable ways of detecting it in human and nonhuman animals. Researchers have kept going, despite the difficulties, because copying the topography of body movements is thought to be an indicator of cognitive complexity, and a potent force in cumulative cultural evolution.

Cognitive complexity

In common with Edward Thorndike, writing at the end of the nineteenth century, biologists, psychologists, and philosophers have long assumed that imitation requires complex cognitive operations that are beyond the capacities of all or most nonhuman animals. No one who supports this view has spelled out what the operations involve. Instead, imitation is said to require 'self-consciousness', 'symbolic thought', or 'intermodal matching'. Although these terms have not been unpacked into a mechanistic or computational theory, they express a powerful intuition that imitation is difficult. As Andrew Meltzoff put it, imitation transforms "the seen but unfelt" movements of the model into "the felt but unseen" movements of the observer. This correspondence problem is maximal for facial gesture imitation, where the observer cannot see her own action at all, but it is also significant for whole-body movements such as bowing (Figure 2) and joining hands behind the back. For facial expressions and whole-body movements, I see very different things when I watch you performing an action, and when I perform the same action myself. Assuming that imitation requires me to know that your action and mine look alike from a third-party perspective, but unable to explain how the imitator could know this — how the cognitive system could transform a sensory into a motor representation — researchers have guessed the process is complicated and given it placeholder labels such as 'self-consciousness'.

Viewed as a sign of cognitive complexity, imitation has been important in research on the evolution

Figure 2. The correspondence problem.
When one agent observes another performing a facial gesture or whole-body movement, such as bowing (left), they see a different spatial configuration than when the observer performs the same movement (right). Confronted with this correspondence problem, it is not possible for the observer to imitate by adjusting his motor output until his own action looks to him like the action of the model. So how does the imitator's cognitive system convert the "seen but unfelt" movements of the model into the "felt but unseen" movements of the self? (Left image courtesy of Depositphotos; right image from anaterate/Pixabay.)

and development of human cognition. Studies purporting to show that nonhuman apes do, or do not, 'ape' are thought to tell us whether advanced intelligence began to evolve before our last common ancestor with other apes. Similarly, reports of gesture imitation in newborn babies have inspired and fortified the idea that major components of the human cognitive toolkit are genetically inherited.

The idea that imitation is a marker of cognitive complexity has also led researchers to distinguish firmly between motor and vocal imitation. Motor imitation is more commonly known simply as 'imitation', copying the topography of body movements. Vocal imitation occurs when birds, cetaceans, and humans copy elements and sequences of speech and songs. Vocal imitation is important for cultural inheritance, but it is not thought to be a sign of cognitive complexity because it does not pose the correspondence problem. I hear similar things when I produce a vocalisation and when I listen to you producing the same vocalisation. Therefore, I could copy a sound you make by simple trial-and-error, varying my vocal output until it matches my memory of the sounds you made. Likewise, emulation does not pose the correspondence problem because I could reproduce your effects on objects (for example, moving food with a rake) by tinkering around until the look of my objects matches the look of yours.

Cumulative culture

Turning from cognition to culture, many biologists have seen imitation as the most important genetic adaptation supporting cumulative culture — see my *Current Biology* Primer on culture, Heyes (2020) — a process that enabled humans to dominate their environments through technology. According to this view, imitation is a cognitive capacity produced by genetic evolution to support cultural evolution. It is an analogue of DNA replication, allowing behaviour to be inherited with high fidelity and improved over generations. Claudio Tennie is the most prominent contemporary exponent of the view that imitation is crucial for cumulative culture: he argues that 'form copying' is distinctively human. Other apes use tools — for example, crack nuts using hammer and anvil stones — but they do not learn tool-use through 'form copying', and therefore their technology has limited potential for improvement. If 'form' refers to body movement topography (rather than sequential features of an object or body movement), this implies that imitation is crucial for the cumulative cultural evolution of technology.

The idea of a close association between imitation and culture has been endorsed and reinvented repeatedly since the beginning of the twentieth century, but in the last decade it has lost favour. One reason for the decline, although dull and definitional, should not be overlooked: now that imitation refers to copying the topography of body movement, the claim that imitation is important for culture has a much more specific meaning. When Richard Dawkins, Robert Boyd and Peter Richerson asserted in the 1980s that cultural evolution depends on imitation they meant only that cultural evolution requires social learning.

But there are more substantial reasons to doubt that imitation played a key role in the emergence of human technology. First, cognitive archaeologists, including Dietrich Stout, have found that contemporary humans require hundreds of hours of hands-on practice to make Acheulian hand axes, the teardrop shaped stone tools providing the first evidence of cumulative culture in hominins. Any contribution of imitation to the development of knapping skill is dwarfed by the perceptual and attentional capacities required to distinguish effective from ineffective strikes, and a lot of patience is needed to persist with such slow learning. Second, transmission chain experiments, pioneered by Christine Caldwell, indicate that children and adults gain as much by observing the products of others' labour as they do by observing the labour itself. For example, when each of a chain of groups builds a tower from raw spaghetti, the height and strength of successive towers increases as much when members of the next group observe the tower-making behaviour of the previous group (imitation possible) as when the next group is allowed to view only the tower made by the previous group (imitation impossible).

So, should we conclude that, after all, imitation is *not* important for cumulative culture? That is the trend among cultural evolutionists such as Kevin Laland, Michael Tomasello and Andrew Whiten. They now list imitation as just one among many psychological ingredients of cumulative culture, with an unspecified role. This one-of-many approach is welcome in recognising that a wide range of psychological processes contribute to culture, but it runs the risk of side-lining imitation before its central contribution to human evolution has been fully investigated.

Task analysis suggests that imitation, narrowly defined, was never a good candidate for the cultural inheritance of technology, but that it is indispensable for the cultural inheritance of gestures. The difference between successful and unsuccessful tools lies in the topography of objects, not of body movements. When a stone knapper is producing a hand axe, whether the next strike detaches a flake, making the blade sharper, or destroys the whole project by shattering the core, depends on the location, force and direction with which the hammer stone hits the core — not on the body movements used to wield the hammer. The right interaction between the hammer and core is easier to achieve with some body movements than others — for example, when the hammer is gripped with the whole hand — but this would swiftly become apparent to the novice through his own experience. In contrast, the difference between successful and unsuccessful gestures depends crucially on how parts of the body move relative to one another. If I lower rather than raise my eyebrows, I am expressing doubt rather than surprise; the ‘ok’ sign is meaningless unless the tips of the forefinger and thumb come together; shaking the upper body is ‘shimmying’ only if the shoulders move back and forward in alternation. Consequently, imitation is likely to play a major role in the cultural inheritance of communicative and ritualistic behaviours — behaviours that are known, through the work of Cristine Legare and others, to have a powerful effect on cooperation within groups.

This task analysis suggests that — like birdsong and whale song dialects and human languages — nonverbal communicative and ritualistic human behaviours may be targets of cumulative cultural evolution, they may get better at promoting group cohesion, because they are inherited through imitation. In addition, communicative and ritualistic behaviours, learned by imitation, may have contributed indirectly to the cumulative cultural evolution of technology by supporting risky forms of cooperation such as long-term teaching and division of labour.

Imitation as a cognitive gadget

The cognitive gadget theory of imitation, also known as the associative sequence learning theory, challenges both the cognitive and the evolutionary assumptions that guided previous research. It suggests that relatively simple cognitive mechanisms enable imitation, and that these mechanisms were assembled from old parts by cultural rather than genetic evolution.

According to the gadget theory, simple cognitive mechanisms are enough for imitation, because imitators do not need to know that their action is similar, from a third-party perspective, to the action of the model. Instead of computing the similarity between seen and felt actions, agents learn binary associations between observed and executed actions via temporal contingency. Whenever an agent gets temporally correlated experience of seeing and doing the same action — for example, sees a shoulder moving forward when moving her own shoulder forward — basic mechanisms of learning connect a visual representation with a motor representation of that action; the two representations enter a matching vertical association. Once a vertical association is in place, sight of the action activates the motor representation enabling imitation of the action. But vertical associations do not only allow imitation of actions performed by the agent in the past (sometimes called ‘mimicry’). Agents learn a large set of vertical associations and these act as a vocabulary for imitation of new actions (‘true imitation’ or ‘imitation learning’). When a novel action sequence is observed, motor representations are activated in the order the action components are perceived. For example, in the case of shimmying, the observer sees: left shoulder forward, left shoulder back, right shoulder forward, right shoulder back. Successive activation of these motor representations allows the observer to learn the new movement sequence as if she were practicing by moving her own body.

‘On the inside’, learning vertical associations requires only the mechanisms of associative learning that produce Pavlovian conditioning in a broad range of vertebrate and invertebrate species. ‘On the outside’ it requires a complex cultural environment to provide a rich supply of correlated sensorimotor experience. For example, correlated experience of seeing-and-doing is provided by optical mirrors, action words, ritual practices involving synchronous action, and child-rearing practices that encourage adults to imitate infants and children.

The gadget theory has been tested over the last 20 years using behavioural and neural measures with adults, children and nonhuman animals. It is consistent with the evidence that nonhuman apes and dogs can be trained to imitate, and that animals raised by humans — apes, dogs, and parrots — are superior imitators. According to the gadget theory, training works by establishing vertical associations, and the active ingredient of ‘enculturation’ is exposure to the artifacts and social practices that foster imitation in children. It is also supported by evidence that human children imitate vocalisations, hand gestures, and actions that make a noise (for example, banging a hand on a table), before they imitate facial expressions and whole-body movements. Self-observation (for example, listening to your own actions or watching your own hand in motion) is sufficient to form vertical associations for the former but not the latter.

Most striking, the gadget theory has been tested and confirmed by experiments showing that the propensity to imitate, and the properties of mirror neurons, can be transformed by novel sensorimotor experience. For example, passive observation of index finger movement normally activates index finger muscles in the observer’s hand. However, research led by Caroline Catmur has shown that, after training in which people respond to index finger movements with little finger movements, and *vice versa*, observation of index finger movement produces more activity in little finger than in index finger muscles. Automatic imitation is converted by sensorimotor learning into automatic counter-imitation.

Figure 3. Neonatal imitation.
In one of many replication failures, a study in 2016 testing 100 human newborns with nine gestures — including tongue protrusion, mouth opening, sad face, and happy face — did not find any evidence of imitation. (Image courtesy of Virginia Slaughter.)

Neonatal imitation

The cognitive gadget theory of imitation is at odds with reports that newborn human babies can copy a range of facial and manual gestures. If newborns can do it, imitation is genetically rather than culturally inherited; a cognitive instinct rather than a cognitive gadget.

Neonatal imitation has been controversial since it was first reported by Andrew Meltzoff and Keith Moore in the 1970s. In the last five years, a group in Brisbane, led by Virginia Slaughter, has tried to resolve the controversy by running a large-scale study, testing 100 newborns, and a meta-analysis of previous studies encompassing 336 effect sizes. The large-scale study found no evidence of imitation across nine actions — including tongue protrusion, mouth opening, sad face, and happy face (Figure 3) — each tested at four time points after birth. The meta-analysis sought and did not find a modulating influence on neonatal imitation of 13 methodological factors previously cited as reasons for replication failure (for example, model identity and response interval). However, the meta-analysis did find a modulating effect of researcher affiliation; a small number of laboratories are more likely than others to find large positive effects. Furthermore, across the full range of previous studies, from 1977 to 2016, there were statistical effects indicating publication bias: that experiments have been conducted and, finding no evidence of neonatal imitation, have not been published.

It is notoriously difficult to provide evidence of absence, and there are certainly developmental psychologists who continue to believe in neonatal imitation. However, in combination with the evidence that imitation depends on sensorimotor learning, outlined above, the Brisbane studies suggest that newborns do not imitate.

Conclusion

Decades of labour to purify the meaning of imitation, and to find reliable methods of detection, were motivated by the belief that imitation involves complex cognitive processes and played a key role in the cultural evolution of human technology. The fruit of this labour has been evidence that the motivating assumptions were not quite right. Recent research indicates that imitation depends on simple cognitive processes, found in a wide range of animals, and that other psychological mechanisms — encoding sequences of object transformations, supporting visual discrimination, and promoting patience — have played a more important role in the emergence of technology. But rather than undermining the importance of imitation, the latest developments make the relationships between imitation, cognition, and culture yet more intriguing (Figure 1). They suggest that imitation plays a dominant role in the cultural evolution of communicative and ritualistic behaviour, and that the capacity to imitate is itself a product of cultural evolution. Like the cognitive processes involved in reading, the mechanisms of imitation are cobbled together from old parts through social interaction during development. Like simple technology, at the population level they are specialised by natural selection operating on culturally inherited rather than genetically inherited variants. Imitation is a cultural gift that goes on giving, a product and a process of cultural evolution.

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