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Imitation: What animal imitation tells us about animal cognition

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Abstract

Imitation of actions is widespread in the animal kingdom, but the mental capacities thereby implied vary greatly according to the adaptive function of copying. Behavioral synchrony in social species has many possible benefits, including minimizing predation risk and using food resources optimally, but can be understood by the simple cognitive mechanism of response facilitation by priming. Imitation can send a social message, either one of short-term meshing or group identity. Where the imitative match is opaque, as in neonatal imitation, the correspondence problem may imply an innate system of behavior matching; but in other cases, no more than priming may be involved, although there are persistent suggestions that great ape imitation implies empathic abilities. Imitation in the service of learning new skills by following another's example can be divided into contextual imitation (when to employ a familiar action, and to what problem) and production imitation (learning of new skills by imitation). Cognitively, the former requires little more than response facilitation, whereas production imitation needs at least the ability to extract the statistical regularities of repeated action and to incorporate the result into hierarchical program-construction. Among our close relatives, only the great apes show much evidence of production imitation of actions, along with the ability to selectively imitate the most rational components of what they observe.

For most biologists, the term 'imitation' refers to morphological adaptations used for camouflage or to mimic the appearance of another species. It is only relatively recently that there has been intense interest in the imitation of *behavior* by animals, usually known as action imitation¹. There are three important reasons to study the imitation of behavior in animals, as well as humans. Firstly, like morphological imitation, it can improve individual fitness under specific conditions². Secondly, imitation of behavior has a potentially important role to play in the evolution and development of culture³. Finally, understanding the mechanics of how animals and humans

imitate behavior can tell us a lot about the mental capabilities of the imitators, so it is of special interest to cognitive psychologists ⁴.

In this review, we concentrate on the last of these three points of interest, discussing the explosion of research that now addresses the imitation of behavior among animals, with respect to the implications for cognitive psychology. We outline the various kinds of imitation that have been described, and discuss what cognitive mechanisms are potentially required for these different forms, drawing from psychological knowledge about imitation in humans where appropriate. One important step in reaching these aims will be to elucidate the potentially confusing array of terms that have been coined to describe different types of action imitation. Following Byrne ⁵, we shall use the three connotations of the term 'imitation' that are evident in dictionary definitions to organize this review; imitation to resemble, imitation to convey a message, and imitation to learn by example.

Imitation to resemble

One objective of imitation in everyday life is to resemble as closely as possible the individual whose behavior is copied. There are several circumstances in which animal imitation of this sort might be adaptive; most are cases where the imitation is immediate and the result is behavioral synchrony. Predators are thought to target individuals that stand out in some way, so behaving just like other members of a flock or herd may reduce risk. A general tendency to match the current actions of others, when in a group, might therefore be expected to evolve in social species. Moreover, by copying the current behavior of other group members, individuals of social species can potentially gain from others' knowledge of a range of costs and benefits that are associated with place, including local level of predation risk, locations of optimal feeding sites, and what is edible there ⁶. It is important to note here that these gains are derived automatically from behavioral matching, not as a result of knowledge transfer.

Behavioral synchrony, or contagion, is in fact reported in a wide range of social animals, and extends to a detailed level of activity copying, such as preening together, or the nearly simultaneous turning of each individual in a flying flock of shorebirds that generates such spectacular aerial acrobatics ⁷. A related phenomenon of goal contagion has been reported in humans, whereby perceiving the goal-directed behavior of another can lead the observer to adopt the same motivation, pursuing the goal as their own ⁸. Goal contagion is most likely to occur when the observer and original actor share group membership, and it is therefore thought to be a mechanism by which groups coordinate their activities and behavior ⁹. Loesch et al argue that this is a specifically human phenomenon because it requires an understanding that a goal can be attained in a number of equivalent ways. Nevertheless, reviewing animal imitation, Whiten and Ham ¹⁰ proposed much the same in animals, using the term goal emulation: an individual, seeing a conspecific gaining some valuable reward, might be influenced to set that reward as its goal. Goal emulation may underlie public information use in animals, whereby an individual uses indirect social information from the behavior and activities of others to make predictions about environmental parameters, such as food palatability or safety of a particular place ^{11,12}.

Cognitive implications of behavioral synchrony

Imitation that produces immediate behavioral synchrony requires an individual to recognize specific actions in others' behavior that are already in its own repertoire. This sort of copying may be understood simply as response facilitation, where seeing an action 'primes' the individual to do the same ^{3,7,13,14}. No special mechanisms are required to understand performance of the action, as the behavior is already part of the copying individual's repertoire. Priming by response facilitation accounts for behavioural synchrony both in animals whose behavioural repertoire is fixed, and those whose repertoire is more flexibly acquired and complex. In the former, observing the action releases the equivalent fixed action pattern in the observer; in the latter, the complete sequence of actions can also be primed as a unit because the behavior is not new to the observer. The case of behavioral copying by goal emulation can also be understood in this

mechanistic way, if seeing the outcome of an action 'primes' the observer to target that outcome as its next goal¹³; again, no special mechanisms are required.

Imitation to convey a social message

The functional significance of 'imitating to resemble' lies in the outcome of the copying; the resulting behavior can directly increase the chance of predator avoidance or benefitting from the environmental knowledge of others. In contrast, when imitating to convey a social message, it is the act of copying itself that is functionally significant, in terms of conveying a social signal. Humans often copy the facial expressions, mannerisms and posture of other people, apparently as a signal of affinity and with the effect of increasing pro-social behavior¹⁵: 'imitation is the sincerest form of flattery'. Many greeting signals and ceremonies of animals might be thought of as imitation of this kind (although these actions are often stereotyped so they may simply be evoked by the social circumstances).

In some instances, the social message is not wholly obvious. Contagious yawning, common among humans, has also recently been observed in chimpanzees¹⁶⁻¹⁸. One possible function is that synchronization of sleeping is adaptive, or was in hominin ancestry when nocturnal activity would risk predation^{19,20}. Yawning is also contagious in dogs, with both human and dog models, but the effect seems much weaker^{21,22}. (There are also reports of contagious yawning in gelada baboons and stump-tailed macaques, although the authors of the latter suggest that the effect in these monkeys may have been due to increased tension or anxiety²³.)

Very young, even newborn, infants copy the facial gestures of adults interacting with them, for instance smiling or tongue-protrusion²⁴. This 'neonatal imitation' may signal alert awareness and cognitive competence, and thereby function to increase maternal investment in the child. Neonatal imitation has also been described in chimpanzees^{25,26} and macaque monkeys²⁷, and during play juvenile orangutans mimic their partners' open-mouth display – an expression homologous to human smiling or laughter²⁸.

Although adult monkeys have sometimes been described as unable to imitate^{29,30}, they react strikingly when their actions are immediately mimicked by human experimenters, and prefer to interact with humans who have previously imitated them, suggesting that signaling social connection by imitating is part of the natural communicative repertoire of monkeys, and it acts to promote affiliation^{31,32}. The recognition of imitation by monkeys is apparently based on detection of structural and temporal contingencies, and is indicated by increased visual attention to the imitator; this has been called 'implicit recognition'³³. All four great ape species are able to go beyond this, 'explicitly' recognizing when they are being imitated, as evidenced by engaging in testing behaviors - behavioral patterns enacted while facing the imitator, that are not part of the described repertoire of the species or that are uncharacteristically long repeats of actions³³.

Behavioral norms and group membership

In all the above cases, any social message conveyed is an immediate one, but humans also show a sort of imitation when they converge on the behavioral norms of their social group. Social behavioral norms are important in helping us decide how we should act, and they convey the message of group membership – and, conversely, out-group exclusion³⁴⁻³⁶. Conformity to group norms of behavior has long been studied in social psychology³⁷.

In chimpanzees and rats, a general tendency to match the actions of the majority of the group has been reported: this has also been described as conformity^{38,39}. Individuals that have already discovered how to open a puzzle box satisfactorily (chimpanzees), or found a food that is palatable (rats), switched to the actions and choices of the majority. In these experiments, the conformity was valueless but the behavior may have been a by-product of a trait that functions in reducing exposure to risk in unpredictable environments. Certainly, both chimpanzees and rats have been noted as conservative in behavior, for instance being remarkably cautious about trying novel foods^{40,41}.

It is tempting to presume that behavioral conformity among the great apes relates to a sense of group identity, as it does in humans. Male chimpanzees certainly show violence to members of other communities in a way that is disturbingly human⁴². However, there is currently only circumstantial evidence to suggest that intercommunity violence is predicated on non-conformity. Crockford et al⁴³ found that the pant-hoot vocalizations of male chimpanzees in three contiguous communities (i.e. in individuals that are likely to interact violently with each other) were acoustically distinct, whereas the pant-hoots of males living in a community 70km away (who would never engage in intercommunity violence with the other) were no more different than expected by chance. Thus, chimpanzees apparently actively modify their pant-hoots to be different from those of neighboring communities and more like their own group, and it is plausible that these group-specific pant-hoots are the basis on which chimpanzees decide to attack or not.

Cognitive implications of imitation as a social signal

The cognitive processes that underlie the numerous forms of social mimicry are likely to vary depending on the actions copied and the motivation behind the copying. If there is a reasonably transparent perceptual relationship between the action as performed by the model and the imitator, then, as in imitation to resemble, response facilitation by behavior priming is a sufficient explanation¹⁴. Transparency of perceptual relationship is required, as there must be a straightforward way of recognizing that the actions are the same, such as an overlap in the perceptual features between the act as done by the model and the imitator⁴⁴. For example, hand actions done by a conspecific and by the self will not look the same, but the actions retain invariances over the difference in visual perspective: quite enough to recognize that they are the same. The discovery of the mirror neuron system, a population of neurons found in macaque monkey cortex that respond equally to a purposive gesture whether performed by the monkey itself or another^{45,46}, is consistent with this mechanism of response facilitation^{47,48}.

With neonatal imitation, however, the facial gestures copied are presumably opaque; there can only be minimal perceptual overlap in visual appearance, as the infants have not yet recognized their own faces in mirrors²⁴. Response facilitation therefore cannot account for this imitation. The resolution of this so called correspondence problem requires an innate system that matches observed facial gestures with the motor commands needed to imitate them. It is difficult to determine how extensive a set of correspondences might exist, when the neonate has such a limited motor repertoire; theorists range from those who attribute hard-wired matching of just a few key facial gestures⁴⁹, to those who posit in the (human) infant the ability to match 1:1 the complete motor repertoire⁵⁰.

Facial mimicry has been linked to empathy, because copying the emotional facial expressions of others can induce the corresponding emotional feeling in the imitator (a form of emotional contagion)⁵¹. Contagious yawning may also be dependent on empathy. Platek et al⁵² demonstrated a correlation in humans between decreased susceptibility to contagious yawning and deficiencies in empathic tendencies, self-recognition, and theory of mind abilities. One test of this is to examine individuals in whom empathy has not fully developed. Normally developing children under the age of four do not show empathy in the same way as adults, and seven-year old children with autism spectrum disorder (ASD) are known to have severely impaired empathy. In both cases, the children have been found not to show contagious yawning^{16,53}. Thus, the observations of facial mimicry and contagious yawning in great apes could be posited as further evidence of their empathic abilities^{28,54}. However, it may be that emotional contagion based on facial mimicry or contagious yawning is largely involuntary and can occur without implying any capacity for theory of mind; understanding of another's emotion is not necessary, and the spread of the feeling may happen without awareness of where it originates from⁵⁵. The fact that dogs yawn contagiously may stem from an increased sensitivity to human behavior and communicative cues as a result of domestication, rather than a consequence of any general empathic ability⁵⁶.

Explicit recognition of imitation in great apes means that they, like human infants, can recognize the contingency between their own actions and those of others in a social interaction, and understand the impact that their actions have on others. Such explicit recognition and understanding of imitation has been suggested to promote - or even form the basis of our

understanding of - social causality, intentionality in others, and the concept of 'self as different from other' ^{4,57,58}. There is no evidence for this explicit recognition in monkeys, which is consistent with other reports that apes have more developed social cognitive skills ¹⁴.

Where lasting consistency in mimicry is seen, a tendency to conform is additionally required. Evidently this can override what has been learnt from individual experience; and the bias to social learning is frequency dependent, being more potent if more individuals are showing the same actions. In humans, conformity is thought to imply an awareness of the beliefs of the group and thus rely on 'mentalizing' or theory of mind abilities ⁵⁵. It is not yet clear if the conformity effects observed in primates or rats are the same as those observed in humans, however, so it is too soon to conclude that conformity as observed in non-human animals is also indicative of mentalizing ³⁸.

Following the example

Learning how to do something from seeing it done might seem the most obvious sense of imitation, yet scientific interpretations of it have varied from a cheap monkey trick to an exalted pinnacle of animal cognition. Even now, it is unclear which species of animal have the ability to learn by imitation. Partly this relates to semantic confusion, between learning *by imitation* and learning *that follows from imitation*. As we have noted already, the tendency to copy the actions of nearby conspecifics occurs widely among animals and can be straightforwardly explained in most cases as a result of priming those responses that match actions seen. Where animals are engaged in instrumental activity, this behavior matching tendency may result in a naïve individual applying actions that are in fact appropriate to the task sooner than it otherwise might. If that brings success the animal will often learn to use these actions again.

A tendency to copy — whether described as imitation, response facilitation or priming — can therefore accelerate learning, and indeed such benefits may have contributed to the evolution of response facilitation in some species. But the learning itself is consequent on getting a favorable result: reinforced trial-and-error learning, in behaviorist jargon. Most experimental tests of animal imitation can be explained in this way, because the experimenters presented the task immediately after the subjects had observed a skilled performer, with rewards contingent on success.

Learning *by imitation* can be shown by introducing a delay before testing, as has been done successfully with both quail and budgerigars ^{59,60}. In these cases, the animal evidently learnt to link an action that was already in its repertoire — for example, pulling, pecking or stepping — with a particular task, by seeing it used. This has been described as contextual imitation, because what the animal learns is *when* and *where* to apply an existing behavioral tactic in its repertoire ¹⁴.

Contextual imitation

Contextual imitation amounts to learning to employ an action already in the repertoire, in different circumstances, as opposed to learning the form of a new action. Contextual imitation may aid problem-solving, whereby a behavior in the species-typical repertoire is applied to a novel problem or used in novel circumstances (as in the budgerigar and quail cases, cited above), after observation of a conspecific doing the same. Dogs have been shown to imitate behaviors already in their repertoire in novel circumstances, in situations when the model was a human or another dog ^{61,62} - although like chimpanzees, they do not imitate intransitive actions from observing another dog perform the action on command ⁶³.

A range of experiments with birds have shown that upon seeing a conspecific using one particular action to obtain food from an unfamiliar container, they will use the same action when it is given the chance to open a similar container, whereas individuals shown a different efficient action acquire that technique instead ⁶⁴⁻⁶⁸.

Similarly, in several species of primate, including chimpanzees, capuchin monkeys *Cebus apella*, and marmosets *Callithrix jacchus*, observing a demonstration has been shown to cause

individuals to apply a particular technique to an unfamiliar problem⁶⁹⁻⁷². For instance, seeing a human use a twisting motion to remove a bolt which locks a box containing food, makes the non-human primate observer more likely to twist rather than pull the bolt out, and vice versa. Crucially, in all these cases, both bird and primate, the two methods are equally effective. This two-action methodology has become the paradigm case for experimentally demonstrating what is sometimes called 'true imitation'^{68,73}. However, in all of these cases it is most likely that a familiar action already in the repertoire is applied to an altered range of environmental stimuli. The result under many circumstances will be improved fitness, since effective actions are prompted into use, but no new actions need be learnt.

Production Imitation

The Holy Grail of animal imitation studies is to discover a species that is capable of learning a *new* motor skill by observation. Another species, that is: there is no doubt that humans can learn in this way, even though in western cultures it is now more common to acquire new skills with some form of verbal instruction. Examples of human skills that seem particularly dependent on learning by imitation are sushi-making, blacksmithing, and stone-working by medieval masons; that is, those that require precise manual manipulations. This kind of imitation, called production-imitation, involves an individual constructing a behavioral routine new to it, out of components in its pre-existing repertoire, from watching a more expert model^{14,74}. Of course, it is unlikely that an entirely novel task will be mastered in a single viewing without practice or relevant prior experience; but crucially, production imitation allows some part or outline of the task to be put together from observation before ever trying it out.

Program-level imitation

The requirements for imitating a good example are quite different to those cases where the function is to resemble another individual or give out a social message. Fine detail is unimportant as long as the right result is obtained, and indeed it is likely that details are better acquired by individual experience. A child, for instance, cannot copy the precise way her mother operates on objects, as she has smaller hands and less strength: precise copying of every action would be maladaptive. Moreover, the potential benefits of learning by imitation vary with task difficulty: where complexity is low, purely individual learning is to be expected, avoiding the costs of finding and watching a skilled model. It is therefore in learning the most technically complex and organizationally involved tasks that imitation should pay.

Complex skills cannot be assembled in a single attempt, so we should expect acquisition to be hierarchical, progressively building up larger and larger components⁷⁵. That is true whatever learning mechanism is involved, but if the *gist* of the right approach can be discerned by imitation, learning can progress by organizational leaps rather than by plodding addition of each action in sequence. Observational learning of the organizational gist of a task has been termed 'program-level imitation'^{74,76}. Program-level imitation is nicely illustrated by an example from vocal imitation, rather than action imitation: when a child copies a word she has not heard before. The child's sound pattern is typically quite different to that of the adult model, with much higher-pitched vowels and often systematic simplification of consonant clusters. This shows that what is copied is the program-level gist of the word, a new way to assemble the motor programs for producing vowels and consonants — which are already in the child's repertoire. Crucially, this process of *synthesis* depends on prior *analysis* that parses the adult's sound into its component units. A tame parrot, in contrast, copies the overall sound contour of a human word: action-level rather than program-level imitation.

Unsurprisingly, the strongest evidence for program-level imitation of actions by animals comes from the technically complex achievements of the great apes. For instance, chimpanzees in northern Congo regularly make two different types of tool in advance of arriving at sites where subterranean termites can be found. A sturdy rod is used to punch a hole deep enough to reach the termites, then a more delicate probe is used to agitate the termites, which bite onto the stem and can thus be fished out⁷⁷. Rwandan gorillas regularly process a local species of stinging nettle: stripping up stems to detach the leaves, twisting off the petioles, sometimes repeating both

these steps several times to accumulate a larger handful, then pulling up the leaf-bundle and folding it over the thumb, finally re-grasping the package before ingestion ⁷⁶. In both chimpanzee and gorilla examples, the actions used at each processing stage are highly specific and it is extremely unlikely that each single individual could invent the appropriate process without some information from an expert model. In these cases, the individuals concerned had prolonged opportunity for casual observation of skilled models; it may therefore be that the production imitation of non-human great apes may be limited to situations where they can watch the skilled behavior many times over.

Rational imitation of actions

18-month infants, when shown how to turn on a light by an adult who leans forward to press the switch with their forehead, often copy the whole performance — even though they could use a hand more easily ⁷⁸. But, as described in the now classic study of Gergely et al ⁷⁹, when the task was modified so that the adult was holding a cloak around their shoulders, 14-month old infants were much less likely to copy the use of the forehead than they were when the adult used her forehead despite having nothing in her hands. It appears that the infant is able to compute that the forehead is only needed *because* the hands are occupied, and can therefore be ignored. Gergely et al concluded that infants evaluate the causal necessity of the model's actions, and only copy those actions they consider to be necessary and thus rational in attaining the goal. It is important to note that this 'rational imitation' only occurred if the action was paired with ostensive cues: if no ostensive cues were given to the infant, they copied the head movement to the same degree in both conditions ⁸⁰.

Something similar to rational imitation has been seen in chimpanzees. Horner and Whiten ⁸¹ presented chimpanzees with a demonstration of how to get food from a puzzle box that was either transparent or opaque: using a tool first to tap the outside of the box and then insert it into the box to retrieve a reward. When the box was opaque, the apes copied both the tapping and inserting actions used by the experimenter; but when it was transparent, revealing that the first action made no contact with the food, they ignored it and copied only stick insertion¹. Possibly, this behavior might have not have relied on rational understanding of causality; for instance, the chimpanzees might have followed the rule, 'where you can see what happens, only copy actions that make contact with the reward; if not, copy everything'. Subsequently, however, Buttleman et al ⁸³ have tested chimpanzees using the original Gergely et al paradigm. Their apes observed a human model operating switches with their feet or head, when their hands were either free or occupied with carrying a bucket. Chimpanzees that saw the model's hands to be occupied, used their own hand to operate the switch; but if they observed an unexpected body part used by a model with hands unconstrained, they often copied the use of this body part. It seems that, like preverbal infants, chimpanzees imitate rationally: in some way, they can understand the logic of how actions achieve their ends, and choose to copy only those components of action that seem to be necessary. Even dogs have now shown selective imitation ⁶¹. Subjects observed a demonstrator dog pull a rod with a paw, whereas the preferred method for dogs is to pull the rod with the mouth. When the demonstrator dog was holding a ball in her mouth, and so 'justifying' the use of the paw rather than the mouth, test dogs did not imitate the use of paw but simply used their mouths. But subjects who saw a demonstration in which the model had no ball in her mouth copied paw action. Whether this ability reflects the long period of their domestication and selection for the ability to respond helpfully to human behavior, or simply taps the native understanding of their wild ancestors, will only be answered by investigating imitation in wolves. The selective imitation of chimpanzees and dogs appears to be based on rational assessment,

¹ Interestingly, when Horner and Whiten gave the same apparatus to children, the 4 year olds did not show the rational deletion of the unnecessary action (tapping the clear box). This has now been termed 'overimitation', whereby children persistently reproduce the unnecessary actions of adults. Overimitation was initially thought to be simply a demonstration of social admiration or imitative habit, but it has recently been argued that children actually encode all of the adult's actions as causally meaningful. See Lyons (2007)⁸² for a discussion of this human phenomena.

but is not apparently reliant on ostensive cues, as in the case of human infants.

Cognitive implications of learning by imitation

As contextual imitation involves using actions that are already in the repertoire, it may parsimoniously be assumed to rely on the same cognitive processes as social mimicry, that is, response facilitation by priming: if the primed action is successful, it will be used again. Where a novel action-sequence is learned, as in program-level imitation, more must be involved. In wild great apes, there are many cases of complex, population-wide skill that imply the use of program-level imitation: but in all of them, repeated observation of skilled model is possible. For this reason, the imitative ability of great apes can be explained by a perceptual process in which the statistical regularities of complex but repeated behavior are detected⁸⁴. At the simplest, this 'behavior parsing' – using the statistical regularities of a multiply-observed action sequence to detect organizational structure – can ground production imitation in any species with the ability to construct hierarchically embedded programs of motor action^{84,85}. Experimentally, the statistical structure of action has been shown sufficient to allow human infants to parse human motion, even in the absence of any understanding of what action is being performed⁸⁶, and it is therefore likely that behavior parsing forms a primitive part of the human imitative ability. The ability to construct hierarchical programs of motor action is probably part of a much wider constellation of general planning and problem-solving mechanisms, which have yet to be studied in any detail in animals. (In humans, they have largely been studied in the context of verbal reports or quasi-mathematical tasks^{87,88})

Behavior parsing itself may not be best viewed as 'part of an imitation mechanism', since what it delivers is of far more general utility. Parsing enables 'perception' of hierarchical programs lying behind output behavior. This is a crucial aspect of discerning the plans of other individuals, if those plans can be imagined. On this interpretation, behavior parsing paves the way for identification of the intentions of other individuals, including the level of intentionality that is sometimes called "theory of mind"⁸⁹. It may therefore turn out that all species that show program-level imitation can also represent the intentions of others, and thereby compute new actions based on these unobservable constructs. This hypothesis is consistent with recent observations that great apes – the taxon for which there is the best evidence of program-level imitation – understand the actions, goals and intentions of others (see^{90,91}).

Human children – and now, chimpanzees and dogs - go beyond the relatively unselective process of behavior parsing when they imitate, demonstrating rational imitation. Rational imitation requires recognition and selective interpretation of the action, the goal state, and the situational constraints and the cause and effect relations between them: essentially, a mental model of causal structure. The role of ostensive cues in rational imitation is not yet fully understood. It may function to indicate to infants that they are about to receive novel information, related to human-specific pedagogy⁹², but further investigation of the use of ostensive cues towards animals is required.

The neurophysiological systems that support the various cognitive mechanisms involved in imitation are not yet fully identified, and the question remains highly contentious. The mirror neuron system (MNS), which relates to response facilitation, has been suggested to underlie multiple forms of imitation, including facial mimicry, neonatal imitation and contextual imitation^{48,93-96}. However, as Southgate and Hamilton⁹⁷ point out, imitation is more than just direct matching of actions across bodies, which is strictly what the MNS allows for; as well as visual analysis and motor control, the goals of actions must be represented, and there must be selection of what and when to imitate. Therefore, at least program-level imitation and rational selection of which actions to imitate must rely on more than just the MNS. Indeed a recent meta-analysis of fMRI studies of action imitation in humans concluded that parietal and frontal brain regions extending beyond the MNS are implicated, particularly the premotor cortex, and superior and inferior parietal lobules⁹⁸.

Conclusion

Animal imitation has much to tell us about animal cognition. Studies of behavioral synchrony, social mimicry and contextual imitation have demonstrated that response facilitation is pervasive. This relatively simple mechanism allows animals to perform a wide range of highly functional behavior; thus, determining the limits of this learning mechanism should prove to be an illuminating exercise for our understanding of animal cognitive processes. A consistent theme in this review has been that chimpanzees, and other great apes where they have also been tested, show imitative abilities beyond those of other animals. Evidence from studies of program-level imitation, explicit recognition of imitation, rational imitation, and perhaps conformity, all suggest that apes are capable of mentalizing about others, and have some understanding of intentionality and causality. The similar performance of dogs on some of these tasks is intriguing, though further investigation is required before we can conclude that dogs share the same capacities as apes. It remains to be seen to what extent other animals that show promise in imitative tasks, such as dolphins and some bird species, share the cognitive skills of apes.

It is important to remember that apparently imitative behaviors may not actually rely on a single cognitive mechanism, nor a single neuronal system. The current classifications of imitation (as well as other social learning mechanisms) are far from perfect³. Much tighter definitions of the various types of imitation are needed, as is much greater understanding of their limitations and interactions with other forms of social and individual learning. Only then will we be able to interpret correctly the results of studies of imitation in animals; to use the conclusions to draw an accurate phylogenetic distribution of imitation; and in turn generate specific hypotheses about the evolution and distribution of particular cognitive capacities.

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Cross-References

Cognitive Biology CogSci-005: Evolution of Cognition

Psychology CogSci-239: Social Learning in Animals

Psychology CogSci-228: Animal Cognition