THE ROYAL SOCIETY

Imitation as behaviour parsing

R. W. Byrne

School of Psychology, University of St Andrews, St Andrews, Fife KY16 9JU, UK (rwb@st-and.ac.uk)

Non-human great apes appear to be able to acquire elaborate skills partly by imitation, raising the possibility of the transfer of skill by imitation in animals that have only rudimentary mentalizing capacities: in contrast to the frequent assumption that imitation depends on prior understanding of others' intentions. Attempts to understand the apes' behaviour have led to the development of a purely mechanistic model of imitation, the 'behaviour parsing' model, in which the statistical regularities that are inevitable in planned behaviour are used to decipher the organization of another agent's behaviour, and thence to imitate parts of it. Behaviour can thereby be *understood statistically* in terms of its correlations (circumstances of use, effects on the environment) without understanding of intentions or the everyday physics of cause-and-effect. Thus, imitation of complex, novel behaviour may not require mentalizing, but conversely behaviour parsing may be a necessary preliminary to attributing intention and cause.

Keywords: great apes; segmentation; hierarchical organization; statistical regularities; intentionality; causality

1. INTRODUCTION

Imitation has fascinated behavioural scientists for more than 100 years (Thorndike 1898), and over this period has acquired many shades of meaning. At the core, however, lie two enigmas.

(i) How is it possible for *actions as seen* to be matched with *actions as imitated*? (the 'correspondence' problem).

(ii) How is it possible for *novel, complex behaviours* to be acquired by observation? (the 'transfer of skill' problem).

Much of the thrust of imitation research in animal behaviour and developmental psychology has focused on the first of these problems, implicitly treating the second as more straightforward.

When attention is restricted to human imitation, this appears at first sight a good strategy. The young child will later develop into an adult who will certainly be able to learn new, highly structured and flexible skills in other ways, including: experimentation and practice, mental planning, explicit teaching or a combination of all three. It is therefore tempting to treat the planning and organizational issues as much the same in imitated and non-imitated behaviour, thus focusing attention on the problem of recognizing correspondence between actions as seen and actions as done. For less sophisticated animals, that becomes a sleight of hand. The ability to organize complex behaviour cannot be assumed for a non-human animal (hereafter, 'animal'), and indeed this may be a greater difficulty even than recognizing correspondence. Moreover,

when the two issues are confronted together, a greater challenge emerges: to understand how the underlying organization of novel, complex behaviour can be perceived, and how what is perceived can be used to guide new learning. This paper will offer some steps towards an eventual solution to this larger problem: how do we detect the organizational structure of observed behaviour in other agents (and consequently acquire new skills by imitation), and how did we acquire this ability?

The long history of imitation research in comparative psychology has, however, bequeathed a useful legacy of terminology, and illustrated that quite effective social learning may be achieved *without* the capacity to imitate. Profiting from this experience can allow several other phenomena to be set aside, allowing clearer focus on the main task.

(a) *Stimulus enhancement, response facilitation and emulation*

In the early history of psychology, persisting today in lay parlance, imitation could refer to almost any case of actions matching in form. E. L. Thorndike's original definition 'learning to do an act from seeing it done' drew attention to the key role which *observation* plays, ruling out cases in which prior observation is unnecessary for behavioural matching to occur (Thorndike 1898). The behaviourist K. W. Spence showed further that rather simple and general behavioural tendencies could aid learning in social contexts. He introduced the notion of *stimulus enhancement*, in which seeing some act done in a particular place or to some particular object would increase the observer's probability of going to that place or interacting with that object (Spence 1937). As he noted, once behavioural exploration is concentrated upon a narrowed range of stimuli, chance discovery of the means of achieving the goal is made much more likely. Numerous cases of social learning, once claimed to show imitation, have proved to

Phil. Trans. R. Soc. Lond. B (2003) **358**, 529–536
DOI 10.1098/rstb.2002.1219

529

© 2003 The Royal Society

be explicable as stimulus enhancement (Galef 1988). Research on animal imitation therefore contracted again, to cases where the form of action matched more or less precisely what was seen. Efforts were thenceforth made to separate out direct behavioural copying from learning about other aspects of the physical situation.

Not all behavioural copying, however, implies that the observer has learned by imitation. A simpler possibility is that a pre-existing response may be facilitated (i.e. made more available) by seeing it done, causing a higher probability of the response occurring subsequently: *response facilitation* (Byrne 1994; Byrne & Russon 1998). Response facilitation involves one of the enigmas of imitation, the correspondence problem, but not the other, the transfer of skill by observation, because to be 'facilitated' the behaviour must exist already within the individual's repertoire. The relationship of response facilitation to stimulus enhancement is evidently close, although here it is a voluntary act that is enhanced or facilitated. Response facilitation and stimulus enhancement may indeed be two manifestations of the same phenomenon: *priming* of neural correlates (Byrne 1994, 1998*b*). Priming neural correlates of aspects of the social situation and environment results in stimulus enhancement; priming neural correlates of action patterns in the current repertoire results in response facilitation. Part of the neural mechanism of response facilitation has apparently been identified, in the mirror neurons found in premotor cortex of rhesus monkeys, *Macaca mulatta* (Gallese *et al.* 1996; Rizzolatti *et al.* 1996, 2002). These cells respond equally to simple, goal-directed manual actions whether made by the monkey itself or an individual it is watching. An experimental paradigm, the two-action method (Dawson & Foss 1965), has shown that facilitation of recently seen, simple manual actions that are part of the observer's normal repertoire does occur in several primate species (e.g. marmosets (Bugnyar & Huber 1997); capuchin monkeys (Custance *et al.* 1999); gorillas (Stoinski *et al.* 2001); and chimpanzees (Whiten *et al.* 1996)). Confusingly, because of the near-exclusive focus on the correspondence problem, this same evidence has been claimed to be the only convincing evidence of imitative capability in animals (see, for example, Heyes 1993, p. 1000). Certainly, the existence of cells that generalize over action-as-seen and action-as-done shows that even monkeys *can* solve this particular correspondence problem. Because manual manipulations are distal to the body the visual appearance of the action will be quite similar, however, and in two-action experiments there is no evidence of learning new skills by anything other than rewarded trial and error. By contrast, compare human neonatal imitation (Meltzoff & Moore 1977; Meltzoff *et al.* 1991) which cannot be accounted for by response facilitation but is thought to function in social bonding rather than skill learning. The possibility that imitation has evolved twice in the human lineage, under quite independent selective pressures for (respectively) social mimicry and skill learning, has even been suggested (Byrne & Russon 1998).

Finally, it has been proposed that an animal watching another individual's actions may more readily or simply learn properties of the physical situation, by *emulation* (Tomasello 1990, 1998), than learn the actions themselves by imitation. For instance, seeing a nut broken may reveal the facts that it is hard, brittle and contains edible material, encouraging rapid future learning of nut-cracking. However, the term emulation has been used with various meanings (Byrne 1998*a*), ranging from simple associative learning (e.g. nut equals food) to acquisition of cognitively complex ideas such as containment. The more complex—and therefore more powerful—of these proposed learning mechanisms may be harder to explain computationally than is imitation itself. A recent meta-analysis of developmental studies could find no clear evidence that children under 5 years old were able to emulate, although they imitated readily (Want & Harris 2002). Moreover, although emulation has been used as a 'null hypothesis' for detecting imitation in great apes, the ability of non-human apes to emulate has been doubted (Byrne & Russon 1998; Byrne 2002*a*). For these reasons, the concept of emulation may not prove useful in understanding the social learning of complex skills in animals or young children.

It is now clear that most animal social learning does not need imitation to explain it, and there is at present no clear experimental demonstration of imitation in any animal, in the full sense of imitation: observational learning of a novel and complex skill, requiring more than priming of actions in the existing repertoire. However, a great deal of observational evidence indicates that at least the great apes have some ability to learn skills by imitation, as well as by other social and non-social learning mechanisms.

(b) *Imitation in great apes*

Socially mediated traditions of behaviour, although known in many species of animal (see, for example, Galef 1980, 1990; Roper 1983; Terkel 1994; Reader & Laland 2000; Rendell & Whitehead 2001), are particularly striking in the chimpanzee *Pan troglodytes* (Whiten *et al.* 1999), and the variation among the tools made and used by different chimpanzee populations is so rich that it has been studied as 'material culture' (McGrew 1992). Although all such variation can be challenged as reflecting subtle and unknown ecological influences (Tomasello 1990), some striking 'incompetences' are more readily understood if imitative learning is sometimes a necessary part of normal acquisition. Thus, it would otherwise be puzzling that chimpanzees in East Africa do not exploit the hard nuts available to them at many sites, which in West Africa are obtained by nut-cracking with stones (Sugiyama & Koman 1979; Boesch & Boesch 1990); and that chimpanzees at some sites discard carefully prepared insect-fishing tools when they become blunted in use, whereas at others the tools are re-sharpened or simply reversed (McGrew *et al.* 1979; McGrew 1998). Mountain gorillas *Gorilla beringei* do not use tools, but their plant preparation shows behavioural organization just as elaborate as chimpanzee tool use, involving several ordered stages, bimanual coordination and manual role differentiation, hierarchical organization of component subroutines, and the flexible omission or substitution of routines according to external circumstances (Byrne & Byrne 1991, 1993; Byrne *et al.* 2001*a*,*b*). As with the chimpanzee data, it is difficult to prove that learning these elaborate skills requires imitation, but two aspects are not easily explained otherwise: (i) although the low-level organization and choice of action is highly variable and idiosyncratic, the

overall behavioural programme is highly standardized within the population (Byrne & Byrne 1993), giving rise to the term 'program-level imitation' for the likely process of acquisition (Byrne 1994); and (ii) even in the case of severe maiming in infancy (an unfortunate consequence of young apes' tendency to explore snares set for other animals), the affected individuals nevertheless acquire the normal technique, i.e. that of their mothers, rather than devise a novel method better suited to their hands' residual competence (Stokes & Byrne 2001; Byrne & Stokes 2002). If there were only one obvious way to consume the plants these observations would be trivial, but in fact there are very many methods, some more obvious to human observers and often attempted by young animals. The standardization to a local population norm and its resistance to change even with severe disability therefore suggests the 'conservative' influence of imitation. Although fewer data are available for the orangutan, the strongest observational evidence of imitative capacity comes from this species: individuals under rehabilitation to the wild after illegal captivity copy a range of complex and elaborate human activities, including some that are strongly discouraged (Russon & Galdikas 1993; Russon 1996). In the forest, orangutans also acquire hierarchically organized action plans (Russon 1998), and one population has been found to possess traditions of tool use very like those of chimpanzees (Van Schaik *et al.* 1996; Fox *et al.* 1999). Given the benefits that this population apparently gains from tool use, the lack of it more generally in orangutans has been attributed to their solitary ranging behaviour, making social transmission of skill inefficient (Van Schaik *et al.* 1999); by contrast, the complete lack of tool using in wild gorillas and bonobos, *Pan paniscus*, may reflect the lack of ecological advantage they stand to gain by using tools (McGrew 1989).

(c) *Imitation without intentionality*

Thus a picture emerges of great apes being able to acquire complex and elaborate local traditions of food acquisition, some of them involving tool use; and it seems highly probable that apes' ability to imitate, so conspicuous under the artificial conditions of human captivity, has its functional origin in efficient food acquisition (Byrne 1997). At the same time, evidence for mentalizing abilities in great apes is much more limited (e.g. Tomasello & Call 1994, 1997; although see Byrne 1995; Suddendorf & Whiten 2001). Therefore, in developing a possible model of the kind of imitation that serves to facilitate skill acquisition, a priority was to eschew mental states as explanatory variables, 'imitation without intentionality' (Byrne 1999*a*), rather than treating an understanding of the model's purposes and understanding of the situation as an early and fundamental part of the process (e.g. cf. Tomasello *et al.* 1993).

The aim has been to develop a purely mechanistic account, meshing where possible with known neural mechanisms, and specified in a sufficiently definite fashion to make future machine implementation a possibility. As an explanatory aid, I will consider the model as applied to one of the complex food preparation tasks of mountain gorillas, beginning with a description of the behaviour and in particular aspects that would gain most from acquisition by imitation. Then, an essential preliminary stage is
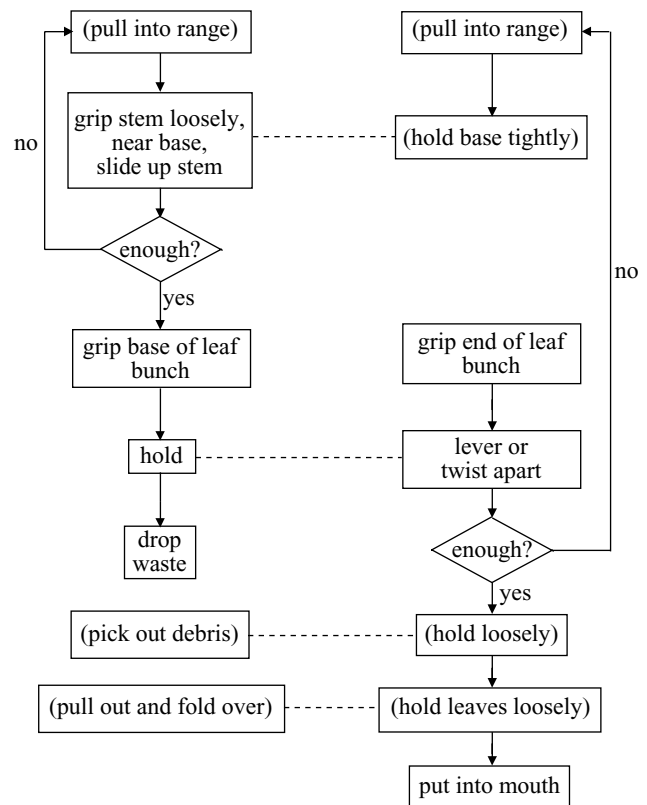

Figure 1. Flow diagram that summarizes the processing sequences used by a right-handed mountain gorilla when preparing bundles of nettle leaves to eat. The process starts at the top of the diagram with acquisition of a nettle plant and ends at bottom right when a folded handful of leaves is put into the mouth. Actions are shown in square boxes; optional actions are in brackets; position of actions to left and right of the figure show where hand preference is significantly lateralized; horizontal dotted lines indicate that the actions of the two hands must be accurately coordinated.

advanced, that of segmenting observed behaviour into a vocabulary of elements. This ability seems much more widespread than the capacity to imitate, and may have evolved for other functions altogether. The 'behaviour parsing' model (Byrne 2002*b*), operating on strings of behavioural elements, is hypothesized to extract the statistical regularities that specifically correlate with organizational structure, and so enable subsequent copying without an understanding of intentions or causal logic. Finally, speculations are advanced about the relationship of these processes to cognition in general.

2. AN ILLUSTRATIVE TASK

Nettles, *Laportea alatipes*, are an important food of mountain gorillas in Rwanda (Watts 1984), rich in protein and low in secondary compounds and structural carbohydrate (Waterman *et al.* 1983). Unfortunately for the gorillas, this plant is 'defended' by powerful stinging hairs, especially dense on the stem, petioles and leaf-edges. All gorillas in the local population process nettles in broadly the same way, a technique that minimizes contact of stinging hairs with their hands and lips (Byrne & Byrne 1991; figure 1). A series of small transformations is made to plant material: stripping leaves off stems, accumulating

larger bundles of leaves, detachment of petioles, picking out unwanted debris, and finally folding a package of leaf blades within a single leaf before ingestion. The means by which each small change is made are idiosyncratic and variable with context (Byrne & Byrne 1993), thus presumably best learned by individual experience. However, the overall sequence of five discrete stages in the process is standardized and appears to be essential for efficiency (Byrne *et al.* 2001*a*). The same applies to the precise bimanual coordination between the hands, in which each hand performs a different role but in temporal and spatial conjunction (manual role differentiation (Elliott & Connolly 1974)). Imitative learning of the *sequence* and the pattern of *bimanual coordination* would therefore be highly beneficial, if not essential for timely acquisition before the young gorilla is weaned and must forage independently at 3–4 years old. Manual laterality is high in almost every individual, often to the point of exclusive hand use, suggesting that the task is a challenging one, and there is a significant population bias towards right-handedness for delicate manipulations (Byrne & Byrne 1991; McGrew & Marchant 1996). However, there is no tendency for an individual's hand preference to match that of its mother (Byrne & Byrne 1991), so this aspect is clearly not imitated. Like other complex feeding tasks in great apes, preparing nettles is a hierarchically organized skill, showing considerable flexibility: stages that are occasionally unnecessary are omitted, and sections of the process (of one or several ordered stages) are often repeated iteratively to a criterion apparently based on an adequate size of food bundle (Byrne & Russon 1998). As noted above, that young gorillas can discern and thereby imitate the hierarchical organization of efficient processing is suggested by the standardization of these aspects in the local population; and their inability to compute novel hierarchical organization even when it would pay is suggested by the lack of any such response to severe, permanent hand injury. Clearly, a good model of imitative learning would include the *hierarchical structure* of the task.

I propose that these cardinal aspects of program-level imitation—sequence, bimanual coordination and hierarchical structure—are extracted from statistical regularities in repeated action. For this parsing process to operate, a preliminary requirement is that the fluid movements of skilled action are 'seen' as composed of strings of *elements*. This segmentation process is considered next.

3. SEGMENTING ACTION INTO ELEMENTS

To be used as building blocks in effective planning, elements of action discerned in another's behaviour must meet one simple principle: each element should *already* be within the repertoire of the observer. By contrast, the 'size' of an element is irrelevant. Under different circumstances, a particular movement of a single finger and an elaborate sequence of bimanual movements might both properly be seen as single elements, if each was a pattern already in the observer's repertoire. When watching an entirely unfamiliar process, the level at which elements were familiar might be that of finger movements; when watching a slight variant of a complex but already familiar activity, the basic elements might themselves be complex processes. Most commonly perhaps, the level at which

observed behaviour matches the existing repertoire would be neither of these, but rather simple and highly practised movements that produce visible effects on environmental objects: that is, simple, goal-directed movements.

The mirror neuron system, noted already as capable of explaining response facilitation (Byrne 2002*c*; Rizzolatti *et al.* 2002), responds to precisely this class of actions. The cardinal property of mirror neurons is that they detect simple, goal-directed movements in the observing monkey's own repertoire, whether the movement is performed by the monkey itself or by another agent that it is watching. It is unlikely that mirror neurons have any role in imitation in monkeys, simply because monkeys have repeatedly failed to show evidence of imitative capacity (Visalberghi & Fragaszy 1990). Rather, it is thought that the evolutionary origin of mirror neurons is related to social sophistication: i.e. that the system functions in revealing the demeanour and likely future actions of conspecifics, by reference to actions the observer monkey might itself have done (Rizzolatti *et al.* 2002). (These qualities are sometimes called 'intentions', though without any implication of mentalizing.)

Despite the apparent lack of imitative ability in monkeys, mirror neurons may be *part* of the process of imitation in some other species. By responding to movement patterns that correspond to actions that the observer can already perform, the mirror neuron system could convert a continuous flow of observed movements into a string of recognized, familiar actions. If seeing a string of familiar actions also allows construction of links between them, then 'action-level' imitation can occur (Byrne & Russon 1998). In action-level imitation, a linear sequence of actions are copied without recognition of any higher-order organization that may be present: the organization is 'flat'. Chimpanzees have been reported to copy the order of actions, even though the sequence was entirely arbitrary and unrelated to success (Whiten 1998), and a detailed learning model has been developed to account for action-level imitation in animals (Heyes & Ray 2000).

The question is, can this sort of 'bottom up', mechanistic analysis go beyond action-level imitation, and explain how behavioural organization can also be copied, i.e. program-level imitation? For arbitrary, random actions or behaviour that is genuinely linear in structure (e.g. the 'fixed action patterns' described by early ethologists), there will be no difference between action-level and program-level copying. However, most human action, and arguably also much of the behaviour of other great apes, is constructed in such a way that aspects of the organization are planned and relate to intended effects during execution. Can this planning be 'seen' in the behaviour of another?

4. PARSING STRINGS OF ACTIONS TO REVEAL ORGANIZATION

Every execution of a motor act, however familiar and well-practised, will differ slightly from others. Nevertheless, this variation is constrained because if certain characteristics are missing or stray too far from their canonical form the act will fail to achieve its purpose. Watching a single performance will not betray these underlying constraints, but the statistical regularities of repeated, goal-

directed action can serve to reveal the organizational structure that lies behind it.

Consider how this might work for an infant gorilla learning about nettle processing. Unweaned great apes spend most of each day within a few feet of their mothers, and (as their main nutrition still comes from milk) they have almost full-time leisure to watch any nearby activities, as well as learn about the structure of plants by their own exploration. By the time a young gorilla first begins to process a nettle plant, at the late age of about 2 years because the stinging hairs discourage earlier attempts, they will therefore have watched many hundreds of plants being processed expertly by the mother. Suppose her behaviour is seen by the infant as a string of elements, each of which is already familiar (i.e. a mirror neuron exists for the element). At this time, the young gorilla's repertoire of familiar elements of action derives from its innate manual capacities, many hours of playing with plants and discarded debris of the mother's feeding, and from its own feeding on other, perhaps simpler plants. The string of elements that it sees when watching its mother eat nettles will differ each time, although her starting point is always a growing, intact nettle stem, and—because she is expert at this task—the final stage is always the same: popping a neatly folded package of nettle leaves into the mouth.

With repeated watching, other regularities begin to become apparent: the mother always uses one hand to fold a bundle of leaf-blades protruding from the other hand, and holds down this folded bundle with her thumb; she always makes a twisting movement of the hands against each other, and immediately drops several leaf-petioles (which she does not eat) onto the ground; she always makes a sweeping movement of one hand, held around a nettle stem which is sometimes held in the other hand even though the plant is still attached to the ground, and this leaves a leafless stem protruding from the ground (see figure 2 for a visual representation of this process). Moreover, these stages always occur in exactly the same order each time: the reverse order to that in which they have been mentioned here. Statistical regularities thereby separate the minimal set of *essential actions* from the many others that occur during nettle eating but which are not crucial to success, and reveal the correct order in which they must be arranged. (The ability of human babies as young as eight months to detect statistical regularities in spoken strings of nonsense words shows that just such sensitivity to repeated orderings is active early in human development (Saffran *et al.* 1996).) The usefulness of detecting regularities applies not only to the linear sequence of movements of each hand, but also the hands' operation together: stages that crucially depend on the hands' close temporal and spatial coordination while doing different jobs will recur in every string, whereas other coincidental conjunctions will not.

Other statistical regularities relate to modular organization and hierarchical organization (see figure 3). Although not present in every string, whenever the operation of removing debris is performed (by opening the hand that holds nettle leaf-blades, and delicately picking out debris with the other hand), it occurs at the same place in the string. Also, on some occasions but not others, a section of the entire string is repeated twice or several times. For
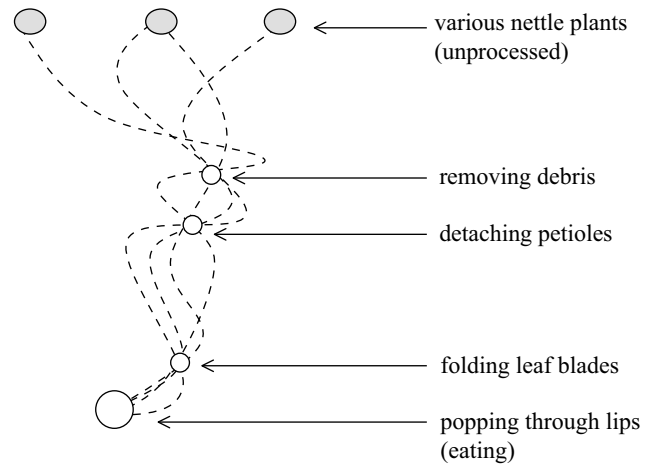

Figure 2. Nettle processing may be viewed as paths through a two-dimensional space of transformations, where each transformation is an action that may be applied. Because each plant is potentially unique in form, each is represented as a different starting point. The manual operations that are applied will vary on each occasion, so no paths overlap perfectly. However, certain operations are critical for success, and these are represented as points where all paths converge. These convergence points define the *essential* actions that must always be performed for eventual success, and may allow them to be recognized among the many inessential, idiosyncratic movements in a typical real sequence.
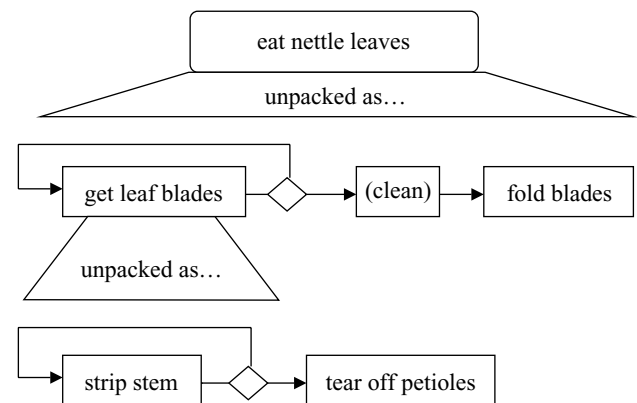

Figure 3. Hierarchical organization of nettle leaf processing must, on current observational evidence, be at least as elaborate as this diagram. The modules 'get leaf blades' and 'fold blades' are known to be independent, because they may on occasion be separated by the optional action, 'clean'. In addition, 'get leaf blades' may or may not be iterated, again implying that this is a distinct module. However, 'get leaf blades' is itself a routine composed of at least two component modules: the evidence that 'strip stem' and 'tear off petioles' are separate modules is that 'strip stem' may or may not be iterated.

instance, the process of 'pulling a nettle plant into range, stripping leaves from its stem in a bimanually coordinated movement, then detaching and dropping the leaf-petioles', may be repeated several times before the mother continues to remove debris and fold the leaf-blades before eating. (Already-processed leaf-blades are transferred to the lower fingers of one hand for retention during the process of acquiring more, an ability that shows that gorillas are able to control individual digits independently.) Subsections of

the string of actions that are marked out in this way may be single elements, or as in this example a string of several elements. Both omission and repetition signal that some parts of the string are more tightly bound together than others, i.e. that they function as *modules*. Optional stages, like cleaning debris, occur between but not within modules. Moreover, repetition of a substring gives evidence of a module used as a subroutine, in this case iterated several times to accumulate a larger handful. Further clues to modular structure are likely to be given by the distribution of pauses (occurring between but not within modules), and the possibility of smooth recovery from interruptions that occur between modules. Gorillas often pause for several seconds during the processing of a handful of plant material, to monitor the movements and actions of other individuals. Finally, a different module entirely may be substituted for part of the usual sequence (e.g. if one hand is required for postural support, then a normally bimanual process may need to be performed unimanually), and if this module is recognized as an already-familiar sequence its substitution again reveals structure; eventually, it may be that a taxonomy of substitutable methods is built up.

This example has been developed as a heuristic exercise, but in fact the existence of statistical regularities that reveal underlying structure is known in this case, because they are precisely the regularities that enabled the scientists to discover the hierarchical structure of nettle processing by adult gorillas (Byrne & Byrne 1993; Byrne & Russon 1998; Byrne 1999*b*). What is proposed in the behaviour parsing model is that the same information can be extracted and used by the apes themselves, and that this ability is what enables a young ape to perceive and copy the sequential, bimanually coordinated, hierarchical organization of complex skills from repeated watching of another. This claim has further implications for how imitation relates to other cognitive activities.

5. POTENTIAL IMPLICATIONS

Just as mirror neurons may be regarded as much more than devices for copying familiar actions (i.e. response facilitation), but as mechanisms for discerning the future behavioural dispositions of other animals, so behaviour parsing may be seen as more than simply part of program-level imitation. Because behaviour parsing reveals the organization of behaviour in other individuals, in terms of actions that the observer can (if it so desires) perform itself, the consequence is that behaviour can better be interpreted in terms of its function and mechanism of operation. In effect, behaviour can be *understood statistically* in terms of its correlations—under what circumstances is a particular organization seen, and what are its normal effects on the environment—without prior knowledge of intentions in the mind of the observed agent, or any understanding of the everyday physics of cause-and-effect relationships between action and consequence. Copying a novel, complex organization of behaviour, and so acquiring a new skill by imitation, may only be a spin-off from a more fundamental ability to understand the world of action. If behaviour parsing enables an agent to 'see through' the surface form of behaviour to an underlying deep structure of actions, then it is perhaps only a

small step to perceiving the plans and intentions that lie behind these structures.

The implications of following these speculations are twofold. First, activities that have been claimed to rely on perceiving the intentions of others (as has been argued for learning by imitation (e.g. Whiten & Byrne 1991; Tomasello *et al.* 1993)), may in fact be possible in a more straightforward, mechanistic fashion. This would ramify the position argued by Bargh & Chartrand (1999), that much more of everyday human action than is currently recognized relies on fast, mechanistic, low-level processes, rather than on elaborate, rational thought processes and deeply intentional understanding. Moreover, if the same competence is discovered in non-human animals, as appears to be increasingly the case, this need not raise awkward questions of non-verbal mentalizing and consciousness. Rather, mentalizing ability may have different and more recent evolutionary origins, functioning to construe actions in various ways (e.g. rationalizing our own and others' actions whose real cause we do not understand, or deliberately misconstruing those actions for our own ends), and be intimately tied to linguistic ability (see Karmiloff-Smith (1993) and Povinelli (2000) for closely related perspectives). The second implication is that, although imitation of novel behaviour and other complex cognitive activity may not require mentalizing, mentalizing may require behaviour parsing as part of the process. The evolution of the ability to parse the behaviour of others, which on current evidence evolved at least as long ago as the shared ancestors of humans and other great apes around 12 Myr ago, may therefore have been a necessary preliminary to the later development exclusively in humans of the ability to mentalize: to attribute intentions and causes to observed actions. Behaviour parsing may still be part of the everyday process of doing so.

REFERENCES

Bargh, J. A. & Chartrand, T. L. 1999 The unbearable automaticity of being. *Am. Psychol.* **54**, 462–479.

Boesch, C. & Boesch, H. 1990 Tool use and tool making in wild chimpanzees. *Folia Primatologica* **54**, 86–99.

Bugnyar, T. & Huber, L. 1997 Push or pull: an experimental study of imitation in marmosets. *Anim. Behav.* **54**, 817–831.

Byrne, R. W. 1994 The evolution of intelligence. In *Behaviour and evolution* (ed. P. J. B. Slater & T. R. Halliday), pp. 223–265. Cambridge University Press.

Byrne, R. W. 1995 *The thinking ape: evolutionary origins of intelligence*. Oxford University Press.

Byrne, R. W. 1997 The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In *Machiavellian intelligence. II. Extensions and evaluations* (ed. A. Whiten & R. W. Byrne), pp. 289–311. Cambridge University Press.

Byrne, R. W. 1998*a* Comments on C. Boesch and M. Tomasello 'Chimpanzee and human cultures'. *Curr. Anthropol.* **39**, 604–605.

Byrne, R. W. 1998*b* Imitation: the contributions of priming and program-level copying. In *Intersubjective communication and emotion in early ontogeny* (ed. S. Braten), pp. 228–244. Cambridge University Press.

Byrne, R. W. 1999*a* Imitation without intentionality. Using string parsing to copy the organization of behaviour. *Anim. Cogn* **2**, 63–72.

Byrne, R. W. 1999b Object manipulation and skill organization in the complex food preparation of mountain gorillas. In *The mentality of gorillas and orangutans* (ed. S. T. Parker, R. W. Mitchell & H. L. Miles), pp. 147–159. Cambridge University Press.

Byrne, R. W. 2002a Emulation in apes: verdict 'not proven'. *Devl Sci.* **5**, 20–22.

Byrne, R. W. 2002b Imitation of complex novel actions: what does the evidence from animals mean? *Adv. Study Behav.* **31**, 77–105.

Byrne, R. W. 2002c Seeing actions as hierarchically organized structures. Great ape manual skills. In *The imitative mind: development, evolution, and brain bases* (ed. A. Meltzoff & W. Prinz), pp. 122–140. Cambridge University Press.

Byrne, R. W. & Byrne, J. M. E. 1991 Hand preferences in the skilled gathering tasks of mountain gorillas (*Gorilla g. beringei*). *Cortex* **27**, 521–546.

Byrne, R. W. & Byrne, J. M. E. 1993 Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): variability and standardization. *Am. J. Primatol.* **31**, 241–261.

Byrne, R. W. & Russon, A. E. 1998 Learning by imitation: a hierarchical approach. *Behav. Brain Sci.* **21**, 667–721.

Byrne, R. W. & Stokes, E. J. 2002 Effects of manual disability on feeding skills in gorillas and chimpanzees: a cognitive analysis. *Int. J. Primatol.* **23**, 539–554.

Byrne, R. W., Corp, N. & Byrne, J. M. 2001a Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. *Anim. Cogn.* **4**, 347–361.

Byrne, R. W., Corp, N. & Byrne, J. M. E. 2001b Estimating the complexity of animal behaviour: how mountain gorillas eat thistles. *Behaviour* **138**, 525–557.

Custance, D., Whiten, A. & Fredman, T. 1999 Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* **113**, 13–23.

Dawson, B. V. & Foss, B. M. 1965 Observational learning in budgerigars. *Anim. Behav.* **13**, 470–474.

Elliott, J. & Connolly, K. 1974 Hierarchical structure in skill development. In *The growth of competence* (ed. K. Connolly & K. Bruner), pp. 135–168. London: Academic.

Fox, E., Sitompul, A. & Van Schaik, C. P. 1999 Intelligent tool use in wild Sumatran orangutans. In *The mentality of gorillas and orangutans* (ed. S. T. Parker, H. L. Miles & R. W. Mitchell), pp. 99–116. Cambridge University Press.

Galef, B. G. 1980 Diving for food: analysis of a possible case of social learning in wild rats (*Rattus norvegicus*). *J. Comp. Physiol. Psychol.* **94**, 416–425.

Galef, B. G. 1988 Imitation in animals: history, definitions, and interpretation of data from the psychological laboratory. In *Social learning: psychological and biological perspectives* (ed. T. Zentall & B. G. Galef Jr), pp. 3–28. Hillsdale, NJ: Erlbaum.

Galef, B. G. 1990 Tradition in animals: field observations and laboratory analyses. In *Interpretations and explanations in the study of behaviour: comparative perspectives* (ed. M. Bekoff & D. Jamieson), pp. 74–95. Boulder, CO: Westview Press.

Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. 1996 Action recognition in the premotor cortex. *Brain* **119**, 593–609.

Heyes, C. M. 1993 Imitation, culture, and cognition. *Anim. Behav.* **46**, 999–1010.

Heyes, C. M. & Ray, E. D. 2000 What is the significance of imitation in animals? *Adv. Study Behav.* **29**, 215–245.

Karmiloff-Smith, A. 1993 *Beyond modularity: a developmental perspective on cognitive science*. Cambridge, MA: Bradford/MIT.

McGrew, W. C. 1989 Why is ape tool use so confusing? In *Comparative socioecology: the behavioural ecology of humans and other mammals* (ed. V. Standen & R. A. Foley), pp. 457–472. Oxford: Blackwell Scientific.

McGrew, W. C. 1992 *Chimpanzee material culture: implications for human evolution*. Cambridge University Press.

McGrew, W. C. 1998 Culture in nonhuman primates? *A. Rev. Anthropol.* **27**, 301–328.

McGrew, W. C. & Marchant, L. F. 1996 On which side of the apes? Ethological study of laterality of hand use. In *Great ape societies* (ed. W. C. McGrew, L. F. Marchant & T. Nishida), pp. 255–272. Cambridge University Press.

McGrew, W. C., Tutin, C. E. G. & Baldwin, P. J. 1979 Chimpanzees, tools, and termites: cross cultural comparison of Senegal, Tanzania and Rio Muni. *Man* **14**, 185–214.

Meltzoff, A. N. & Moore, M. K. 1977 Imitation of facial and manual gestures by human neonates. *Science* **198**, 75–78.

Meltzoff, A. N., Kuhl, P. K. & Moore, M. K. 1991 Perception, representation, and the control of action in newborns and young infants: towards a new synthesis. In *Newborn attention: biological constraints and the influence of experience* (ed. M. J. Weiss & P. R. Zelazo), pp. 377–411. Norwood, NJ: Ablex Press.

Povinelli, D. 2000 *Folk physics for apes*. Oxford University Press.

Reader, S. & Laland, K. 2000 Diffusion of foraging innovations in the guppy. *Anim. Behav.* **60**, 175–180.

Rendell, L. & Whitehead, H. 2001 Culture in whales and dolphins. *Behav. Brain Sci.* **24**, 309–382.

Rizzolatti, G., Fadiga, L., Fogassi, L. & Gallese, V. 1996 Premotor cortex and the recognition of motor actions. *Brain Res.* **3**, 131–141.

Rizzolatti, G., Fadiga, L., Fogassi, L. & Gallese, V. 2002 From mirror neurons to imitation: facts and speculations. In *The imitative mind: development, evolution, and brain bases* (ed. A. Meltzoff & W. Prinz), pp. 247–266. Cambridge University Press.

Roper, T. J. 1983 Learning as a biological phenomenon. In *Animal behaviour, vol. 3. Genes, development and learning* (ed. T. R. Halliday & P. J. B. Slater), pp. 178–212. Oxford: Blackwell Scientific.

Russon, A. E. 1996 Imitation in everyday use: matching and rehearsal in the spontaneous imitation of rehabilitant orangutans (*Pongo pygmaeus*). In *Reaching into thought: the minds of the great apes* (ed. A. E. Russon, K. A. Bard & S. T. Parker), pp. 152–176. Cambridge University Press.

Russon, A. E. 1998 The nature and evolution of intelligence in orangutans (*Pongo pygmaeus*). *Primates* **39**, 485–503.

Russon, A. E. & Galdikas, B. M. F. 1993 Imitation in free-ranging rehabilitant orangutans. *J. Comp. Psychol.* **107**, 147–161.

Saffran, J. R., Aslin, R. N. & Newport, E. L. 1996 Statistical learning by 8-month-old infants. *Science* **274**, 1926–1928.

Spence, K. W. 1937 Experimental studies of learning and higher mental processes in infra-human primates. *Psychol. Bull.* **34**, 806–850.

Stoinski, T. S., Wrate, J. L., Ure, N. & Whiten, A. 2001 Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *J. Comp. Psychol.* **115**, 272–281.

Stokes, E. J. & Byrne, R. W. 2001 Cognitive capacities for behavioural flexibility in wild chimpanzees (*Pan troglodytes*): the effect of snare injury on complex manual food processing. *Anim. Cogn.* **4**, 11–28.

Suddendorf, T. & Whiten, A. 2001 Mental evolution and development: evidence for secondary representation in children, great apes, and other animals. *Psychol. Bull.* **127**, 629–650.

Sugiyama, Y. & Koman, J. 1979 Tool-using and tool-making behaviour in wild chimpanzees at Bossou, Guinea. *Primates* **20**, 513–524.

Terkel, J. 1994 Social transmission of pine cone feeding behaviour in the black rat. In *Behavioural aspects of feeding* (ed. B. G. J. Galef, M. Mainardi & P. Valsecchi), pp. 229–256. London: Harwood Academic.

Thorndike, E. L. 1898 Animal intelligence: an experimental study of the associative process in animals. *Psychol. Rev. Monogr.* **2**, 551–553.

Tomasello, M. 1990 Cultural transmission in the tool use and communicatory signaling of chimpanzees? In *'Language' and intelligence in monkeys and apes* (ed. S. T. Parker & K. R. Gibson), pp. 274–311. Cambridge University Press.

Tomasello, M. 1998 Emulation learning and cultural learning. *Behav. Brain Sci.* **21**, 703–704.

Tomasello, M. & Call, J. 1994 Social cognition of monkeys and apes. *Yearbook Phys. Anthropol.* **37**, 273–305.

Tomasello, M. & Call, J. 1997 *Primate cognition*. New York: Oxford University Press.

Tomasello, M., Kruger, A. C. & Ratner, H. H. 1993 Cultural learning. *Behav. Brain Sci.* **16**, 495–552.

Van Schaik, C. P., Fox, E. A. & Sitompul, A. F. 1996 Manufacture and use of tools in wild Sumatran orangutans. Implications for human evolution. *Naturwissenschaften* **83**, 186–188.

Van Schaik, C. P., Deaner, R. O. & Merrill, M. Y. 1999 The conditions for tool-use in primates: implications for the evolution of material culture. *J. Hum. Evol.* **36**, 719–741.

Visalberghi, E. & Fragaszy, D. M. 1990 Do monkeys ape? In *'Language' and intelligence in monkeys and apes* (ed. S. T. Parker & K. R. Gibson), pp. 247–273. Cambridge University Press.

Want, S. C. & Harris, P. L. 2002 How do children ape? Applying concepts from the study of non-human primates to the developmental study of 'imitation' in children. *Devl Sci.* **5**, 1–13.

Waterman, P. G., Choo, G. M., Vedder, A. L. & Watts, D. 1983 Digestibility, digestion-inhibitors and nutrients and herbaceous foliage and green stems from an African montane flora and comparison with other tropical flora. *Oecologia* **60**, 244–249.

Watts, D. P. 1984 Composition and variability of mountain gorilla diets in the central Virungas. *Am. J. Primatol.* **7**, 323–356.

Whiten, A. 1998 Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **112**, 270–281.

Whiten, A. & Byrne, R. W. 1991 The emergence of metarepresentation in human ontogeny and primate phylogeny. In *Natural theories of mind: evolution, development and simulation of everyday mindreading* (ed. A. Whiten), pp. 267–281. Oxford: Blackwell.

Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P. & Bard, K. A. 1996 Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **110**, 3–14.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999 Cultures in chimpanzees. *Nature* **399**, 682–685.