REVIEW

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Imitation without intentionality.
Using string parsing to copy the organization of behaviour

Abstract A theory of imitation is proposed, string parsing, which separates the *copying* of behavioural organization by observation from an *understanding* of the cause of its effectiveness. In string parsing, recurring patterns in the visible stream of behaviour are detected and used to build a statistical sketch of the underlying hierarchical structure. This statistical sketch may in turn aid the subsequent comprehension of cause and effect. Three cases of social learning of relatively complex skills are examined, as potential cases of imitation by string parsing. Understanding the basic requirements for successful string parsing helps to resolve the conflict between mainly negative reports of imitation in experiments and more positive evidence from natural conditions. Since string parsing does not depend on comprehension of the intentions of other agents or the everyday physics of objects, separate tests of these abilities are needed even in animals shown to learn by imitation.

Key words Imitation · Skill learning · Intention · Cause and effect

Introduction

The history of animal imitation has seen a succession of reinterpretations. Each time, a subset of the various behaviours considered to reflect imitation has become understandable by some newly proposed theoretical mechanism (Galef 1988; Visalberghi and Fragaszy 1990; Whiten and Ham 1992). In most cases, the general acceptance of the new mechanism has been on the basis of parsimony – that it is a simpler explanation – rather than by

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applying a test diagnostic of it (Roitblat 1998). Imitation as an explanation is "not simple" because it is taken to rely on one or more unobservable or otherwise mysterious cognitive mechanisms. Mechanisms proposed to underlie true imitation include the mental perspective translations involved in "seeing the world from another's viewpoint", the ability to conceive of the goals and intentions of other individuals (theory of mind), and the visual-kinaesthetic transformation allowing conversion of visually registered actions into an organized programme of commands to effector muscles (Bruner 1970; Heyes 1996; Tomasello et al. 1993a).

In the last century, the term imitation would seem to have been defined in the rather vague way that it is still used colloquially: almost any case of two animals doing the same thing close together in time was treated as imitation. E.L. Thorndike's practical definition "learning to do an act from seeing it done" focused attention on the key role which observation plays, ruling out all those cases in which prior observation is unnecessary for behavioural matching to occur (Thorndike 1898). But observation of what, precisely: the agent's movements, or the objects to which they are applied? This distinction was raised by K. W. Spence's 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 focused upon a narrowed range of stimuli, chance discovery of the means of achieving the goal is made much more likely, even if the other individual's actions themselves go unnoticed or unremembered; and numerous cases of social learning proved explicable as stimulus enhancement (Galef 1988). M. Tomasello further drew attention to the power of the physical situation to enable learning, introducing the concept of *emulation*: that is, what may be learnt from the consequences observed happening to things in the environment, as a result of another individual's actions, but without learning the actions themselves (Tomasello 1990). Thus, if an individual sees a coconut smashed against a rock, breaking to disclose edible flesh,

then by stimulus enhancement it may focus its subsequent actions on the site (below a coconut tree) and the object (coconuts), and by emulation it may now know that coconuts are breakable and edible – all without learning the particular method of breaking, the behaviour, employed by the model. In the light of this new theory, to test whether a putative case was truly imitation, researchers would need first to replicate the whole situation, but minus the bodily actions: if the learning was still as effective, then the original case need not be seen as imitation. The discovery that naïve tits (*Parus*) learnt to peck open the foil caps of milk-bottles as quickly after finding bottles already pecked open as by watching experienced tits open them (Sherry and Galef 1984) vindicated this approach. Most recently, even a direct effect of seeing a particular action has been challenged as insufficient to diagnose imitation. R. W. Byrne showed that, in the same way that one stimulus may be enhanced over another, increasing the probability that the individual would interact with it, so one response (i.e. a voluntary action in an individual's existing repertoire) may be enhanced or primed by seeing it done, causing a higher probability of the response occurring subsequently (Byrne 1994). This *response facilitation* may underlie the various effects found using the experimental "two-action method" (Byrne and Tomasello 1995), sometimes claimed to be the only convincing evidence of imitative capability in animals (e.g. Heyes 1993, p. 1000). Part of the neural mechanism of response facilitation has already been identified, the so-called *mirror neurons* in monkey cortex (Gallese and Goldman 1998; Perrett et al. 1989; Rizzolatti 1981); these cells respond equally to the same action, such as picking up a peanut or grooming hair, whether this is done by the monkey itself or an individual it is watching. The theory of response facilitation has emphasized the need to require novelty when claiming animal behaviour as imitation (though from everyday experience we know that we can also imitate familiar actions, if we so wish).

By this point, the set of animal behaviours that can unequivocally be ascribed to imitation has been much reduced in number. (Though note that in many of the excluded cases the possibility of imitation is not yet ruled out, only this would be a less parsimonious explanation.) Indeed, if the process of reinterpretation in terms of "simpler" mechanisms continues, the set may eventually become empty. It is the contention of this paper that that outcome would be a positive one, provided each of the proposed mechanisms is definite (i.e. mechanical) rather than mysterious and unspecified, and as such more testable than imitation itself (see also Mac Aogain 1998) Further, if *all* the possible mechanisms by which an animal could "learn to do an act from seeing it done" were properly understood, a more balanced, Bayesian approach could be applied to deciding in a given circumstance just which mechanism had been important. This would get away from the current unfortunate necessity to argue in terms of which null hypothesis is most plausible a priori, and which explanation is most parsimonious of extra theoretical baggage, neither of which are easy judgements to

make. It is in this spirit of aiming towards eventual completeness that the theory expounded in this paper is offered: *imitation by string parsing*.

The current challenge is to see how imitation – i.e. some significant subset of those behaviours not already explained by one of the mechanisms already specified – may be achieved in a way that can be specified clearly and mechanically. In the process, it would be ideal to avoid the need of unduly elaborate mental mechanisms, such as the rich intentionality of understanding the plans and goals of another individual, or vague and mysterious ones, such as visual-kinaesthetic translation. I will first develop the string parsing model in relatively abstract terms; then consider what sorts of input data would be necessary for such a system to work, thereby developing predictions of the circumstances in which its operation might be expected and what effects it should produce; and finally examine some empirical data that might be explained as a product of string parsing.

A theory of imitation: string parsing

Consider an animal watching another individual's behaviour, and suppose that this behaviour is novel to the viewer, in that the behaviour as a whole does not form part of its repertoire – although the component actions that make up the organized structure of the behaviour may well do. If the observing animal were subsequently to show the behaviour, without any intervening schedule of rewards or punishments from trial and error interactions with the environment, then none of the existing non-imitative mechanisms could account for it. How might it have been copied?

Assume that the animal is capable of seeing the other's behaviour as made up of a sequence of simpler elements. One obvious way it might do so is if each element were an action already forming part of its own repertoire, and at some level of detail *any* action must be comprised of units which a conspecific has in its repertoire. Alternatively, the elements might simply be discriminably different states of the physical world affected by the behaviour; this difference will be explored further, after the model has been introduced. The basic input for string parsing is the linear sequence of elements, A, B, C, D, E, F... and so on. Strings of this kind are remembered and thereby compared, in a search for data-reduction by the discovery of patterns. Out of these one-dimensional, linear strings of elements is generated an organized structure in which the links are correlational – a "statistical sketch" of the action (Fig. 1).

Any one string may be entirely ambiguous as to what structure underlies it, but as more and more strings are cross-correlated, the regularities can betray the organization. Even for complex behaviour which is hierarchically organized (Byrne and Russon 1998; Dawkins 1976; Lashley 1951), the underlying structure imposes a distinctive signature on the linear sequence of elements that serves to show how the fluid stream of action may be
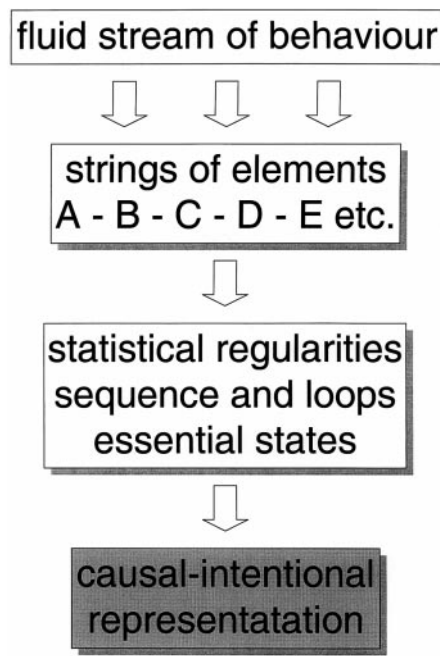
Fig. 1 Schematic diagram of the stages of imitation. Transformations are shown as *downward arrows*: firstly, into strings of elements (sequencing), next, into a statistical sketch of the underlying process (string parsing), last, into a full causal-intentional representation. It is argued that this final stage (*shaded box*) is not necessary for effective imitation of novel, complex behaviour

"carved at the joints". For instance (and no doubt there are many other principles than these):

1. In a hierarchical organization, modules occur in which the elements seem to more tightly bound together, whereas at a junction between modules the link is weaker (e.g. A=B=C–D=E=F; elements joined by = are tighter bound together than those joined by –). Interruptions occurring at these junction-points will permit smooth resumption once the distraction is past; in contrast, interruptions within a module will force the animal to "begin at the beginning again", either the beginning of the module or of the entire program. Partly, this is an inevitable consequence of hierarchical organization: it is easier to keep track when interrupted between one subroutine and the next; in addition, the elements of frequently used subroutines will tend to become "chunked" as larger units of behaviour (e.g. Welford 1968, p. 179). Thus, interruptability is a correlate of structure.

2. In a flexible, hierarchical organization of behaviour, unnecessary stages or modules can be omitted, on the basis of local circumstances. So, in repeated strings that are broadly similar, certain sections will occur in some strings but not others, signalling the underlying modular structure (e.g. numerous instances of both A,B,C,D,E,F and A,B,E,F signals A=B–C=D–E=F).

3. Modules, used as subroutines in a hierarchical organization, may be employed iteratively until some criterion is reached (cf. the test-operate-test-exit unit of Miller et al.

1960), and repeated "loops" around a subroutine give a distinctive sequence of sequential elements: a series of repeated short strings, embedded within the main sequence (e.g. A,B,C,B,C,B,C,D,E signals that B=C is an iterated subroutine).

4. In many cases, planned behaviour leads to the achievement of a goal. Thus, consummatory activity of some sort (e.g. eating a food item), coming after a sequence of elements, indicates a proper end to that sequence. In some cases, the proper start to a sequence might also be visible in behaviour, if no other activity occurred immediately beforehand; thus some "complete" strings of elements corresponding to goal-directed behaviour can be identified. More generally, the appropriate phase in which sequences need to be meshed to detect the recurring patterns may be indicated in this way.

5. In minor and trivial ways, every execution of a behaviour is slightly different. The characteristics that *always* occur, in regular positions in every string of elements leading to the same outcome, can therefore be identified as necessary ones, whereas those that do not are revealed as unnecessary. Thus, by comparing a series of strings that lead to the same outcome, the ordered sequence of necessary elements that leads to it can be identified.

6. A subroutine may be used in more than one program, or one program may be used as a subroutine in another. Thus, once some strings have been identified as forming discrete modules or more complex structures, then these patterns can be picked out in as-yet-unparsed strings of elements.

A string-parsing algorithm which is sensitive to these regularities will inevitably generate a statistical sketch which tends to mirror the actual organization of any planned, complex behaviour[1]. (For random strings of elements, no statistical sketch would emerge.) Depending on the complexity of the behavioural organization, however, numerous instances may be needed to provide sufficient data to extract all the crucial regularities.

The organization of complex behaviour can in principle therefore be "perceived" in a rather literal way, including the starting conditions, the outcome or goal, and the statistical regularities of elements that connect the two. In this manner, the behaviour may be copied – at *program level* (Byrne 1998). If each element were an action in the observer's repertoire, use of the statistical sketch to build a novel behavioural routine is particularly straightforward. The system of mirror neurons in pre-motor and associated temporal cortex of macaque monkeys (Rizzolatti 1981; Rizzolatti and Gentilucci 1988; Perrett et al. 1989) provides a feasible neural basis for this process of segmenting fluid action into a string of discrete elements, each one an action in the observer's repertoire – effec-

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[1] An algorithm which operates according to some of these principles, LAWE, has apparently been effective in simulating the children's learning of arithmetical procedures, such as long division, by observation of worked examples (E. Furse, unpublished work).

tively, "reading the letters" of action by means of response facilitation, action by action. If the output of segmentation by mirror neurons were the input to the string parsing process, then the statistical sketch would mirror behavioural organization directly. Alternatively, if each perceived element were a state of the physical world – for example, how an object looked after some manipulation had been applied to it – then the statistical sketch would specify the organization and sequence of transformations necessary to reach the goal. What actions are needed to make each transformation would then still need to be acquired, based on prior knowledge of how to attain these subgoals, or by a process of trial and error learning. But even in this case, the overall organization by which the actions are assembled into a behavioural routine would be derived by string parsing.

The mental apparatus to (in effect) cross-correlate among very large numbers of sequences will need to function automatically and efficiently without demands on central capacity; just as with response facilitation, a specialized neural system is perhaps likely. Also, while the emphasis in this paper is on the structural information which can be extracted by string parsing, the mechanism of extracting correlational structure from sequences of observed behaviour seems unlikely to be entirely different to the associative mechanisms underlying classical conditioning (see Dickinson 1980). For instance, it might be that the underlying correlation-extraction mechanisms overlap considerably, but some species of animal lack the additional capacity to assemble any hierarchical, co-ordinated action plans, and thus fail to show program-level imitation. These relationships will be interesting to explore in the future.

Of course, when adult humans "see" the structure that lies behind fluid behaviour sequences, they typically also go on to interpret the structure causally and intentionally (Fig. 1). We just perceive complex actions as organized, so that:

1. The sequence seems to be *logical*, with one thing following from another (because it causes/permits it).

2. The whole performance seems intentionally *aimed* at a final result, one which makes sense for the doer.

Sometimes, of course, the understanding behind such ascriptions may be flimsy. As a first approximation, humans might often assume correlational sequences to be causal, and assume the intermediate but necessary states to be subgoals. These assumptions would usually be correct. Further, humans have other sources of information that may aid this final stage of causal-intentional interpretation: information about what people often want to do, how things are labelled with linguistic terms, or what they themselves have been taught formally about causes and logic.

If understanding were based on a statistical sketch alone, comprehension would clearly be limited. In such a sketch, the reasons *why* an action is done once or many times, *how* a choice is made between possibilities, *why* an interruption occurs here rather than there, are all "understood" in a local sense only. This sense of understanding does not start from what the individual intends, or depend on knowing the everyday physics of the transformations that are made on the environment. Nevertheless, since by string parsing it is possible to detect organization, without necessarily understanding the cause-and-effect of physics or the intentions of psychological agents, an apparently intentional understanding can be derived by a mechanical, correlational process. For an animal unable to represent the causal-intentional logic of situations, this might provide a real benefit in allowing imitation of certain important skills. In the next section, I will examine the circumstances in which this benefit might be obtained.

Limitations on imitation by string parsing

Most of the proposed criteria, by which an underlying structure can make itself evident at the surface level of behaviour, depend on having an extensive corpus of data available. By definition, a process that uses multiple repetitions of intrinsically "the same" sequence of actions, to clarify which elements are obligatory ones and which are trivial variations in response to changing circumstances, requires the opportunity to see the job done many times. Consummatory activity, marking the proper end of a goal-directed sequence, will give a useful hint as to the correct phase in which to align repeated sequences, but whether the start is clear in the surface form of behaviour will be much more variable. Both the occurrence of iteration, and the omission of optional stages, will depend on particular features of the problem, and cannot be relied on to appear in every sequence. And obviously, interruption is unlikely to occur frequently, since animals will tend to seek locations for their activity where they are not interrupted. Thus the cardinal requirement for string parsing to work usefully is *repeated views* of the activity.

Self-evidently, these views must be clear ones to be useful. In the laboratory, that can usually be ensured, but in the natural environments in which any copying mechanisms must have evolved an animal cannot rely on repeated, *clear views* of another's activity except in rather specific circumstances. Further, if the activity does not produce *visible effects* on the environment at every stage, then the only elements that can serve for string parsing are bodily movements, not states of the physical world. This is important, because in practice it may sometimes be easier to see the objects that are affected than the movements that caused the effects, while in other cases the actions but not their effects may be visible.

Finally, in order to collect the necessary quality of data for any string parsing mechanisms to operate on, an animal will have to pay close attention to another's activity for long periods. Thus, the activity must in some way be intrinsically interesting or *attention-grabbing* for the observer.

What activities are naturally likely to promote prolonged attention, to be clearly visible or produce notice-

able effects, and to recur many times in essentially similar organizational form? And what classes of individuals will have the opportunities to make these observations? Wild mammals typically spend the largest fraction of their time budget engaged in foraging. This activity includes two components that may benefit from social learning, search strategy and processing technique; depending on the range of diet items consumed, both searching and processing may present multiple occurrences of similar actions. Since successful foraging results in ingestion of food items, it is likely to be intrinsically attention-grabbing for any mammal, except a baby wholly nourished by milk. However, feeding competition is a major limitation on socially living species, which often therefore forage at much greater inter-animal distances than when engaged in other activities. The obvious individuals to whom this does not apply are dependent offspring. Thus one likely site for a benefit from string parsing would be social learning of maternal feeding skills by offspring approaching weaning. Social activity is also prominent in the time budgets of many species, and in most catarrhine primates this includes a manual activity that recurs very frequently: grooming. To be effective, this activity does require bimanual co-ordination and deft manipulations made in a systematic fashion, but to what extent it includes skills that need to be learnt, socially or otherwise, is unknown. In this case, the range of opportunities for prolonged observation are greater. More narrowly applicable still, among great apes every adult needs to fashion a sleeping nest or bed each night; since these are arboreal structures in most populations, only dependent offspring could observe the details of any other individual's efforts at nest construction. Again, it is unknown at present to what extent this procedure is under relatively tight genetic control, like the nest and bower building of various species of birds, and to what extent individual and social learning is important.

Of these suggestions for circumstances that might provide potential sites for program-level imitation by string parsing, there are extensive data at present only for the acquisition of maternal feeding skills. This has been studied in a number of species, and in the next section attention will focus on the acquisition of feeding skills in an attempt to locate real cases of imitation by string parsing. Many mammals and birds are not required to perform any complex behaviour to access food resources, or if they do, it is performed in a relatively stereotyped fashion by all species members. Some remarkable exceptions do exist, however, encouraging speculation about learning by imitation. Some of these will be examined as potential sites for the operation of string parsing mechanisms.

Potential examples of copying by string parsing

These are not meant to be in any way an exhaustive set, but since they involve social learning of relatively complex skills they present prime cases for which explanation is needed.

Rats in pine forests

Black rats (*Rattus rattus*) in pine forests around Jerusalem have been found to process pine cones in a systematic way, rather in the manner of various species of squirrel (*Sciurus*), in order to reach the seeds (Aisner and Terkel 1992 b). The method involves detaching the cone from the branch without dropping it, carrying it to a secure branch, then systematically stripping off scales in a spiral, beginning from the base and proceeding upwards. This is not a species-typical behaviour of black rats, and indeed naïve rats do not learn it when given unopened cones, even if food-deprived. Cross-fostering the offspring of naïve and experienced mothers on each other has shown that the skill is socially rather than genetically transmitted (Aisner and Terkel 1992 a). It is clear that stimulus enhancement and response facilitation are inadequate as explanations, since an organized process must be acquired, whereas string parsing would be well able to account for the normal acquisition of the skill: the process is visible both in actions and effects, it involves attention-grabbing food items, and is performed many times by the mother.

Interestingly, naïve young rats can also learn the skill if they are taken through a structured series of encounters with part-stripped cones, beginning with an almost-completely processed cone, and then in subsequent cones steadily reducing the number of rows of scales already removed (Aisner and Terkel 1992 a). Seeing the behavioural sequence is therefore not strictly necessary, and on this basis it might be argued that young rats learn by emulation. However, note that the order in which the cones need to be presented to achieve this result is precisely the *reverse* of the order in which these products naturally appear during cone processing. Indeed, Terkel (1994, p. 252) notes that "this is not a situation that occurs in nature". Thus, humans can *teach* rats how to process a cone without the rats ever seeing it done, but there is no reason to think natural coincidence could achieve the same effect; in 10 years of working on the problem and surveying the pine forests, J. Terkel and his co-workers have hardly ever found partially opened cones.

To argue that emulation could account for the normal process of learning, it would be necessary to present a series of part-processed cones in the normal processing order. And even if this did allow the rats to learn, it would – on its own – be insufficient to show that young rats normally learnt by observing the products of behaviour rather than the behaviour itself. Firstly, since the young rat would normally see the part-processed cones while the mother processes them, not discarded on the ground, the ideal experiment would present the physical transformations that a cone undergoes during normal processing, in the absence of rat behaviour. This could be done by graphic editing, if rats could successfully attend to video images. Secondly, it might be that the rats could learn equally by observing their mother's behaviour, without seeing what happens to the pine cone as a result. Again, graphic editing could be used, here to present behaviour without physical transformations of the object. The

mother rat picks up a pine cone, which blurs so that we cannot see where on the cone she starts to gnaw, nor that the cone rotates as she does so – although her own actions remain sharp and clear. These experiments have not been performed, and since they involve odd and potentially difficult situations for a rat to deal with (rats, for instance, do not appear to comprehend video images as monkeys or apes do), they may never be.

The fact that these crucial experiments are so difficult to carry out, and so far removed from the natural circumstances of learning, may be signalling an important message. The experiments are only "crucial" in the light of the disputes in recent literature between whether learning was by means of emulation, in which novel properties of objects are learnt, or imitation, in which novel behaviour is learnt (Tomasello 1998; Tomasello et al. 1993 a). But when applied to behaviour that shows systematic organization over time, the distinction may not be useful. In the real world, an ordered series of physical transformations of an object ending up with an edible package, simply does not occur except when produced *by behaviour*. And ordered sequences of behavioural actions do not occur in the absence of the objects and physical transformations for which they make sense. Arguing about whether learning is by means of "program-level imitation" or "program-level emulation" would completely miss the point (Byrne and Russon 1998; Russon, in press). What is important is that a novel organization of behaviour can be acquired by observation. Which precise aspects of the stimulus situation facilitate this observation is of course of interest, and it may be that the physical consequences of each behavioural act are sometimes easier to see clearly than the movements themselves. But that would not make it appropriate to describe the process as emulation, since what is learnt is a transformational sequence, not a property or "affordance" of an object.

Terkel (1994) himself concluded that, most likely, young rats learn by stealing half-processed cones from their mothers. If so, then plausibly they would begin by stealing cones whose processing is nearly complete, with seeds visible, but – as the sight of less and less fully processed cones becomes associated with eating, and thus rewarding – gradually extend to earlier stages of the process. Rather than learning by emulation, young rats would be learning by trial and error exploration structured by the mother's behaviour of allowing access to part-processed food. This explanation is plausible, but it remains possible that the rats learn by program-level imitation, based on a string parsing analysis of the numerous processing sequences that young rats have the opportunity to watch. Detailed ethological observations of mother and pup rats interactions over pine cones will be needed to discriminate between these hypotheses, although structured trial and error is perhaps more likely. On present evidence, Israeli cone-eating rats do not show program-level imitation by string-parsing, but their data are close enough to serve as a useful baseline for its identification.

Gorillas in herb meadows

Mountain gorillas (*Gorilla g. beringei*) in the Virunga mountains of central Africa live in areas where almost no fruit is available, by exploiting herbaceous vegetation (Watts 1984). In these temperate and sub-Alpine zones the herbs largely lack toxic secondary compounds, and some are relatively rich sources of protein (Waterman et al. 1983). However, the commoner plants are defended physically, either by specific adaptations that reduce palatability (stings, spines) or as a structural consequence of their clambering growth form (tiny hooks, woody exterior to pith stems). The techniques gorillas use to circumvent these defences are complex in more than one sense (Byrne and Byrne 1993): each involves several discrete stages of processing, in which many different manual actions are organized into mechanically efficient combinations, mostly involving bimanual co-ordination between the two hands used in complementary roles, and the overall organization is hierarchical, with subroutines used iteratively at some stages. As with most skilled human manual behaviour, high degrees of behavioural lateralization are found (Byrne and Byrne 1991). Each of several common herbs requires a different, but more or less equally complex technique, yet all individuals have reached adult levels of proficiency by the age of weaning, as measured by the time to process the average handful (Byrne and Byrne 1991). Gorillas forage alone in dense herb vegetation, but mothers allow their infants to accompany them constantly and to observe their food processing (Byrne, in press).

In this case, no experiments could be done on a wild population of an endangered species; however, there is no serious likelihood that the various different techniques are genetically transmitted. Even if a single complex technique might be acquired by natural selection in a somewhat *r*-selected mammal (Leon 1976), like a black rat, the probability of several different techniques evolving in a sub-population of a mammal as *K*-selected as a great ape must be vanishingly small. Note also that each technique is only valuable for dealing with a particular species, and all these herbs are restricted to a limited altitudinal zone on a few mountains.

The precise actions used to achieve each stage of processing, and the laterality of the whole, bimanual program, vary idiosyncratically between animals and show no sign of running in families. However, the overall organization of each technique is remarkably standardized across the study population, despite the fact that the choice of which general action to apply next is massively under-determined by the stimulus. This pattern – close matching at the organizational level but with individual variation in the details – is just what would be expected from acquisition by string parsing, and indeed these data were originally used to argue for program-level imitation of the techniques (Byrne and Byrne 1993; Byrne and Russon 1998). On the other hand, the mechanism proposed by J. Terkel to explain ontogeny of pine cone stripping can be ruled out: the gorilla data come from an ethological study, where we can be sure that unweaned gorillas did not steal part-processed

plants from their mothers (never, in 510 h focal and much incidental observation; mothers did sometimes steal high-quality plants from unweaned infants, however!). Nor was any teaching observed, even of a weak form such as making available part-processed foods to infants (Byrne, in press). In the case of some of these hard-to-process plants, infants would be able to examine processing debris (*Peucedanum*, *Carduus*); however, this debris is not of a sort to "scaffold" acquisition, and for other plant foods no debris is produced (*Laportea*, *Galium*). The remaining alternative is that infant gorillas might derive a whole series of complex techniques, structurally identical to those of their parents purely by individual exploration and emulation learning. This is hard to discount without experiments involving food deprivation – these plants are clearly unpleasant and often painful for young gorillas to handle – but can hardly be said to be a parsimonious explanation, compared to the definite mechanical process of copying by string parsing.

Chimpanzee traditions of tool use

Unlike any other non-human animal, chimpanzees (*Pan troglodytes*) use tools for a wide range of mechanical and social purposes (McGrew 1992). Among this range are three particularly complex and elaborated skills: using plant probes to "fish" for termites (*Macrotermes* and *Pseudocanthotermes*) and *Campanotus* ants (Goodall 1964; Nishida 1973), using woody sticks to "dip" for *Dorylus* ants (McGrew 1974), and using hammer and anvil stones to crack *Panda* and *Coula* nuts (Boesch and Boesch 1983; Sugiyama and Koman 1979). In all three cases, an organized sequence of actions is required, beginning from selection of tool or the material from which it is made, and as with gorilla plant feeding the choice of each action is under-determined by the stimulus: this is most obvious in the case of tool-making or tool selection in advance of arriving at the site of use. Also reminiscent of the gorilla skills is the strong behavioural lateralization of these tasks, unlike other chimpanzee manual action which is typically unlateralized (Marchant and McGrew 1996)[2]. Only for nut-cracking has active teaching been reported (Boesch 1991), but it is very rare, only two cases over 11 years, and evidently not the major means of acquisition. However, numerous inter-population differences in tool-using and other behaviours have long implied that social learning was important in maintenance of these traditions, and the more complex of them were taken to rely on imitation (Nishida 1986).

M. Tomasello challenged this interpretation, suggesting emulation as sufficient explanation: since the traditions did not show distinctive styles in different populations, all that need be learnt by observation was physical properties of sticks, rocks, nuts and insects (Tomasello 1990). Subsequent comparative analyses have shown this to be incorrect, at least in the case of the fishing and dipping techniques, which show clear local styles unrelated to plausible ecological constraints (McGrew 1998). For instance, in different populations probing tools are re-sharpened by biting frayed tips, rotated to use the other end, or simply discarded (McGrew et al. 1979). Most tellingly, the same species of *Dorylus* ants are eaten with different techniques of dipping in different populations . In East Africa, the ants are allowed to swarm up a long wand which is then swept through a precision grip of the other hand to accumulate a handful of ants for rapid chewing (McGrew 1974). In West Africa, a shorter stick is used, one-handed, and the ants are bitten off the end (Boesch and Boesch 1990; Sugiyama 1995; Sugiyama et al. 1988). This method is less efficient, yet the tradition is widespread and persistent; it is evident that the behavioural skills are maintained by imitation – but of what sort?

Just like the gorilla techniques of plant processing, the traditions of insect feeding and nut-cracking in chimpanzees involve multiple repetitions, of easily visible manual actions, most of which produce visible effects, and they finally result in food ingestion: they thus fit all criteria for string parsing. Since female chimpanzees perform substantially more tool use than males (McGrew 1979), young chimpanzees would have especially many opportunities to acquire the techniques. To account for the acquisition of these techniques, at least program-level imitation by string parsing is necessary, and on current evidence it would also seem sufficient.

Discussion

Imitation of complex behaviour – with sequential structure, hierarchical organization, and co-ordination of complementary actions by different effector organs – can under certain circumstances be achieved by a definite method which depends only on observable events: string parsing. Just those circumstances are met among mammals in the case of several complex feeding skills, in species as diverse as rats and apes. In the case of pine-cone-opening by black rats, a satisfactory alternative explanation exists: pups stealing part-processed food remains from the mother would find their skill acquisition structured towards eventual success. In the current absence of evidence of imitation of skills in the entire mammalian radiation – with the exception of the great apes – this explanation is presumably more likely. Other cases where string parsing is a candidate explanation include several techniques of plant processing by gorillas, for which learning from part-processed food is not possible and the only alternative account is the implausible one of individual exploration and emulation learning; and several tool-using traditions of chimpanzees in which population differences of style and technique also rule out that possibility. It has often been argued that skill learning by imitation

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[2] However, insect-fishing for *Campanotus* ants is unlateralized (Nishida and Hiraiwa 1982), and smashing open of *Strychnos* fruits against anvils of stone or wood is lateralized (McGrew et al. 1999).

is restricted to great apes (Byrne 1995; Byrne and Russon 1998; Parker 1996; Whiten and Byrne 1991); the thesis developed here is that string parsing is a sufficient explanation for these data, and that deeper understanding of demonstrator intentions and the cause and effect of the actions are not necessarily involved.

String parsing is a *definite* process, in that it relies on specified features and a mechanical process. These include: sequential order of actions, with recurring patterns in these sequences; recurring elements (as opposed to variable ones) in all corresponding sequences; interruptibility and optionality of parts of sequences; identifiable temporal links with consummatory actions, and so forth. All these features are *observable*, and what is needed is simply a statistical process, effectively cross-correlation of sequential information, in order to extract regular patterns. No reference is here made to mental transformations of perspective by unspecified means, or to comprehension of invisible mental states of other agents.

For string parsing to work, it is necessary for the fluid stream of behaviour to be perceived as segmented into discrete items: only then can the statistical regularities of strings of these items be extracted, and recurring patterns of behaviour related to goals in the environment. One possibility is that any action that an individual can itself perform can also be recognized in the observed behaviour of another (response facilitation); the existence in macaque monkey cortex of mirror neurons, which make just this generalization, makes this the simplest and most likely underpinning of imitation by string parsing in great apes. The absence of any evidence of imitation in monkeys seems puzzling at first sight, but would be explained if response facilitation by mirror neurons evolved, not for skill learning, but for interpretation of social intentions and demeanour (Gallese and Goldman 1998). Effective segmentation is crucial to imitative learning, and just as cognitive scientists studying imitation may have trouble with the segmentation issue, so may novice learners. Some of the exaggerated prosody and form typical of human behaviour that is done as teaching might be best understood as a means of conveying the appropriate segmentation (as suggested also by Parker and Russon 1996, p.437). With the segmentation problem thereby solved, imitation becomes a more practical method of acquiring much more subtle and difficult skills. More recent adaptations, restricted to the great ape clade, may allow detection by string parsing of underlying structure in behaviour segmented by mirror neurons, and to build the hierarchical planning structures of program-level imitation.

Perhaps now this completes the array of theoretical apparatus necessary to understand all the animal behaviour that is labelled as "imitation"? That hope is no doubt slightly too optimistic, but it may be worth taking as a working hypothesis the more restricted proposition that "string parsing, in conjunction with the simpler mechanisms of social learning already known, can account for all cases of skill learning by imitation". Copying of facial and other gestures, and social mimicry in general, has been suggested to have a social function and an evolutionary origin independent of skill learning (Byrne and Russon 1998; Meltzoff and Gopnik 1993).

String parsing can also help make sense of some of the puzzling variation of outcomes reported from experimental attempts to test whether great apes can imitate. Laboratory experiments seldom present their subjects with the multiplicity of highly similar observations that string parsing requires as data. Even where this is in principle available to the naïve animal, there may be little to hold its attention if the actions are only indirectly related to rewarding outcomes. And although actions are naturally visible, if they have no immediate consequences in the environment their precise nature may be difficult for an observer to discern. Failures to detect imitation in the laboratory are to be expected (see Russon and Galdikas 1995, for a similar conclusion). In the most extreme case, where a test apparatus was designed to make its whole mechanism of operation invisible to the observer (a control designed to prevent emulation learning), leaving only external movements of a stick to see, orangutans completely failed to imitate, even an individual with long experience of humans and their artefacts (Call and Tomasello 1994, 1995). In striking contrast, orangutans at a rehabilitation project imitated a bewildering range of human activities (Russon 1996; Russon and Galdikas 1993): sawing wood, washing clothes, cutting and tidying weeds on a path, and so on. These activities all possessed the characteristics that make string parsing possible: they were repeated, often many times a day, and all stages were visible and clearly related to their outcomes.

Chimpanzees imitate key aspects of some traditions of tool-using in the wild, yet in captivity they have often failed to imitate to order (Tomasello and Call 1997). Here, the few successes may be revealing about the causes of more general failures. After a particular method of opening a puzzle box, with prominent external catches and food inside, was demonstrated, imitation was not clear in chimpanzee subjects; but when *repeated* attempts were scored after further demonstrations had intervened, evidence of sequence copying gradually emerged (Whiten 1998). The effect was not large, but then the number of sequences observed in total was tiny compared to those of termite-fishing or hammering that a young chimpanzee watches in the wild. [Note also that Russon (1996) suggested that recurrent attempts at reproduction may be a standard feature of learning by imitation.] Chimpanzees that have experienced extensive interactions with humans during their development do imitate demonstrated actions with simple human artefacts, whereas mother- or nursery-reared individuals seem unmoved (Call and Tomasello 1996; Tomasello et al. 1993b). But consider the difference in experience of these individuals. Those brought up with humans are used to a wide range of ways of interacting with human artefacts already, their "repertoire" of patterned actions is thus greater. Ostensibly the same demonstration, then, is very much less complicated for them, since much of the situation is already familiar. The difference in performance may equate to their operating in a different "zone of proximal development" (Vygotsky 1978).

The fact that the structural organization of skilled behaviour can be extracted by string parsing, with no need of an understanding of the "everyday physics" of cause-and-effect, means that imitation per se can no longer be used as a non-verbal test of such comprehension. Even in the elegant experiment of Meltzoff (1995), in which 18-month-old infants see adult models *failing* to complete some action sequence, yet they copy the intended (but not seen) act, it may be argued that the complete sequence might already have been acquired by string parsing. As an alternative, it would be possible to use the experiment devised by Want and Harris (1998), in which a subject is shown how to poke an object out of a horizontally mounted transparent tube, in which there is a "trap" (a task originally devised by Visalberghi and Limongelli 1994, to study monkey and ape understanding of causality). Only if the poking is done from one end can the object be obtained. Some children saw the action performed perfectly, while others saw the model put the stick first into the wrong end, then remove it and poke from the other end; thus both groups saw successful performance, but for one an error was nearly made each time. On the basis of string parsing alone, the children in this latter case should have treated the aborted poke into the wrong end as part of the successful sequence. Yet in fact these children did not copy the incorrect insertions, and interestingly they actually learnt significantly more quickly than those who saw only error-free demonstrations. The implication is that what they learnt was an understanding of how a trap can prevent success, not simply a patterned sequence of actions. This task has yet to be tried with non-humans, but should serve as one way of distinguishing causal understanding from imitation by string parsing alone.

Drawing a sharp theoretical line between imitation by string parsing and causal/intentional understanding may enable a better appreciation of how they articulate in practice. It seems possible that, in the absence of instructional teaching by language, an organism could not in principle understand the purpose of another's behaviour and how it physically achieved this purpose if it could not first parse the behaviour into its appropriate components. Consequently, it may not be possible to find organisms that can achieve a causal/intentional understanding of complex behaviour but cannot imitate it. Moreover, once imitation is seen as something that can take place without prior causal/intentional understanding of what is imitated, then it may be that the process of imitation is sometimes helpful for acquiring such understanding. That is, an organism may imitate a complex behavioural process *without* understanding it, and by doing so come to grasp better the cause-and-effect nature of the process and its purpose. Indeed, imitating behaviour "mindlessly" may be one way of gaining a fuller understanding of its purpose.

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