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WHAT CAN IMITATION DO FOR COOPERATION?

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Does imitation play a significant role in human ultra-cooperation? Is our ability to copy body movements an important part of the matrix of cognitive skills that deliver collective action and information sharing on an unprecedented scale? For at least a century, psychologists and biologists have said a firm ‘yes’. This chapter also says ‘yes’, but questions the traditional picture of how and why imitation supports cooperation. I’ll argue that imitation is not a ‘module’ or cognitive adaptation for cooperation, that it contributes to collective action and information sharing in a wider variety of ways than has been typically assumed, and that its celebrated contribution – to the cultural inheritance of technological skills – may be only a very small part of what imitation does for cooperation.

Two types of imitation have been identified, which I’ll call ‘simple’ and ‘complex’¹. It is widely assumed that simple imitation and complex imitation are cognitive adaptations - that they are based on distinct cognitive processes, which evolved independently via gene-based selection to fulfil different social functions. Simple imitation is thought to function as ‘social glue’ – to enhance an individual’s sense of belonging to a social group - in a way that could facilitate collective action. Complex imitation is thought to be an adaptation for a certain kind of information sharing - the cultural inheritance of technological skills.

Section 1 reviews recent research showing that simple and complex imitation are based on the same core cognitive mechanisms, and section 2 considers whether these and other imitation-related mechanisms constitute cognitive adaptations. Section 3 looks at recent studies of simple imitation suggesting that a virtuous circle of unconscious imitation and prosocial attitudes keeps the members of human social groups in a constant state of readiness for collective action and information sharing. Section 4 argues that complex imitation contributes to human cooperation primarily

by promoting the cultural inheritance of communicative-gestural, rather than instrumental-technological skills, and that it is particularly effective when it is dumb, i.e. not guided by rational mechanisms.

More broadly, this chapter discusses both the proximal psychological mechanisms and the evolutionary consequences of imitation. I argue that the proximal mechanisms are more ancient (primarily sections 1 and 2), and that the evolutionary consequences are more diverse (sections 3 and 4), than has typically been assumed. These two themes are related, but in a specific way. With one exception (section 4.2), I am *not* suggesting that imitation has particular evolutionary effects *because* it depends on ancient and relatively simple psychological mechanisms. In most cases, complex, recently evolved cognitive adaptations could in principle have the same evolutionary consequences. They could, but the experimental evidence indicates that they don't – that imitation does not, in fact, depend on cognitive adaptations. The point I want to make is that simple, old psychological mechanisms are enough; imitation need not be based on complex cognitive adaptations in order to support human ultra-cooperation.

1. **Cognitive mechanisms of imitation**

1.1 Simple and complex imitation

Simple imitation is also known as 'mimicry' (Tomasello 1996), 'automatic imitation' (Heyes et al. 2005), 'priming' and 'response facilitation' (Byrne & Russon 1998). It occurs when an observer copies body movements that are already part of his behavioural repertoire. For example, when two people are in conversation, it is

common for each to copy the other's incidental gestures, such as ear-touching and foot-wagging (Chartrand & Barge 1999). Simple imitation is currently a focus of study in social cognitive psychology and cognitive neuroscience, where most people assume that the mechanisms underlying this kind of imitation consist of simple connections between event representations (Chartrand & Van Baaren 2009).

Complex imitation is also known as 'imitation learning' (Tomasello 1996), 'true imitation' (Zentall, 2006), 'observational learning' (Carroll & Bandura 1982) and 'programme-level imitation' (Byrne & Russon 1998). It occurs when an observer copies a 'novel' sequence of body movements; a sequence she had not performed before observing the model. For example, in one of many experimental demonstrations of complex imitation, adults observed and then reproduced a novel sequence of semaphore-like movements of the hand and arm (Carroll & Bandura 1982). Complex imitation is a focus of study in developmental and comparative psychology, where it is assumed to involve a variety of complex psychological mechanisms. These include symbolic coding, programme extraction, perspective-taking, and intention-reading.

The assumption that complex imitation depends on complex psychological processes has been motivated by task analysis rather than empirical data. To imitate observed body movements, my cognitive system has to translate visual information from the model into motor output that looks the same as the model's behaviour from a third-person perspective. In cases where the first-person and third-person views of an action are very different (e.g. facial and whole-body movements), it is far from obvious how the cognitive system solves this 'correspondence problem'; how it works out which of my potential actions corresponds to the one I saw you perform (Heyes & Bird 2007). 'Symbolic coding', 'programme extraction', 'perspective-taking' and

‘intention-reading’ are all broad-brush candidate solutions to the correspondence problem. They are broad-brush in that no one has specified in any detail what these processes involve. They are candidate solutions because each is thought to involve abstract, flexible representations of action, and it is plausible that representations of this kind could solve the correspondence problem by an up-and-down route. In other words, the cognitive system could solve the correspondence problem by taking a relatively low-level visual representation of an observed action, recoding it ‘up’ into an abstract representation – a symbolic code, programme, perspective or intention - and then recoding it ‘down’ into a motor programme.

The difficulty of the correspondence problem varies with the difference between first-person and third-person views of an action sequence; a difference that is maximal for facial gestures and minimal for vocalisations. The challenge posed by the correspondence problem does not vary with sequence novelty. The cognitive system has to solve the correspondence problem for simple as well as complex imitation - to enable copying of familiar as well as novel body movements. Curiously, it is seldom acknowledged that simple imitation poses the correspondence problem. As a result, when researchers suggest that ‘mimicry’ is mediated by a simple, evolved cognitive mechanism (e.g. Tomasello 1996; Byrne & Russon 2006), it is not clear whether they have overlooked the correspondence problem, or are suggesting that the mechanism in question solves this problem in an unspecified but simple way².

1.2 Associative sequence learning

Recent research in experimental psychology and cognitive neuroscience has provided evidence in support of a new ‘associative sequence learning’ (ASL) model of

imitation (see Figure 1; Heyes & Ray 2000; Catmur et al. 2009). This model suggests that the correspondence problem is solved in the same way for both simple and complex imitation, and that the solution does not involve up-and-down recoding. According to ASL, the correspondence problem is solved for any given action by a direct connection between a visual and a motor representation of that action. These connections, or ‘matching vertical associations’, are forged in the course of development by the same domain- and species-general processes of associative learning that produce Pavlovian and instrumental conditioning in the laboratory (see Schultz & Dickinson (2000) for a review of associative learning). These processes strengthen excitatory connections between pairs of event representations when the occurrence of the two events is correlated, i.e. when they occur relatively close together in time (contiguity) and one event is predictive of the other (contingency).

Insert Figure 1 here

In terms of their internal structure, the processes of associative learning could just as easily produce non-matching as matching vertical associations. If the sight of one action, X, is correlated with the performance of a different action, Y, associative learning will strengthen the connection between a visual representation of X and a motor representation of Y, supporting counter-imitative rather than imitative behaviour. According to ASL, matching vertical associations predominate because certain features of the human developmental environment ensure that we more often experience correlations between observation and execution of the same action, than of different actions (Heyes 2005). For example, experience of the former kind comes from direct self-observation (e.g. looking at your own hands in motion), mirror self-

observation (using reflective surfaces), being imitated by others (especially facial imitation of infants by adults), synchronous activities of the kind involved in dance, sports and military training, and indirectly via the use of action words (Ray & Heyes 2010). The ASL model suggests that it is the relative paucity of these kinds of experience in the lives of nonhuman animals that explains why their imitation repertoires are more limited than those of humans.

ASL assumes that in cases of complex imitation, when an observer copies a novel sequence of actions, the operation of matching vertical associations is guided by processes that encode the serial order of visual stimuli. These ‘horizontal’ processes learn what the novel action sequence ‘looks like’. The representation they construct would be sufficient for subsequent recognition of the sequence, and to distinguish it from sequences containing the same components in a different order. However, for *imitation* of a novel action – to turn vision into matching action - the visual sequence representation formed by horizontal processes must activate, in the appropriate order, a matching vertical association for each element of the sequence.

Unlike several of the processes invoked by up-and-down accounts of complex imitation, horizontal mechanisms are not dedicated to the processing of body movements or even of social stimuli. The ASL model assumes that the same horizontal mechanisms encode the serial order of inanimate stimuli. It does not deny that processes like ‘intention-reading’ are sometimes involved in overt imitative performance. In adult humans, the activation of motor representations via MVAs makes imitation possible, not obligatory, and intention-reading will sometimes determine whether overt imitative behaviour is inhibited or allowed to occur. What the ASL model implies is that, while processes like intention-reading sometimes modulate both imitative and non-imitative behaviour, they don’t play a distinctive,

necessary or integral role in imitation. Specifically, they don't help to solve the correspondence problem.

Unlike previous accounts of the cognitive mechanisms mediating imitation, ASL has been explicitly tested against alternative models. These experiments have examined both simple and complex imitation, using behavioural and neurophysiological measures, and probed the model's claims about both vertical and horizontal processes. Supporting the idea that matching vertical associations are forged by associative learning, these studies have shown that novel sensorimotor experience can enhance (Press et al. 2007), abolish (Heyes et al. 2005) and even reverse (Catmur et al. 2007; 2008) simple imitative behaviour. It has been widely reported that humans typically show 'automatic imitation' of various hand and foot movements: in tasks that require us to ignore the sight of these movements, we nonetheless respond faster and more accurately when the required action matches an observed body movement. Hand opening is faster when observing hand opening than when observing hand closing, foot lifting is faster when observing foot lifting than hand lifting, and so on. These imitative effects appear to be relatively impervious to the actor's intentions, but they can be changed by retraining. For example, without explicit training, passive observation of index finger movement activates muscles that move the index finger more than muscles that move the little finger. However, after training in which people were required to respond to index finger movements with little finger movements, and vice versa, this pattern was reversed. Observation of index finger movement activated little finger muscles more than index finger muscles, implying that associative learning had converted automatic imitation into automatic counter-imitation (Catmur 2007; 2008).

Similarly, experiments examining complex imitation have provided evidence that it involves the same kind of sequence learning processes as non-imitative tasks (Leighton et al. 2010); that these processes do not depend on intention-reading (Leighton et al. 2008); and that they do not show the flexibility one would expect if complex imitation were achieved by an up-and-down route (Bird & Heyes 2005). For example, when people are required to imitate a sequence of movements involving the selection of a pen and its placement in one of two containers they show exactly the same pattern of errors as when they are instructed to perform the same movements by flashing geometric shapes. Error patterns are indicative of underlying cognitive processes. Therefore these results indicate that the same sequence encoding mechanisms are recruited in imitative and non-imitative tasks, and by stimuli that do and do not support the attribution of intentions (Leighton et al. 2010). Regarding flexibility, Bird & Heyes (2005) found that people who had observed a complex sequence of key-pressing movements could reproduce that sequence only when they used exactly the same digits as the model. For example, when the model used her fingers, they could imitate the sequence with their fingers but not with their thumbs.

2. **Cognitive adaptations for imitation**

If the ASL model is broadly correct, the core mechanisms of imitation – the processes that solve the correspondence problem – are not cognitive adaptations. They were not favoured by natural selection because individuals with those mechanisms out-reproduced others by virtue of being better able to imitate. Matching vertical links are a product of associative learning. Associative learning is almost certainly an adaptation, but for the detection of causal relationships between events, not for

imitation specifically. The horizontal sequence processing mechanisms may also be an adaptation, and of a more specific kind. Very few species show sequence processing capabilities even remotely comparable to those of humans (Pearce 2008). However, the evidence that these horizontal processes are domain-general – that they operate in the same way on sequences of animate and inanimate stimuli – suggests that they are not an adaptation for imitation.

Viewed through the lens of the ASL model, the human capacity for imitation is ‘epistemically engineered’ (Sterelny 2003) or socially constructed. Consider the contexts in which we receive correlated experience of seeing and doing the same action, the experience that creates matching vertical associations: direct self-observation, mirror self-observation, being imitated by others, and synchronous activities of the kind involved in sports, dance and military training (Ray & Heyes 2010). They are all contexts created or tightly regulated by cultural artefacts and practices. Direct self-observation is the least ‘social’ context, but it is still subject to powerful cultural constraints. In contemporary Western cultures, infants spend a large proportion of their waking hours gazing at their own hands in motion (White et al. 1964), an activity that would rarely be possible in cultures, past and present, where infant swaddling is the norm.

Although it now seems unlikely that the core mechanisms of imitation are cognitive adaptations, it is still possible that both cultural and genetic evolutionary processes have played a part in making us ‘Homo imitans’ (Meltzoff 1988), a species that can imitate an extraordinary range of actions with remarkable facility. It is possible that some of the social practices that foster the development of imitation have been favoured by cultural group selection. For example, groups that trained their novices to dance and fight via synchronous drills may have been more successful than

other groups, in part because these drills made the novices better imitators. In addition, gene-based individual selection could have favoured the evolution of mechanisms – in adults and infants - that speed-up learning of matching vertical associations. Candidate mechanisms of this kind include an attentional bias towards hands-in-motion (del Giudice et al. 2009), which could promote learning by self-observation, and tendencies to produce and to attend to ‘natural pedagogical’ cues (Csibra & Gergely 2009). These tendencies could make imitation of infants by adults a more potent source of matching vertical associations. On the production side, natural pedagogical cues include ‘motherese’, the high contrast intonation we tend to use when addressing infants and children, and on the receptive side, they include attentional biases towards both motherese and direct gaze.

Two features of these response tendencies and attentional biases are worth noting. First, they could be mediated by relatively simple perceptual and motoric behaviour-control mechanisms; a tendency to orient towards a particular class of stimulus does not require anything as complex as intention-reading. Second, even if we call these low-level mechanisms ‘cognitive’, and assume that they are biological adaptations, it would make them cognitive adaptations, but not cognitive adaptations *for imitation*. The hands-in-motion, motherese and direct gaze attentional biases may speed-up learning to imitate, but it’s unlikely that this was a significant factor in their evolution. The hands-in-motion bias is likely to be an adaptation for precise visuomotor control of action, and natural pedagogical cues appear, as their name suggests, to be a generic method of ensuring that infants attend to, and therefore learn from, adults.

It has recently been suggested that humans have ‘a special kind of motivation for imitation’ (p. 2412, Tennie et al. 2009; see also Carpenter 2006). It appears that,

unlike chimpanzees, human children do not merely imitate in order to acquire more effective methods of solving instrumental problems. Experiments demonstrating ‘over-imitation’ or ‘over-copying’ (e.g. Lyons et al. 2007) - the imitation of incidental details of a model’s technique - suggest that human children are ‘socially motivated’. Above and beyond any instrumental benefits, children imitate because they just want to act in the same way as others.

This is a plausible and interesting suggestion. It has been assumed for too long that differences between chimpanzees and children in imitation tasks are due to ability rather than motivation (Shea 2009), and it is not difficult to imagine how a desire to be like others could enhance the fidelity of cultural inheritance of behaviour. However, it is far from clear that over-imitation represents a motivational adaptation, rather than a product of enculturation. From early infancy, children are selectively rewarded by adults for imitation. For example, Pawlby (1977) found that, whenever infants performed an action shortly after it had been performed by their mother, the mother responded with smiles and a general tone of encouragement, and that ‘a sense of special achievement was conveyed to the infant’. Confirming the effects of this kind of training to imitate, Waxler and Yarrow (1975) found in a free play session that infants who were rewarded more frequently for imitation exhibited imitation more often and across a broader range of behaviours. Thus, social motivation to imitate may well be human-specific, and an important part of the story about human cultural inheritance, but we shouldn’t assume it is an adaptation.

In sections 1 and 2 I’ve argued that neither the core nor the peripheral mechanisms of imitation are dedicated cognitive adaptations - they did not evolve via gene-based selection specifically to make imitation possible. Recent evidence suggests that the core mechanisms – those that solve the correspondence problem -

are products of cultural epistemic engineering, and that the peripheral mechanisms – that assist the engineering process – are non-specific and/or also cultural in origin. If imitation mechanisms are not cognitive adaptations, they could not be cognitive adaptations that have ‘evolved for’ cooperative functions; social bonding in the case of simple imitation, and cultural inheritance in the case of complex imitation. However, as I hope to show in sections 3 and 4, this does not in any way undermine the view that imitation promotes human cooperation.

3 Cooperative effects of simple imitation

Anecdotal reports and folk wisdom have long suggested that people inadvertently copy each other’s gestures and mannerisms, and that this tendency somehow facilitates their interaction. In the last 10 years, research on this kind of simple imitation – known as the Chameleon effect (Chartrand & Bargh 1999), or nonconscious mimicry (Van Baaren et al. 2009) – has made enormous progress. Carefully controlled experiments in semi-naturalistic settings have confirmed that the effect is pervasive, and post-interaction interviews provide no evidence that imitatees are aware of being copied, or that imitators are aware of, or intend to, imitate. Yet more important, recent experiments have shown that simple imitation is causally related to ‘prosocial’ or cooperative attitudes and behaviour (Chartrand & Van Baaren 2009; Van Baaren et al. 2009).

The causal relationships go in both directions: being imitated makes people more cooperative, and when people are thinking and feeling in a cooperative way, they are more likely to imitate others. When a person has been imitated by an interaction partner, they like the partner more (Chartrand & Bargh 1999), judge them

to be more persuasive (van Swol 2003), and report that the interaction was smoother and more enjoyable (Tanner et al. 2008) than when they were not imitated. In negotiation exercises, dyads in which one person was asked to imitate the other secured better outcomes, both for themselves and for the group (Maddux et al. 2008). Further evidence that the cooperative effects of being imitated do not only benefit the imitator comes from a study showing that, when they have been imitated, people are more willing to help others with simple tasks, and donate more money to charity (van Baaren et al. 2004).

Other studies have examined the effect of cooperative attitudes on imitation. These show that people imitate a person they like more than a person they don't like, members of an in-group more than members of an out-group (Likowski et al. 2008; Stel et al. 2010), and more after they have been primed with words such as 'we' and 'ours', than after priming with words such as 'me' and 'mine' (Leighton et al. 2010). They also indicate that people imitate more when they are feeling ostracised or socially excluded, and under these circumstances they imitate members of the group that has excluded them more than members of other groups (Lakin et al. 2008). This implies that, even when people are apparently unaware of giving or receiving simple imitation, their behaviour is sensitive to the fact that imitation tends to elicit cooperative attitudes from the imitatee.

These bidirectional causal relationships raise the possibility that, when the members of a social group are in face-to-face contact, they are constantly maintaining one another in a cooperative frame of mind – in a state of readiness for collective action and information sharing - via a virtuous circle of simple imitation and prosocial attitudes. The idea that this virtuous circle functions to maintain, rather than to change, cooperative groups is consistent with research examining imitation across

group boundaries. This shows, not only that the members of other ethnic (Heider & Skowronski 2008) and religious (Yabar et al. 2006) groups are imitated less than the members of ones own group, but also that being imitated by a member of a different ethnic group makes the imitatee like that imitator less, rather than more (Likowski et al. in press).

Very little is known about the psychological mechanisms supporting the virtuous circle. Even if we assume that matching vertical associations are the mechanism that makes imitation possible, we still need to understand how being imitated produces cooperative attitudes, and how cooperative attitudes engender imitation. Because the virtuous circle seems to be so well-tuned to maintaining cooperative relationships, so fit for purpose, it's tempting to assume that these mechanisms are dedicated, and perhaps sophisticated, cognitive adaptations. Future research may support this assumption, but that is far from inevitable. The virtuous circle could be underwritten by two relatively simple, non-specific psychological gadgets: contingency detection and disinhibition.

Contingency detection, the capacity to detect when the movements of another person co-vary with ones own, could be the basis for the imitation to cooperation relationship. In other words, the imitatee's cognitive system need not know that the imitator's movements are topographically similar; only that movements of the imitatee's body predict those of the imitator's body. There is evidence that infants can detect contingencies between their own actions and those of external objects from an early age, and that detecting these contingencies is associated with positive emotion (Gergely & Watson 1999). If the contingency detection mechanism that generates these emotional reactions is the same one that mediates associative learning, then

there is reason to believe that it is both simple and phylogenetically ancient (Rolls 2000).

Disinhibition, or the release of inhibitory control, could underwrite the relationship between cooperative attitudes and imitative behaviour. This suggestion is consistent with evidence that patients with lesions of the prefrontal cortex, an area involved in the inhibition of over-learned or automatic response tendencies, show compulsively imitative behaviour (De Renzi et al. 1996). These inhibitory processes are complex, and more highly developed in humans than in any other species. However, the possibility I am raising is that cooperative attitudes promote imitation, not by using these complex inhibitory processes, but by switching them off. When we like someone, or perceive that person to be 'like me', there is a release of inhibition which allows the activation of motor representations via matching vertical associations to produce overt imitative behaviour. Thus, when we are cooperatively motivated, imitative tendencies, which are normally suppressed, are allowed to 'get out' and influence observable behaviour.

To find out whether basic mechanisms such as contingency detection and disinhibition are driving the virtuous circle, it will be necessary to test whether contingent, nonimitative behaviour has the same prosocial effects as imitation, and whether cooperative attitudes 'release', not only imitative behaviour, but also other over-learned reactions to social and inanimate stimuli. If experiments of this kind confirm that the virtuous circle depends on simple, non-specific mechanisms, it would help to explain the early co-evolution of human cooperation. As Sterelny (2003) has pointed out, language and cultural inheritance of information are, not only instruments of cooperation, but also mighty cooperative achievements. For a complete account of the origins of human cooperation, we need to find the precursors of these cooperative

feats, the processes that got human cooperation off the ground. If it is based on simple psychological mechanisms, the virtuous circle linking simple imitation with cooperative attitudes is a strong candidate for this ground-breaking role.

4 Cooperative effects of complex imitation

Discussion of the cooperative effects of complex imitation has been dominated by the possibility that complex imitation plays a crucial role in a certain kind of information sharing – the cultural inheritance of instrumental or technological skills. Much contemporary psychological research on this issue compares the behaviour of children and chimpanzees in tasks where they are allowed to observe an expert performing a novel instrumental action (e.g. manipulating objects to obtain a reward), and then attempt to obtain the reward themselves. Focal questions are whether children are more likely than chimpanzees to imitate than to ‘emulate’ (defined below) the expert’s behaviour, and, if so, whether this difference provides evidence that the capacity to imitate is a key psychological requirement for the cultural inheritance of instrumental skills (e.g. Tennie et al., 2009; Whiten et al., 2009).

4.1 Imitation and emulation

The distinction between imitation and emulation (Tomasello 1996) is, I think, a very important one, but it is sometimes drawn in a confusing way. Performance of an instrumental task involves two kinds of transformation: a sequence of changes in the spatial properties of the actor’s body parts (body movements), and of the objects on which he is acting (object movements). At its valuable root, the imitation / emulation

distinction draws attention to *what* is copied by the observer of instrumental task performance: the body movements (imitation) or the object movements (emulation) or both. So far, so good. But this *what* distinction is sometimes confounded with a *how much*, distinction: between the copying of a sequence and the copying of an endpoint. When the *what* and *how much* distinctions are pulled-apart, we have four possibilities: endpoint imitation – copying the endpoint of a sequence of body movements; endpoint emulation – copying the endpoint of a sequence of object movements; sequence imitation – copying a sequence of body movements; and sequence emulation – copying a sequence of object movements.

When the *what* and *how much* distinctions are confounded, ‘imitation’ refers to copying of a sequence of body movements, including the endpoint, while ‘emulation’ refers to copying of the endpoint, only, of a sequence of object movements (end/object). Thus, imitation is cast as ‘process copying’ and emulation as ‘product copying’ (Tennie et al. 2009), and it seems that imitation is more likely than emulation to result in high fidelity transmission of behaviour; transmission of the kind needed for cumulative cultural evolution. If an observer copies only the endpoint of a model’s action (the terminal configuration of the fingers, or of the parts of an instrument, or both), and there is more than one sequence that can culminate in this endpoint (the order and dynamics of the body part and/or object movements), it is almost inevitable that the *sequence* will be transmitted with lower fidelity. The fact that sequence copying is likely to lead to higher fidelity transmission of sequences than endpoint copying is important in its own right. However, it does not imply that body movement copying is associated with higher transmission fidelity than object movement copying.

Once the confusion between *what* and *how much* is penetrated, it becomes clear that the comparison that matters with respect to the cultural inheritance of skills is between sequence imitation and sequence emulation, and it is my hunch that, for most instrumental skills, sequence imitation will result in *lower* copying fidelity than sequence emulation. A novice watching an expert potter, flint knapper, basket weaver or computer programmer would do better to attend to, and copy, the sequence of object movements effected by these skills than to focus on the expert's body movements. A combination of both sequence imitation and sequence emulation is likely to be associated with the highest transmission fidelity, but if for some reason - local, developmental or evolutionary - it has to be one or the other, my money is on sequence emulation coming out on top. Perhaps there are exceptions, but it seems that in the case of instrumental skills, actions on objects, the cultural wisdom lies in the object transformations rather than the body movements. If this is correct, copying the sequence of object movements (sequence emulation) will either ensure that the sequence of body movements is also inherited, or it won't matter, from the perspective of cultural evolution, how the object movements are effected by the actor's body.

To test the hunch that sequence emulation is more important than sequence imitation for the cultural inheritance of instrumental skills, it would be helpful to use eye-tracking to find out what novices are looking at most when they are learning a technological skill by observation. Are they, for example, studying more closely the movements of the flint-knapper's fingers, hands and arms, implying sequence imitation, or the angle and velocity at which one stone makes impact on the other, implying sequence emulation?

If my hunch is correct, imitation is much less important for the cultural inheritance of instrumental / technological skills than was previously thought. However, once the *what* and *how much* distinctions have been dissociated, it becomes clear that imitation, sequence imitation, is likely to be indispensable for the cultural transmission of the other major category of skills – ‘communicative’ or, more broadly, ‘gestural’ skills. Many potent, culture-specific signs and rituals do not involve objects. They consist exclusively of conventional (i.e. instrumentally arbitrary) sequences of body movements, and therefore cannot be learned by sequence emulation.

These gestural skills are seldom considered by psychologists interested in cultural inheritance, but their importance in defining groups and promoting cooperation is recognised in anthropology and the humanities (Corbeill 2004). They include the sequences of body movements that enable group members to communicate without words, and thereby to coordinate their activities when there are no words (e.g. when the message is ineffable, and before language co-evolved), and when words are dangerous (e.g. when a group is stalking prey). They also include the sequences of body movements, such as those involved in ritualistic dancing, that enable group members to bond – to achieve the states of trust and commitment required for cooperative action - through the expression of common religious beliefs, and the sharing of heightened states of arousal. In addition to providing proximal support for cooperative action – by communicating information, promoting trust and commitment, and indicating who is and who is not part of the cooperative group – these gestural skills may also contribute to the kind of within-group homogeneity and between-group diversity necessary for the evolution of cooperation via cultural group selection (Boyd & Richerson 1985).

4.2 Smart and dumb (complex) imitation

I've called the imitation of novel actions 'complex imitation' because it's traditionally assumed that the imitation of novel actions involves more complex psychological mechanisms than the imitation of familiar actions, and, in some measure, I agree with this tradition. The ASL model outlined in section 1.2 suggests that, although the same core mechanisms solve the correspondence problem for simple and complex imitation, something extra – horizontal, or serial order, processing - is needed to explain complex imitation.

Horizontal processing is complex in the sense of being computationally demanding, but in other respects it is dumb. Encoding the serial order of visual events, including observed body movements, is demanding on working memory and executive processes. However, horizontal processing can occur without consciousness or an intention to learn, and doesn't help the novice to make rational choices about what they should and should not imitate. The ASL model implies that rational decisions of this kind are an optional extra, not an intrinsic part, of complex imitation; rational decision-making and imitation have distinct co-evolutionary roots, and in adults as well as children and nonhuman animals, complex imitation often occurs without awareness or deliberation (Bird & Heyes 2005).

In this respect, the ASL model is very different from theories suggesting that complex imitation necessarily involves the observer representing what the model intended to achieve (Tomasello 1996), or to teach the observer (Csibra & Gergely 2009). These theories suggest that complex imitation is smart in the selfishly rational sense; that an observer won't imitate an action unless she either understands what the

outcome will be, and desires that outcome, or has reason to believe that copying the model's action represents the most efficient means for her to achieve a current goal.

Shea (2009) has pointed out that smart imitation – imitation regulated by selfishly rational calculation - is likely to have negative effects on the fidelity of cultural inheritance, and therefore on the 'evolvability' of cultural skills and practices. Studies reporting smart imitation imply that novices pick and choose which observed behaviours to copy, using the model as a source of elements and ideas, but reinventing rather than faithfully adopting the expert's method of getting the job done (e.g. Gergely et al. 2002). In contrast, dumb imitation – imitation that does not depend on rational calculation – has a better chance of allowing culturally accumulated wisdom to be propagated across generations of learners. I'd like to add two things to Shea's analysis. The first is a footnote, and the second a more substantive hypothesis about the importance of dumb imitation with respect to cooperation.

The footnote is to point out that dumb imitation is not unselective imitation; it won't result in novices copying every incidental detail of a model's behaviour. On any given occasion when an expert demonstrates a skilled action, she may fumble or sneeze, and, at a low-level of analysis, the trajectories of her body movements will be slightly different from those she uses on other occasions. However, to learn any significant skill by imitation, a novice must watch many repetitions of the skilled action, performed by a single model or by a number of different models. Across these demonstrations the important elements of the action will persist while the incidentals will vary. Therefore, any horizontal sequence learning process sensitive to the frequency of elements and element transitions – i.e. any sequence learning process worthy of the name – will be selective; it will encode the core, recurrent features of the sequence, filtering out accidents, idiosyncracies and random variation.

The hypothesis is that, unlike smart imitation, dumb imitation can produce group markers – badges of group membership – that would be extremely difficult to fake. The members of a social group often have subtle behavioural characteristics in common; they walk with a certain gait, fiddle with their hair in a certain way, or use facial expressions that are minutely different from those of other groups. These group-specific characteristics can modulate cooperative behaviour - by eliciting trust and other prosocial attitudes - but they are poor targets for smart imitation. In many cases, the distinctive features of a group's behaviour can't be consciously detected, and therefore can't be copied (i.e. faked) by outgroup members via a process that depends on conscious, rational calculation. It's possible that, in other cases, careful scrutiny permits the detection of group-specific behaviour, but deliberate imitation of this behaviour would yield an inauthentic caricature of the original³. However, these behavioural badges *can* be acquired via dumb imitation. The horizontal processes described by the ASL model allow a novel behaviour to be learned by observation, and to be imitated without awareness or deliberation. Instead they depend on the frequency with which the novel behaviour is observed. In the case of group-specific postures, gestures and mannerisms, frequency of observation is likely to covary with time spent in the company of group members – a fair indicator of genuine group membership.

5 Summary

For many years, those interested in the evolutionary origins and consequences of imitation have focussed on the imitation of novel actions, and its potential contribution to the cultural inheritance of technological skills. Drawing on recent

research in experimental psychology, social cognitive psychology and cognitive neuroscience, I have tried to adjust this focus in several ways. First, I have suggested that the imitation of novel actions (complex imitation) is continuous, in terms of its origins and underlying mechanisms, with the imitation of familiar actions (simple imitation), and therefore a full assessment of the cooperative functions of imitation must encompass them both. Second, I have reviewed research on simple imitation indicating that the members of human social groups are constantly copying each other's gestures and mannerisms. This 'unconscious mimicry' both promotes, and is promoted by, prosocial attitudes, creating a virtuous circle that maintains group members in a state of readiness for cooperative action. Finally, I have argued that complex imitation is unlikely to play a major role in the cultural inheritance of technological skills, but that it is crucial for the cultural inheritance of gestural skills – sequences of body movements that promote cooperation via communication and social bonding, and, potentially, by creating the conditions necessary for cultural group selection. Provided that it does not depend on conscious, deliberative processes, complex imitation may also allow subtle, group-specific features of body movement to function as highly reliable badges of cooperative group membership.

Throughout the discussion, I have presented arguments and evidence suggesting that, although imitation has many adaptive effects, it is not 'an adaptation' (*sensu* Williams 1966). The core mechanisms of imitation - those that translate visual input from a model into matching motor output - are constructed by associative learning, a domain-general cognitive process, from sensorimotor experience provided by the sociocultural environment. Much of this experience depends on artifacts (e.g. mirrors) and practices (dance training) that are themselves cooperative achievements.

Therefore, the human capacity to imitate both engenders, and is engendered by, cooperation.

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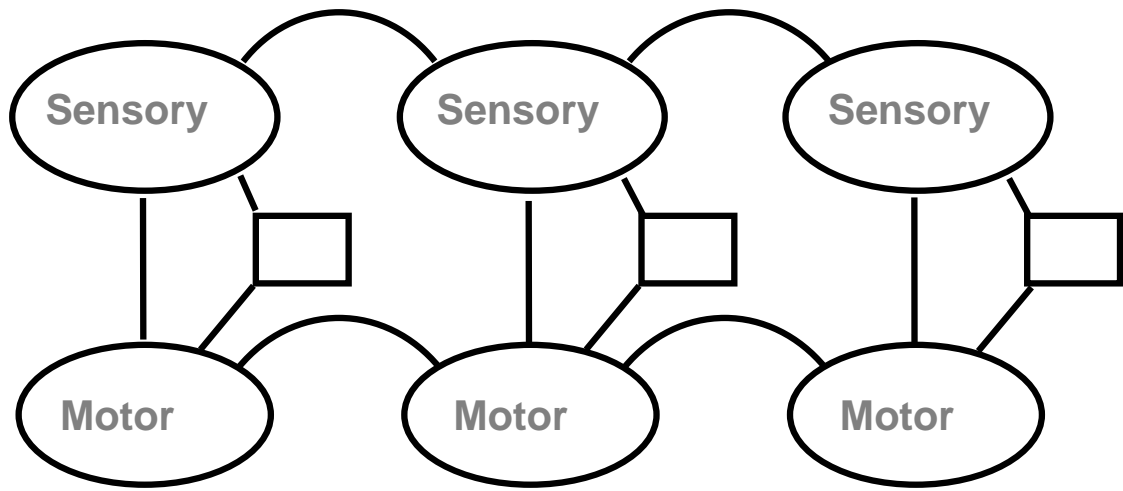
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Figure legend

Figure 2. The associative sequence learning (ASL) model of imitation. The upper row of ovals depicts sensory (visual), and the lower row motor, representations of successive units in a sequence of body movements. The straight vertical lines, connecting sensory and motor representations of the same action unit, are the matching vertical associations (MVAs) that solve the correspondence problem for both simple and complex imitation. The curved lines represent the horizontal learning processes involved in complex imitation. These encode the sequence of visual events (upper row) and, via the matching vertical associations, the sequence of motor events (lower row), during action observation. The boxes represent acquired equivalence cues, which are not discussed in this article.



Footnotes

¹ 'Imitation' refers to copying by an observer of a feature of the body movement of a model. 'Copying' implies a specific causal relationship between observation of a feature of a model's body movement, *fm*, and execution by the observer of a body movement with the same feature, *fo*. This excludes, not only cases in which *fm* and *fo* co-occur by chance, but also other examples of 'social learning' in which *fo* is caused by observation of a property of the model other than *fm*, or in which the effect of observing *fm* is not specific to the production of *fo* (Heyes 2001).

² Meltzoff and Moore are exceptional in having pointed out very clearly that simple imitation of facial expressions poses the correspondence problem. Like those who discuss the correspondence problem in the context of complex imitation, they assume that it is solved by an up-and-down route, involving 'supramodal coding' (Meltzoff & Moore 1997).

³ Thanks to Ben Fraser for this suggestion.