TARGET ARTICLE

Imitation in infancy: the wealth of the stimulus

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Abstract

Imitation requires the imitator to solve the correspondence problem – to translate visual information from modelled action into matching motor output. It has been widely accepted for some 30 years that the correspondence problem is solved by a specialized, innate cognitive mechanism. This is the conclusion of a poverty of the stimulus argument, realized in the active intermodal matching model of imitation, which assumes that human neonates can imitate a range of body movements. An alternative, wealth of the stimulus argument, embodied in the associative sequence learning model of imitation, proposes that the correspondence problem is solved by sensorimotor learning, and that the experience necessary for this kind of learning is provided by the sociocultural environment during human development. In a detailed and wide-ranging review of research on imitation and imitation-relevant behaviour in infancy and beyond, we find substantially more evidence in favour of the wealth argument than of the poverty argument.

Introduction

Imitation – copying the topography of observed body movement – has powerful effects on cognitive, emotional and social development.[1] We imitate actions on objects, allowing us to engage with cultural artefacts and to master technologies, as well as the gestures, postures and movement sequences that define culturally appropriate social interaction. Imitation of gestures leads to rapport (Chartrand & Van Baaren, 2009), and to emotional contagion, providing the foundation for durable emotional reactions to classes of objects and events (Hess & Blairy, 2001). It has even been argued that recognition of the visual similarity between self and other, produced by imitation, promotes mutual understanding and contributes to the development of theory of mind (Goldman, 2005; Meltzoff, 2005; Prinz, 2005).

In order to imitate, a neurocognitive system must be able to solve the *correspondence problem*; to take visual information about body movements and use it to generate motor output that looks the same from a third party perspective (Heyes, 2005). Some actions are perceptually transparent with respect to imitation (Heyes & Ray, 2000); they have exteroceptive effects in common when observed and executed. For example, I can see myself raise my forearm, and it looks a lot like what I see when you raise your forearm. To imitate an action like this, I could use vision to compare your arm movement and my arm movement, and, despite differences in size and orientation, produce a rough copy of your behaviour. However, a comparison process of this kind could not solve the correspondence problem for perceptually opaque actions, such as facial gestures, that yield input in different modalities when observed and executed. When they are performed, perceptually opaque actions are experienced primarily or exclusively through the kinaesthetic senses, and when they are imitated, the model's action and the observer's action look the same only from a third party perspective. Thus, imitation of perceptually opaque actions cannot be guided by sensory information about the degree of similarity between the model's and the observer's behaviour. To imitate perceptually opaque actions requires a neurocognitive mechanism that relates the seen and unfelt to the felt and unseen.

It has been widely believed for some 30 years that the human capacity to solve the correspondence problem, and thereby to imitate, depends on a complex, innate cognitive mechanism. Evidence that human neonates can imitate a range of facial gestures (e.g. Meltzoff & Moore,

[1] Observers can imitate (i.e. reproduce the topography) of both transitive and intransitive actions. That is, an observer can copy the way in which the parts of the model's body move relative to one another, both when the modelled action is applied to an object and when it is a gesture. Imitation is commonly distinguished from 'emulation' (e.g. Tomasello, 1996). In cases of emulation, the observer copies 'ends' rather than 'means'; she reproduces the effects of an action on an object, but not the topography of the actor's body movements. Emulation and the imitation of transitive actions are thought to play a role in the cultural inheritance of technological skills, while the imitation of intransitive actions is thought to promote social bonding (e.g. Chartrand & Van Baaren, 2009).

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1983) apparently provides the foundation for a strong *poverty of the stimulus argument* to this conclusion (Chomsky, 1975): If infants are able to imitate within hours or days of entering the world, their imitative capacity could not be based on learning; if they can imitate a range of behaviours, the innate endowment must be something more complex than a couple of reflexes.

This poverty argument has been widely accepted in spite of a number of forceful challenges. Many researchers have been unable to replicate the neonatal imitation findings (e.g. Koepke, Hamm, Legerstee & Russell, 1983; McKenzie & Over, 1983), and critical exchanges regarding both methodology and interpretation began in *Science* shortly after the first data were published (Anisfeld, 1979; Jacobson & Kagan, 1979; Masters, 1979; Meltzoff & Moore, 1979) and continue to the present day (Anisfeld, 2005; Jones, 2009; Rogers, 2006). Although important, these critical studies have been limited in empirical and theoretical scope. Each has focused on a particular feature of the neonatal imitation data (e.g. replicability), and offered an alternative explanation for the apparently imitative behaviour of neonates, rather than an encompassing alternative model of the origins of adult imitative competence.

The current review has a wider empirical base and more general theoretical objectives. In the first half of the article, headed 'Poverty of the stimulus', and in the Supporting Material, we re-examine all aspects of the research traditionally understood to support the poverty argument in relation to imitation. This research has involved infants in the first 6 weeks of life. In the second half we broaden the perspective to include studies of later infancy (up to 2 years), and of the effects of experience on imitation in adulthood. These data, we argue, support a *wealth of the stimulus* argument with respect to imitation. They suggest that there is sufficient information in the individual's environment, and particularly in their social interactions, to support ontogenetic development of the capacity for imitation without the guidance of a specialized, innate cognitive mechanism.

This re-examination of imitation in infancy is timely because the assumption that imitation is innate is having an increasing impact in research on the mirror neuron system (Ferrari, Visalberghi, Paukner, Fogassi, Ruggiero & Suomi, 2006; Lepage & Theoret, 2007; Nagy & Molner, 2004; Williams, Whiten, Suddendorf & Perrett, 2001. For critiques of research relating the mirror neuron system and imitation, see Southgate & Hamilton, 2008; Southgate, Gergely & Csibra, in press). Furthermore, an alternative model of the origins of imitation is gaining support in experimental psychology and cognitive neuroscience. In the second half of the paper, we outline this alternative, *associative sequence learning* model (ASL; Heyes & Ray, 2000), which explains how the capacity to imitate could develop ontogenetically.

Poverty of the stimulus

The poverty of the stimulus argument is a skeleton; it concludes that the capacity to imitate depends on a complex innate cognitive mechanism, but says nothing more about the nature of that mechanism. Meltzoff and Moore's (1997) *active intermodal matching* model (AIM) puts some flesh on these bones. Meltzoff (2005, p. 55) has argued that the behavioural similarity that is diagnostic of imitation, in some cases apparent only from a third party perspective, is 'the soul of imitation', and that imitation must be mediated by a mechanism that 'knows about' this similarity. AIM describes this mechanism as 'innate equipment' and characterizes its functioning: 'Newborns detect equivalences between observed and executed acts. When newborns see adult biological motion, including hand and face movements, these acts are mapped onto the infant's body movements. This mapping is manifest by newborn imitation. Newborn imitation suggests an innate common code of human acts whether these body transformations are performed by self or observed in other' (Meltzoff, 2002, p. 9). AIM suggests that the common or *supramodal* code specifies *organ relations*, the configuration of body parts produced by a body movement, but it does not give further details of this code, or of a mechanism that would allow organ relations to be derived from observed body movement.

Meltzoff's (2002) position on the development of social cognition is a form of *starting-state nativism*, in which the conceptual changes that produce theory of mind begin at birth but continue, under the guidance of imitation, for some years. However, with respect to imitation specifically – the mechanism that solves the correspondence problem by detecting 'equivalences between observed and executed acts' – it appears that AIM represents *final-state nativism*. AIM allows that, through repetitive body play, or *body babbling*, infants learn relationships between their self-generated movements and the organ relations that result. However, the passages quoted in the preceding paragraph suggest that, according to AIM, the mechanism that maps your movements onto mine is present in a mature form at birth.

If AIM is correct, then one would expect the behaviour of neonates to have certain characteristics: (1) Range. For each of a range of actions, neonates will respond to that action by producing a similar action. '[H]uman infants are imitative generalists. The hallmark of normal human infants is that they imitate a range of novel and arbitrary acts' (Meltzoff, 1996, p. 347). (2) Specificity. For each action in this range, it should be the topography of the model's behaviour – rather than, for example, its location or intensity – that enables production of topographically similar behaviour by the infant. In other words, each example of matching action (responding to modelled action x by performance of x) should be an example of imitation. (3) Developmental continuity. If

the mechanism that mediates imitation in infants is also the mechanism that mediates imitation in adulthood, one would expect the range of imitated actions to be maintained in the course of development. (4) Intentionality. If, as AIM suggests, the innate imitation mechanism is an active, matching-to-target process, the topography of the neonate's successive responses to a modelled action should become progressively more similar to the topography of the modelled action. (5) Phylogenetic distribution. It has been suggested in connection with AIM that humans are 'Homo imitans' (Meltzoff, 1988), and that monkeys 'do not imitate' (Meltzoff & Decety, 2003, p. 491). This implies that the innate mechanism postulated by AIM is present only in humans, or only in humans and our close primate relatives. If this is correct, then species that are only distantly related to humans should either be incapable of imitation, or their imitative behaviour should be mediated by mechanisms distinct from those supporting human imitation. Each of these predictions is discussed in turn in the sections that follow.

Range

The vast majority of experiments investigating neonatal imitation have compared the frequency with which an infant produced a particular gesture after the gesture had been modelled with one of the two baseline measures of gesture frequency used in Meltzoff and Moore's (1977, Experiment 2) seminal report of neonatal imitation. In that study, *cross-target* comparison showed that infant tongue protrusions following modelling of tongue protrusion exceeded tongue protrusions after modelling of mouth opening (and vice versa for mouth opening), and exceeded baseline spontaneous gesture production when the model remained passive.

We review 37 experiments that tested for neonatal imitation of 18 gestures. In the Supporting Material we review each of these studies in detail, on a gesture-by-gesture basis. The results of this review – which are summarized in Table 1, and in the remainder of this section – suggest that neonates match tongue protrusion, but do not imitate a range of actions.

Of the 18 gestures investigated, half have not yielded any positive reports of neonatal imitation (chin tapping, cheek swelling, close eyes, arm waving, making and unmaking a fist, ear touching, chest tapping, hand-to-face, hand-to-and-from-midline). Of the nine remaining gestures, five have produced mixed results in which negative reports outnumber positive reports (mouth opening, hand opening and closing, lip protrusion, sequential finger movement, and blinking). For example, there have been twice as many failures to find imitation of mouth opening as successful attempts. In many of these cases, including mouth opening, positive findings are likely to have been generated by response competition rather than imitation (see Supporting Material). Another gesture, imitation of index finger extension, has been

tested only once and then only relative to baseline production, not cross-target comparison.

Only three gestures – lateral head movement, facial expressions of emotion, and tongue protrusion – have yielded more positive than negative findings. Close examination of the experimental procedures (see Supporting Material) indicates that the head movement effect is likely to be due to perceptual tethering, and that the facial expression effect, when present, may be an artefact associated with the method used to score infant behaviour. The results of the many studies of tongue protrusion leave no doubt that when newborn infants see tongue protrusion they are likely to protrude their own tongues. However, as the next section indicates, even the tongue protrusion effect lacks the specificity that defines an imitative response.

Specificity

The AIM model, and the poverty argument more generally, suggests that there is an innate mechanism that solves the correspondence problem. The correspondence problem arises when observation of the topography of an action provokes or enables the observer to produce an action with the same or similar topography. Therefore, matching behaviour in neonates does not bear on AIM or the poverty argument unless it is specific, i.e. unless it is the topography, rather than some other feature of the model's behaviour, such as its location or intensity, that plays a causal role in producing topographically similar behaviour in the infant.

There is now a substantial body of evidence indicating that the one robust effect in the neonatal imitation literature – tongue protrusion matching – is not specific, and therefore does not support the poverty argument.

In the earliest study of specificity, Jacobson (1979) compared the frequency of infant tongue protrusion in response to modelled tongue protrusion and to a number of alternative, animate and inanimate, stimuli. Having found tongue protrusion responses to, for example, the movement of a felt tip pen or small white ball towards and away from the infant's mouth, Jacobson suggested that tongue protrusion stimuli elicit tongue protrusion responses, and other oral behaviours, by virtue of an *innate releasing mechanism* (IRM); because they resemble an approaching nipple, tongue protrusion stimuli elicit feeding responses including tongue protrusion. On this account, tongue protrusion matching shows some degree of specificity – the topography of the stimulus plays some role in eliciting the topographically similar response – but the matching effect is due to a simple reflex rather than a complex innate mechanism.

More recent work provides evidence that tongue protrusion matching is much less specific than Jacobson's study implied; that it depends on the intensity or salience, rather than the topography, of observed tongue protrusion (Jones, 1996). Jones has shown that infant tongue protrusion, but not mouth opening, increases following

Table 1 *Summary of experiments seeking evidence of imitation in human neonates up to 6 weeks old. The 'Gesture' column identifies the target or modelled movement. All gestures have been included for which there is at least one report that infants produced the target action more frequently after observing the target action than after observing an alternative action (cross-target comparison). Experiments in the 'Positive' column reported a positive cross-target comparison, and experiments in the 'Negative' column did not find a significant difference in cross-target comparison. The number in italics at the top of each cell in the Positive and Negative columns gives the total number of experiments in that cell. Studies are listed in alphabetical order. Each study is identified by the name of the first author and the last two digits of the year of publication. In cases where the published paper included more than one experiment, a digit following the author/year citation indicates the number of the experiment in which the result was found. Decimal digits indicate the stage in the sampling period where an effect was found in a longitudinal study. The 'Notes' column summarizes the results of detailed review, reported in the main text and Supporting Material.*

Gesture	Positive	Negative	Notes
Tongue protrusion	*21* Abravanel (84)2 Abravanel (91)1, 2 Anisfeld (01) Heimann (89).1, .2 Jacobson (79) Kugiumutzakis (99).1–.4 Legerstee (91) Maratos (82).1,.2 Meltzoff (77)1, 2 Meltzoff (83) Meltzoff (89) Meltzoff (92) Meltzoff (94) Vinter (86) (dynamic stimuli)	*11* Abravanel (84)1 Fontaine (84) Hayes (81)1, 2 Heimann (85) Koepke (83)1, 2 Lewis (85) McKenzie (83) Ullstadius (98) Vinter (86) (static stimuli)	Reliable but non-specific effect due to innate releasing mechanism or oral exploratory responses to arousing stimuli
Mouth opening	*9* Kugiumutzakis (99).1–.4 Legerstee (91) Meltzoff (77)1, 2 Meltzoff (83) Meltzoff (94) (duration)	*20* Abravanel (84)1, 2 Abravanel (91)1, 2 Anisfeld (01) Fontaine (84) Hayes (81)1, 2 Heimann (85) Heimann (89).1,.2 Koepke (83)1, 2 Lewis (85) Maratos (82).1,.2 McKenzie (83) Meltzoff (92) Meltzoff (94) Ullstadius (98)	Side-effect of reliable tongue protrusion matching: recovery of mouth opening responses after suppression during tonguing
Hand opening and closing	*1* Vinter (86)	*4* Abravanel (84)1 Jacobson (79) Vinter (86) (static stimuli) Fontaine (84)	Not reliable. When present, likely to be due to interdependence of facial and manual gestures
Lip protrusion	*2* Meltzoff (77)1 Reissland (88)	*3* Heimann (89).1,.2 Koepke (83)1	Not reliable. When present, likely to be due to scoring method
Sequential finger movement	*1* Meltzoff (77)1	*2* Koepke (83)1 Lewis (85)	Not reliable. When present, likely to be due to scoring method
Blinking	*4* Kugiumutzakis (99).1-.4	*2* Abravanel (84)1 Fontaine (84)	Not reliable. Could be a side-effect of attentional response to tongue protrusion model
Lateral head movement	*3* Meltzoff (89) Maratos (82).1,.2		Likely to be due to perceptual tethering
Facial expressions of emotion	*2* Field (82) Field (83)	*1* Kaitz (88)	Not reliable. When present, could be due to scoring method

exposure to flashing lights (Jones, 1996) and, in a conceptual replication, to bursts of music (Jones, 2006). In combination with data showing that infants look longer at tongue protrusion than at mouth opening, and that toy presentation elicits more tongue protrusion than mouth opening responses (Jones, 1996), these findings suggest that modelled tongue protrusion is just one of many types of stimulus that arouse or interest infants, and thereby elicit oral exploratory behaviour, including tongue protrusion responses.

Developmental continuity

If, as AIM suggests, the mechanism that mediates imitation in infants is also the mechanism that mediates imitation in adulthood, one would expect the develop-

ment of imitation to be continuous. In contrast with this prediction, the literature suggests that gestures that were apparently imitated in the newborn period 'drop-out', or cease to be imitated, at about 3 months, and then begin to be imitated again at around 6 months (Abravanel & DeYong, 1991; Abravanel & Sigafoos, 1984; Fontaine, 1984; Heimann, Nelson & Schaller, 1989; Jacobson, 1979; Kugiumutzakis, 1999; Maratos, 1982).

In response to these findings, Meltzoff and Moore (1992) have argued that the capacity to imitate remains constant during infancy, but changes in social behaviour mask this ability, noting their impression that, at 2–3 months, infants try to engage the experimenter in social games. In a procedure designed to motivate infants to imitate beyond the neonatal period, 10-week-old infants were found to imitate tongue protrusion and mouth opening in response to static and dynamic versions of gestures modelled by mothers and strangers. However, these data do not provide a compelling case for developmental continuity. The infants were drawn from the youngest age at which imitation has been found to drop-out, and the methodological changes make comparison with neonatal studies difficult. Furthermore, the hypothesis that imitative capability is masked by increasing sociability does not explain why imitation recovers at 6 months, why a decline in imitation occurs at different ages for different gestures, or why declining rates of imitative tongue protrusion and mouth opening reflect declining rates of spontaneous production of these gestures (Maratos, 1982). Therefore, the developmental drop-out phenomenon is consistent with the proposal that tongue protrusion imitation in the neonatal period is due to an innate releasing mechanism (Jacobson, 1979) or to an exploratory response to arousing stimuli (Jones, 1996; Keven, Crawford & Akins, under review).

Intentionality

AIM suggests that neonatal imitation is mediated by an innate, active, matching-to-target or error-correction process. If this is correct, the topography of the neonate's successive responses to a modelled action should become progressively more similar to the topography of the modelled action. There is very little evidence that this is the case.

Nagy, Compagne, Orvos, Pal, Molnar, Janszky, Loveland and Bardos (2005) reported that neonatal imitation of index finger extension became progressively more accurate during the experimental session. The data showed that, on average, infants produced their first incomplete finger extension when the action had been modelled four times, and their first accurate match when the gesture had been modelled six or seven times. Viewed as evidence of a matching-to-target process, these findings are problematic. Over trials, the infants were both repeating the response and accumulating exposures to the movement stimulus. Therefore, apparent improvement in accuracy could be due to an increase in vigour

with response repetition, or to perceptual learning – to the formation of a better perceptual representation of the modelled movement with repeated exposures – rather than to an error-correction process in which feedback from earlier responses is used to enhance the accuracy of later responses.

In an experiment that is said by the authors to provide the best evidence of neonatal imitation, Meltzoff and Moore (1994) reported that infants' imitation of sideways tongue protrusion showed improving topographic accuracy over successive trials. Their analysis assumed that the following behavioural categories constitute a scale or sequence progressing towards accurate imitation of sideways tongue protrusion: small non-midline tongue protrusion, small tongue protrusion to the side, large midline tongue protrusion, large tongue protrusion to the side. It then went on to examine whether the infants' performance in successive trials conformed to this sequence. The principal problem with this approach relates to the scale. For example, it is not clear that, as an imitative response to sideways tongue protrusion, a small tongue protrusion to the side is less, rather than more, accurate than a large midline tongue protrusion. However, it is clear that the former response is less vigorous than the latter. Therefore, if the infants tended to produce small sideways tongue protrusions before larger midline tongue protrusions, this could have been because response vigour, rather than accuracy, increased over trials (Anisfeld, 2005).

Homo imitans

There is now relatively unambiguous evidence of the imitation of simple movements in a wide range of taxa, including: birds (Akins & Zentall, 1998; Campbell, Heyes & Goldsmith, 1999; Lefebvre, Templeton, Brown & Koelle, 1997; Mui, Haselgrove, Pearce & Heyes, 2008); neonatal monkeys (Ferrari et al., 2006); neonatal chimpanzees (Bard, 2007); and adult chimpanzees (Carpenter & Tomasello, 1995; Custance, Whiten & Bard, 1995; Whiten, Custance, Gomez, Bard & Teixidor, 1996).

The cognitive complexity of the innate supramodal coding mechanism proposed by AIM is difficult to reconcile with the finding that our distant relatives imitate motor behaviours using homologous, rather than analogous, mechanisms. For example, like humans, birds are capable of deferred imitation (Akins & Zentall, 1998; Richards, Mottley, Pearce & Heyes, 2009), and have the potential both for 'automatic imitation' (Mui et al., 2008) and for imitative performance that is modulated by the observed consequences of the model's action (Dorrance & Zentall, 2001; Saggerson, George & Honey, 2005).

Particularly challenging for AIM and the poverty argument are the results of a recent study reporting neonatal imitation effects in rhesus macaques that are similar to those observed in human neonates (Ferrari et al., 2006). The monkeys in this study were tested for

matching of five movements at four intervals post-partum. They showed a matching effect only for tongue protrusion and lip smacking (the latter was not scored independently) and only on the third day post-partum. Thus, like human neonates, the newborn monkeys did not match a range of actions, and their matching behaviour was not developmentally durable. This suggests that, if homologous mechanisms are responsible for matching in human and monkey newborns, these are innate releasing or arousal mechanisms, rather than an innate supramodal matching mechanism of the kind postulated by AIM.

As we have seen in the foregoing review (and in Supporting Material), evidence relating to the range, specificity, developmental continuity and intentionality of putative examples of neonatal imitation is also consistent with the hypothesis that they are generated by processes distinct from those that mediate imitation in later infancy and in adulthood. Thus, close examination of the experimental literature on neonatal imitation indicates that, with respect to the origins of adult imitative competence, the poverty of the stimulus argument is not persuasive.

Wealth of the stimulus

The wealth of the stimulus argument proposes that an infant's interaction with the world, and especially with other agents, is the engine that drives cognitive development for imitation. Several theories are broadly consistent with this argument (Jones, 1996; Piaget, 1962; Prinz, 2005) but we will focus on the associative sequence learning model (ASL; Heyes 2005, 2010; Heyes & Ray, 2000) because it gives the most explicit account of how experience could provide a solution to the correspondence problem, and offers a general theory of imitation, applicable to infants and adults. In this second half of the paper, we first outline the ASL model, and then consider three kinds of evidence that support the model and, more broadly, the wealth of the stimulus argument in relation to imitation.

Associative sequence learning

The AIM model suggests that the correspondence problem is solved by a mechanism that computes similarity; that can work out, via an unspecified endogenous process, what any seen action feels like when it is performed. In contrast, the ASL model suggests that the correspondence problem is solved piecemeal and by a simple mechanism – associative learning. The success of this simple mechanism depends, not on powerful and specialized internal resources, but on the developing infant's environment, especially their sociocultural environment. To build an adult who can imitate a range of actions, the developmental environment must provide for each of the to-be-imitated actions experience in which its observation and execution are contiguous and

contingent. In other words, to be able to imitate an action x, I must have seen x and performed x close together in time (contiguity), and the two events, seeing and doing x, must have been contingent. The latter condition means, roughly, that the probability of my seeing x while doing x must be higher than the probability of my seeing any other single action while doing x. We will refer to experience that meets these conditions as 'seeing and doing the same action'.

As indicated in Figure 1, ASL suggests that seeing and doing the same action leads, via standard processes of associative learning (Schultz & Dickinson, 2000), to the establishment of a *matching vertical association*; a bidirectional excitatory link between a sensory (typically visual) representation of x and a motor representation of x. Once this link is in place, activation of the sensory representation by observation or recollection of the action is propagated to the motor representation, making it possible, but not obligatory, for the observer to produce the observed action.

It is important to note that ASL does not assume that there are internal constraints favouring the establishment of matching over non-matching vertical associations. If the individual experiences a contiguous and contingent relationship between seeing x and doing an alternative action y, she will form a non-matching vertical association linking x and y, and a tendency to counter-imitate, to do y whenever she sees x. Therefore, ASL implies that, although the topographic similarity between observed and executed action is the cardinal diagnostic feature of imitation, the associative mechanisms that make imitation possible via matching vertical associations do not encode or 'know about' similarity. If people are more inclined to imitate than to counter-imitate, this is because our developmental environments have exposed us to more matching, x–x, than non-matching, x–y, sensorimotor relationships.
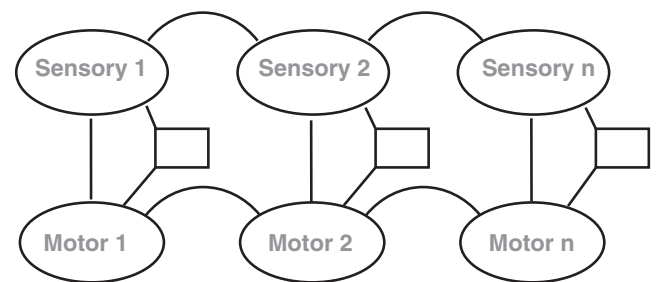

Figure 1 *The associative sequence learning (ASL) model of imitation. Vertical lines represent matching vertical associations, i.e. excitatory links between sensory and motor representations of the same action. Rectangles indicate stimuli, such as words, that mediate acquired equivalence learning. Curved lines represent 'horizontal' sequence learning processes. The ASL model explains imitation of novel actions – actions that represent a new combination of elements – with reference to these horizontal processes (e.g. Heyes, 2005). They are not a focus of discussion in the present paper because it is rarely claimed that infants imitate novel actions.*

Effects of training and expertise on imitation and the mirror neuron system

Experiments with adult human participants, using behavioural and neurological measures, have provided strong support for this core counter-intuitive component of the ASL model. For example, they have shown that non-matching or *incompatible* sensorimotor training – in which the participant repeatedly performs one action while observing another – can abolish and even reverse both imitative behaviour and the action matching properties of the mirror neuron system (MNS).[2] For example, Heyes, Bird, Johnson and Haggard (2005) showed that a brief period of incompatible sensorimotor training – in which participants responded to hand opening stimuli by closing their hands, and to hand closing stimuli by opening their hands – abolished *automatic imitation*, e.g. the involuntary tendency to make an open hand response faster to an opening than a closing hand stimulus. Gillmeister, Catmur, Liepelt, Brass and Heyes (2008) demonstrated a comparable reduction in automatic imitation of hand and foot actions following incompatible sensorimotor experience, while Catmur, Walsh and Heyes (2007) showed that, in the case of little and index finger abduction movements, incompatible sensorimotor experience can reverse automatic imitation, producing a systematic, involuntary tendency to counter-imitate the observed action.

In the latter study, Catmur *et al.* (2007) measured automatic imitation using muscle-specific, motor evoked potentials (MEPs), induced by single pulses of transcranial magnetic stimulation (TMS) to the primary motor cortex. MEPs of this kind have been used as a marker of the functioning of the MNS (Fadiga, Fogassi, Pavesi & Rizzolatti, 1995). Therefore, this study provides evidence that incompatible sensorimotor experience can reverse, not only automatic imitation, but also the responsivity of the MNS. For example, after training, observation of index finger movements produced larger MEPs in the little finger muscle than in the index finger muscle.

Further evidence that incompatible sensorimotor training can reverse the action matching properties of the MNS came from a study using functional magnetic resonance imaging (fMRI; Catmur, Gillmeister, Bird, Liepelt, Brass & Heyes, 2008). Observation of hand movements is normally associated with a stronger MNS response than observation of foot movements. After training in which participants performed a hand response to a foot stimulus and a foot response to a hand

stimulus, Catmur *et al.* found foot-dominance, rather than hand-dominance, in both premotor and parietal areas of the MNS.

Providing further support for ASL, a number of recent studies have shown that expertise in a particular action domain increases the responsivity of the MNS during observation of actions from that domain (Cross, Hamilton & Grafton, 2006; D'Ausilio, Altenmuller, Olivetti & Lotze, 2006; Haslinger, Erhard, Altenmuller, Schroeder, Boecker & Ceballos-Baumann, 2005; Margulis, Mlsna, Uppunda, Parrish & Wong, 2009; Vogt, Buccino, Wohlschlager, Canessa, Shah, Zilles, Eickhoff, Freund, Rizzolatti & Fink, 2007). For example, Calvo-Merino, Grezes, Glaser, Passingham and Haggard (2006) used fMRI to compare the MNS responses of male and female ballet dancers while they were observing male-specific and female-specific ballet moves. Left premotor cortex, as well as parietal and cerebellar areas, showed a greater BOLD response when participants viewed their own gender's movements than when viewing those of the other gender. This suggests that visual experience of an action is less important than motor experience and/or sensorimotor experience in modulating MNS responses to observation of that action.

Thus, the results of expertise studies complement those of training studies. Expertise studies show that experience of a kind that is available in natural environments has powerful effects on the MNS. Training studies indicate, in accordance with ASL, that it is sensorimotor experience, rather than purely sensory or purely motor experience that is crucial in producing these effects.

Sources of imitogenic experience in infancy

Previous discussions of the ASL model delineated a number of potential sources of *imitogenic experience*, contexts in which individuals commonly see and do the same action, and therefore have the opportunity to form the matching vertical associations that make imitation possible: direct self-observation, mirror self-observation, synchronous action, acquired equivalence experience, and being imitated (e.g. Heyes & Ray, 2000). The following brief survey of research on motor behaviour and social interaction in infancy suggests that imitogenic experience of these kinds is freely available in early life.

Direct self-observation

Human anatomy is such that we can see many of our own actions, from something very like a third party perspective, as we perform them. Therefore, direct self-observation provides ideal conditions for the establishment of matching vertical associations relating to perceptually transparent actions such as arm/hand and foot/leg movements.

Observational studies have shown that infants spend a large proportion of their time watching their limbs move, and that they actively explore the changing sensorimotor

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[2] It is widely believed that imitation can be mediated by the MNS (for a contrary view, see Southgate & Hamilton, 2008; Southgate, Gergely & Csibra, in press). There is little direct evidence that this is the case, but it is certainly plausible that some, if not all, imitation is mediated in this way. The ASL model offers an account of the development of both imitation and the MNS (Catmur, Walsh & Heyes, 2009; Heyes, in press).

correspondences produced by this activity (Rochat, 1998). Strikingly, White, Castle and Held (1964) reported that 2–3-month-old orphans spent the majority of their waking hours looking at their own hands. Experimental evidence further confirms that newborn infants have a marked visual preference for hands and are motivated to keep them in sight (Van der Meer, Van der Weel & Lee, 1995). Neonates resist pressure applied to move a visible, but not an occluded, arm, and they move their arms far more when they can see them than when they can't. Furthermore, when in darkness, except for a narrow beam of light visible only when broken, newborns control their movements to keep their hands visible, readjusting their position in keeping with movements of the beam (Van der Meer, 1997).

Mirror self-observation

Unlike direct self-observation, mirrors are a source of matching vertical associations for perceptually opaque actions, such as facial gestures and whole body movements. Mirror self-recognition (Asendorpf, Warkentin & Baudonnière, 1996) is not necessary for mirrors to contribute to this kind of learning. However, mirrors can yield the necessary experience only if the learner engages in a variety of activities before the mirror and is attentive to her reflection. A number of studies show that infants meet these conditions. For example, Amsterdam (1972) found that 85% of infants between 6 and 12 months responded to their mirror image as a sociable playmate, smiling at and making playful approaches to the 'other child' while vocalizing delight and enthusiasm. In their second year, infants responded to their mirror images with a variety of 'self-admiring' and 'embarrassed' behaviours. Similarly, Reddy (2000) reported coyness in response to the mirror at 2 months, with gaze and head aversion at the height of the smile, followed by immediate re-engagement, and arm movements to the face. Furthermore, infants' attraction to mirrors is sustained over time: 6-month-olds spend as much time interacting with mirrors as 1-month-olds, and the older infants engage in a broader range of activities while looking at their reflections (Schulman & Kaplowitz, 1976).

Synchronous action

Synchronous action occurs when two or more individuals react in the same way to an event; for example, when supporters of a football team stand, raise their arms and cheer a goal. When one member of the group looks at another during synchronous action, activation of the sensory representation of the action is paired with activation of the motor representation.

This kind of imitogenic experience is likely to be especially important in the post-infancy period, when the children are encouraged to participate in the group activities where dance movements and athletic skills are practised in synchrony. However, social referencing

behaviour ensures that infants will see a caregiver's facial expression when both adult and infant respond reflexively to startling or emotionally charged events (Ainsworth & Bell, 1970), and adult scaffolding of infants' interactions frequently generates synchronicity. For example, O'Toole and Dubin (1968) reported that in 55% of spoon-feeding sequences, both the caregiver and the infant opened their mouths in response to the spoon.

It is important to note that synchronous action is distinct from 'synchronic imitation' (Asendorpf et al., 1996; Nielsen & Dissanayake, 2004; Slaughter, Nielsen & Enchelmaier, 2008). According to the ASL model, synchronic action is an input to, and synchronic imitation is an output from, the repertoire of matching vertical associations that solve the correspondence problem.

Acquired equivalence experience

The ASL model suggests that matching vertical associations are often formed indirectly, via acquired equivalence experience (Hall, 1994), in which a stimulus is paired on some occasions with the sight of an action, and on other occasions with performance of that action (Heyes & Ray, 2000). As a consequence of this experience, presentation of the stimulus simultaneously activates the sensory and the motor representations of the action, and thereby enables a matching vertical association to be forged between them.

Like synchronous action, acquired equivalence experience is likely to be especially important after infancy, when children are learning action words. A word such as 'frown', heard on some occasions when the child sees another frowning, and on other occasions when she is herself frowning, is an ideal bridge between observed and executed action. However, acquired equivalence experience is available to infants via the natural sounds of actions; for example, the slap of a hand on a table, or the pop of lips suddenly parted (Piaget, 1962). Evidence that sounds of this kind are imitogenic comes from experiments showing that infants imitate actions accompanied by sounds more readily than silent actions (Devouche, 1998; Jones, 2007).

Being imitated

The evidence suggests that being imitated by adults is an especially rich source of imitogenic experience in infancy. Infants spend a large proportion of their waking hours in face-to-face encounters with adults, 65% of this time is spent actively interacting, and caregivers shape these face-to-face interactions to contain frequent, salient and enthusiastic imitation episodes (Uzgiris, Benson, Kruper & Vasek, 1989). The frequency of these episodes is remarkably high. Pawlby (1977) found that an imitation episode occurs roughly once a minute in mother–infant face-to-face interaction, and the vast majority of these episodes, 79%, involve mothers imitating infants. Similarly, Uzgiris et al. (1989) found that in early infancy

mothers were roughly five times as likely to imitate their infants as the other way around, and that this proportion had not substantially declined when the infants were 11–12 months old.

Caregivers appear to be imitatively opportunistic, searching for ways to incorporate infant behaviour into imitative exchanges. Observation of mother–infant dyads suggests that when an infant is involved in repetitive facial/body play, mothers insert their own copy of the infant act, simulating reciprocal imitation and maximizing opportunities for their infants concurrently to see and do, and do and see, an action (Pawlby, 1977). As infants develop in the frequency and range of behaviours they produce, mothers take the opportunity to imitate them yet more (Flynn, Masur & Eichorst, 2004; Uzgiris *et al.*, 1989). When encouraging infant imitation, mothers respond sensitively to infants' visuomotor experience of action; for example, when showing a familiar behaviour, mothers leave time for the infant to reproduce the action if it has been performed with a novel object, but not if it involves a familiar action–object coupling (Zukow-Goldring & Arbib, 2007). This study found that if the action itself was novel, mothers frequently acted conjointly with their infants, or 'embodied' the act, putting the infant through the movements to experience the visuomotor correspondence.

Maternal reports show that matching by their infants and imitation games are highly salient and enjoyable to mothers, the majority of whom believe that their infants imitate them even when matches are no more frequent than would be expected by chance (Lewis, 1979). In addition to increasing the frequency of behavioural matches in infants' experience, maternal enthusiasm for imitating and being imitated would be expected to foster the learning of matching vertical associations in two ways, via reward and *marking*.

First, mothers deliver powerful and selective rewards when their infant's behaviour matches their own. Pawlby (1977) found that mothers reacted to infant 'imitations' (real or imagined) with delight, pride and manifest pleasure; they were met with smiles and a general tone of encouragement. According to the ASL model, reward is not necessary for the formation of matching vertical associations, but it will significantly increase the rate of learning. Consistent with this, 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.

Second, mothers mark their imitation behaviours by using highly salient, exaggerated and enthusiastic gestures. Consequently, it has been suggested that mothers show *motionese*, a non-vocal equivalent of *motherese*, in infant-directed action (Brand, Baldwin & Ashburn, 2002). Brand *et al.* found that, when demonstrating actions involving novel objects to infants rather than adults, participants used 'high relief'

behaviours that were more interactive, higher in enthusiasm, proximity, range of motion, repetitiveness and simplicity. Salient stimuli enter into associations more readily than less salient stimuli (Rescorla & Wagner, 1972). Therefore, the ASL model suggests that marking or motionese will have a substantial, facilitating effect on the learning of matching vertical associations. Consistent with this, Waxler and Yarrow (1975) found that maternal enthusiasm during action demonstration was positively correlated with the variety of acts imitated by 19-month-old infants.

It is important to note that, according to the ASL model, infants do not need to detect or recognize that they are being imitated in order for this experience – which appears to be plentifully available in typical development – to support the learning of matching vertical associations.

The development of imitation in infancy

Widespread acceptance of the poverty argument may have led research on imitation in post-neonatal infancy to be neglected. Imitation is commonly used as a measure, of memory or perceptual functioning, but more rarely as a focus of enquiry in its own right (Jones, 2009). However, the ASL model makes three predictions about the development of imitation in infancy that can be assessed against currently available data. First, the accuracy of imitation, and the range of behaviours that can be imitated, should increase over time as individuals acquire experience of seeing and doing the same actions. Second, imitation of perceptually transparent actions should precede imitation of perceptually opaque actions only to the extent that infants are more likely to have had experience of seeing and doing the former. Third, variation in the development of imitation across infants should depend on amount of imitogenic experience, and in particular on the quality of social interactions in which adult and infant commonly see and do the same action.

Change over time

At 6 months, infants emulate actions on objects (Barr, Dowden & Hayne, 1996; Barr, Vieira & Rovee-Collier, 2001; Barr, Rovee-Collier & Campanella, 2005), and show a rudimentary capacity to imitate the topography of body movements. In particular, imitation of actions with sounds has been reported at this age, including imitation of mouth opening in response to observation of mouth opening plus a popping sound (Kaye & Marcus, 1978) and patting a surface (Uzgiris, 1972). The ASL model suggests that infants are able to match these actions at a relatively young age because the auditory cues – e.g. the popping noise and the sound of patting – have provided acquired equivalence experience, and thereby enabled the early formation of matching vertical associations.

From 6 months onwards, infants become increasingly imitative (Masur, 2006). There is a significant linear increase in the frequency of imitation from 7.5 months (Killen & Uzgiris, 1981), and the frequency doubles by the end of the first year (Uzgiris, Vasek & Benson, 1984). The range of actions that infants imitate also increases throughout infancy (Jones, 2007; Masur, 2006). The majority of infant motoric imitation towards the end of the first year involves actions on objects (Uzgiris, 1972; Masur, 2006), where self-observation, scaffolded and synchronous action with caregivers is likely to have provided many opportunities to learn matching vertical associations.

Transparency and opacity

Piaget (1962) suggested that infants imitate *visible* actions sooner than *invisible* actions. The distinction between visible and invisible actions is not identical to the distinction between perceptually transparent and perceptually opaque actions (Heyes & Ray, 2000). However, Piaget's hypothesis motivated a number of studies showing that there is a general tendency for infants to imitate transparent actions before they imitate opaque actions (Uzgiris, 1972; Jones, 2007). For example, studying infants to 18 months, Jones (2007) found that perceptually transparent gestures, such as waving bye-bye, were imitated up to 6 months earlier than opaque gestures, such as tongue protrusion, even though the opaque actions were less demanding motorically.

Piaget (1962) assumed that opaque actions are intrinsically more difficult to imitate; that it is harder, in the case of opaque actions, for the internal mechanisms mediating imitation to work out which motor commands will produce an output that is similar, from a third party perspective, to the model's action. In contrast, the ASL model assumes that the internal mechanisms mediating imitation – associative learning mechanisms – forge matching vertical associations in the same way, and with the same ease, for opaque and transparent actions. However, the ASL model is consistent with a general tendency towards earlier imitation of transparent actions because one of the major sources of imitogenic experience, direct self-observation, contributes to the formation of matching vertical associations for transparent but not for opaque actions. Therefore, it is likely that, on average, infants will acquire matching vertical associations for transparent actions before opaque actions.

Particularly strong evidence in favour of the ASL model comes from studies comparing the onset of imitation for gestures within the category of perceptually opaque actions. Imitation of mouth opening and lip smacking *when accompanied by sounds* has been reported at roughly 6 months and 8 months (Piaget, 1962; Kaye & Marcus, 1978), whereas ear touching is not imitated until a year later (Uzgiris, 1972). This suggests that perceptually opaque actions are not uniformly, and therefore intrinsically, difficult to imitate. Rather, it is consistent with the idea that, even among perceptually opaque actions, the age at which a particular action begins to be imitated depends on the richness of the infant's imitogenic experience of that particular action. Matching vertical associations for mouth opening and lip smacking are likely to be formed relatively early because these actions are common targets for imitation of infants by adults (O'Toole & Dubin, 1968), and, because they have typical auditory correlates, acquired equivalence experience can facilitate the learning process.

Quality and quantity of social interaction

A recent quantitative genetic study using a twin sample found that, in accounting for individual differences in imitation at 2 years, the largest variance component, 42%, related to the shared environment, 28% of the variance was due to environmental factors unique to each twin, and only 30% of the variance was due to genetic influence (McEwen, Happe, Bolton, Rijsdijk, Ronald, Dworzynski & Plomin, 2007). Interpreting these data, the authors suggest, in common with the ASL model, that individual differences in imitation depend primarily on the amount that an infant has been imitated in the course of his development. An older study points to the same conclusion by showing that, by the end of the first year, the most imitative mothers have the most imitative infants (Masur, 1987).

Experiments involving infants deprived of typical interaction with adults provide further support for the view that being imitated is an engine for the development of imitation. For example, Field, Hernandez-Reif, Vera, Gil, Diego, Bendell and Yando (2005) found that in co-morbid depression, high anxiety and high anger mothers spent less time imitating their infants than mothers whose depression was associated with low anxiety and low anger. Infants of high anger mothers imitated less than infants of low anger mothers, and infants of high anxiety mothers showed a similar trend towards less imitation than infants of low anxiety mothers.

Similarly, a study of infants with physical disabilities underlines the importance in the development of imitative ability, not just of adult contact, but of the experience of being imitated. Cress, Andrews and Reynolds (1998) found that parents of infants with physical disabilities who were raised in typical home environments reported that they almost never imitated any of their infant's gestures or movements. At 19 months, these infants showed deficits in imitation of movements entirely within their range of physical capabilities.

It has long been recognized that social motivation is important in guiding our decisions about what and when to imitate (Carpenter, 2006; Nielsen, in press; Uzgiris, 1981). The ASL model and the research reviewed in this section suggest that social interaction plays a yet more fundamental role – through social interaction we construct the mechanisms that make imitation possible.

Conclusions

In the first half of this paper (and Supporting Material), a detailed review of the literature on behavioural matching in the neonatal period showed that it contains very few reliable effects, and that even these effects do not appear to have the characteristics of imitation; they are indicative of generalized, exploratory responses to arousing stimuli, and response competition, rather than the kind of specific, topographic matching that defines imitation in adulthood. In contrast, in the second half – examining research on motor behaviour, social interaction and imitation throughout infancy and beyond – we found evidence consistent with a wealth of the stimulus argument, that imitation is an ontogenetic achievement, based on sensorimotor learning in a richly imitogenic sociocultural environment.

The findings of this review have implications with respect to research on typical and atypical development, the cognitive neuroscience of mirror phenomena, the design of artificial agents, and the evolution of cognition. They lend support to the growing body of work showing, through a combination of dynamic systems modelling and empirical studies of infant behaviour, that sensorimotor learning is a powerful force in human social and cognitive development (Smith, Thelen, Titzer & McLin, 1999; Thelen, 2001). They also raise the possibility that sensorimotor training may be an effective intervention for atypically developing groups with imitation impairments.

Turning to cognitive neuroscience and artificial agents, insofar as it can be assumed that imitation depends on the MNS, our findings suggest that, rather than being innate (Lepage & Theoret, 2007; Nagy & Molner, 2004), this system acquires its visuomotor matching properties through experience (Catmur, Walsh & Heyes, 2009; Heyes, 2010). This hypothesis is already being applied in the development of imitating humanoid robots (Chaminade, Oztop, Cheng & Kawato, 2008). However, research on artificial systems has focused on direct self-observation as a source of imitogenic experience, whereas our review suggests that imitation by adults is an especially rich source of imitogenic experience in human infancy.

In accordance with the ASL model, our review suggests that sociocultural interaction, including the experience of being imitated, is of crucial importance in the development of imitation. If this is correct, it has two implications with respect to the evolution of cognition. First, it suggests that the capacity to imitate is culturally inherited in a direct way: that the members of each cultural generation acquire the capacity to imitate through exposure to the imitative behaviour of members of the previous generation. This is consistent with evidence that *enculturated* chimpanzees are better imitators than mother-reared chimpanzees (e.g. Tomasello, 1996). Second, and more broadly, the evidence that imitation depends on sociocultural sensorimotor learning lends weight to the view that natural selection has shaped the human mind, not by producing complex, specialized cognitive 'modules' (e.g. Cosmides & Tooby, 1994), but by favouring relatively simple behaviour-control mechanisms that channel the effects of domain- and taxongeneral cognitive processes (Heyes, 2003; Sterelny, 2003).

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