Causes and consequences of imitation

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Recent behavioural and neuroscientific research concerning imitation has revealed evidence of experience-dependent imitation in chimpanzees and birds, wide ranging imitation deficits in autism, and unintentional imitation in adult humans. This review examines these findings and also evaluates evidence of neonatal imitation and intentional imitation in infancy, and evidence suggesting that the left inferior frontal gyrus is specialized for imitation. At the theoretical level, the empirical findings support the view that the perceptual–motor translation that is a unique and defining property of imitation depends primarily on direct links between sensory and motor representations established through correlated experience of observing movements and carrying them out.

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Imitation is a focus of research in many disciplines: comparative, cognitive, developmental, evolutionary and social psychology; cognitive neuroscience; ethology; primatology; and robotics. As a result of its multidisciplinary origins, the literature on imitation is rich but scattered. The present article attempts to provide an integrative overview. The first section ('Components') summarizes, separately for each of the principal contributing disciplines, major empirical findings of the last few years. The second part outlines recent theoretical accounts of the psychological mechanisms of imitation ('Causes'), and of the relationship between imitation and theory of mind ('Consequences'), and evaluates these in relation to the evidence reviewed in the first section. Definitions of imitation are discussed in Box 1.

Components
Phylogeny
Recent research on imitation in nonhuman animals has made substantial progress in its century-long quest to establish which taxa, if any, are capable of imitation[1,2] by providing relatively unambiguous evidence of imitation in primates[3–7] and birds[8–11].

The primate data suggest that chimpanzees can imitate to the extent that they have had prior experience of interacting with humans[12,13] and/or explicit training to imitate. Custance *et al*.[4] successfully trained chimpanzees to imitate 15 human-modelled gestures (e.g. raise two arms, pat stomach) using the method of successive approximation, and found that the same animals subsequently imitated, without shaping, gestures that had not been in the training set. Chimpanzees that have not been explicitly training to imitate, but which have had extensive contact with humans, can reproduce human movements on objects[6,7,14]. A report that chimpanzee neonates can imitate facial expressions[15] is based on a sample too small for statistical evaluation, and, even if the results were

reliable, they could be due to copying of a single action, tongue protrusion (see *Development* below).

Turning to birds, there is evidence that, without explicit training, pigeons and quail imitate the appendage (beak or feet) used to depress a lever[8,9], and that European starlings[10] and Carib grackles[11] imitate features of beak (closed pecking versus open prying) and head (down versus up) movement when removing a stopper from a food source. In each case, the imitated body movements were part of the relevant species' natural foraging repertoire, and the subjects were accustomed to feeding in flocks. Therefore, it is possible that they had learned to imitate these movements during group feeding prior to the experiments.

On the basis of the current evidence from nonhuman animals, the psychological mechanisms that provide the potential for imitation could be phylogenetically general or products of convergent evolution in avian and hominid lines. Convergent evolution is implied by the fact that imitation has been demonstrated only in birds and primates, but the implication is weak. These taxa have been studied much more intensively than others, and the evidence that imitation in chimpanzees depends on implicit or explicit training raises the possibility that other mammals could also imitate if they had experience comparable to these primates. Whatever the phylogenetic distribution of the innate bases of imitation, the chimpanzee data suggest that they are 'open programs'[16] requiring substantial environmental input before the phenotype is capable of imitative performance.

Normal development
Since the late 1970s, Meltzoff and Moore have published a series of studies suggesting that neonates can imitate a range of facial expressions (including tongue protrusion, lip protrusion and mouth opening)[17,18]. These were replicated in many other laboratories, but Anisfeld's recent re-analysis of the entire corpus of neonatal imitation data reported that (1) tongue protrusion is the only gesture for which there is reliable evidence that observation increases the frequency of subsequent performance in neonates, and (2) the absence of reliable effects for other facial gestures is not due to test insensitivity[19,20]. If tongue protrusion is the only body movement that newborns can imitate, it is plausible that the mediating process is an innate releasing mechanism; an inborn stimulus-response link, wherein the response coincidentally resembles the stimulus from a third party perspective.

Box 1. Definitions of imitation

In this article, '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 those in which *fo* is caused by observation of a property of the model other than *fm*, and in which the effect of observing *fm* is not specific to the production of *fo*.

Example

Suppose that, first an adult, and then an infant, pushes a ball off a table with their hand. The infant's use of her hand (*fo*) would be imitative only if it was provoked specifically by observation of the adult using his hand (*fm*). It would not be an example of imitation if: (1) what caused the child to use her hand was observation of the adult's body in close proximity to the ball, or of the ball falling off the table (*fo* is caused by a property other than *fm*); or (2) observation of the adult's hand movement diverted attention to the ball, or caused a generalized increase in the infant's activity, which could be detected, not only in the infant displacing the ball with her hand, but also in oral exploration of the ball or increased vocalization (*fm* is not specific to the production of *fo*).

Alternatives

The foregoing definition is consistent with most usage of the term 'imitation' in comparative and developmental psychology, and in computational and cognitive neuroscience, but narrower, more theory-driven definitions are sometimes applied. These stipulate that, even when there is evidence of a specific causal relationship between observation of *fm* and production of *fo*, an instance of matching behaviour is not imitation if it could have been based on an innate releasing mechanism[a], prior learning[b], or any mechanism *not* guided by appreciation of the model's intention[c].

Imitation versus emulation

Researchers have become increasingly aware that, when an observer sees body movement generating object movement, his or her reproduction of the action might be causally related, not to the model's body movement (imitation), but to the observed object movement (emulation)[c]. Indeed, under these circumstances, emulation may be more probable. This is suggested by recent research showing that, regardless of whether people are watching arm, hand or finger movements, passively or for subsequent imitation, they tend to fixate on the end-point of the trajectory[d]. When action on an object (transitive action) is observed, the object typically lies at the end-point of the movement. Therefore, these eye-tracking data raise the possibility that emulation tends to overshadow imitation when transitive actions are observed. This is consistent with a recent report that children imitate arm movements less accurately when the movements are made to physical objects than to unmarked locations[e].

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Many infancy researchers, including Meltzoff and Moore, continue to believe that neonates can imitate a range of facial expressions via a cognitively complex process[18,21,22]. However, data published since Anisfeld's critique favour his view. These studies report further evidence that neonatal imitation is confined to tongue protrusion[23], failure to find imitation of tongue protrusion[24], and that the tongue protrusion effect is not sufficiently specific to constitute imitation[25]. Data from Heimann and Ullstadius[26] suggest that neonates can imitate mouth opening as well as tongue protrusion, but they also support the innate releasing mechanism hypotheses by showing that individual differences in imitation at 12 months of age are related to those at 3 months but not to individual differences among neonates.

Turning from neonates to toddlers, there are reports that 18-month-old infants selectively imitate movements that they believe to have been performed intentionally by the model, and therefore that imitation can be used as a non-verbal test for intention or desire attribution, a component of theory of mind[27,28] (see Box 2).

Atypical development

The third focus of recent developmental research, imitation deficits in autism, also concerns the relationship between imitation and theory of mind. Autism is a heritable developmental disorder known to be associated with severe impairments in the attribution of mental states[29]. Reviewing the literature in 1988, Baron-Cohen concluded that autistic individuals are more impaired than mental

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## Box 2. Imitation as a non-verbal test for theory of mind

Experiments by Meltzoff[a], and Carpenter *et al.*[b] have been claimed to demonstrate that imitation can be used as a non-verbal test for the attribution of intention, a component of theory of mind, and that such tests reveal the attribution of intention by infants as young as 18 months old.

Success versus failure

Meltzoff's findings can be summarized with reference to one of the objects used in his procedure, a dumbbell toy, consisting of two wooden cubes, each with a length of plastic tube extending from it, and fitting into/around the other tube. The 'target action' on this object involved pulling the two pieces apart, and it was performed by as many 18-month-old infants who had seen an adult model pretending to try and fail to separate the two pieces – '*Demonstrate* (*intention*)' – as by infants of the same age who had seen the model performing the target action successfully – '*Demonstrate* (*target*)'. One interpretation of these results is that the infants in the *Demonstrate* (*intention*) group inferred that it was the model's desire or intention to perform the target action, were motivated to reproduce the intended act, and therefore decided to perform the target action rather than reproduce the movement they had actually seen. Alternatively, the infants in both *Demonstrate* (*intention*) and *Demonstrate* (*target*) might have learned by model observation to apply outward force to the ends of the dumbbell.

Human versus mechanical model

Another experiment by Meltzoff[a] showed that the target action was produced by
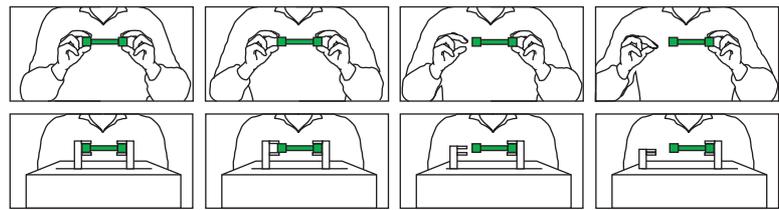
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Fig. I. Stimulus sequences observed by infants in the *Demonstrator* (*intention*) (top row) and *Demonstrator* (*mechanical slippage*) (bottom row) groups of the second experiment of Meltzoff *et al.* Reproduced, with permission, from Ref. a. (See text for details.)

more infants who had seen a human model trying and failing to pull apart the dumbbell – *Demonstrate* (*intention*) – than by infants who had seen two mechanical pincers grasping the ends of the dumbbell and then slipping off – *Demonstrate* (*mechanical slippage*). It seems that infants are more likely to attribute intentions to humans than to mechanical devices, and therefore this result has been interpreted as supporting the idea that toddlers attribute intention. However, the observers in group *Demonstrate* (*mechanical slippage*) not only saw pincers contacting the dumbbell but also an adult model refraining from doing so (see Fig. I). Therefore, it is plausible that, from adult observation, *Demonstrate* (*intention*) learned to apply outward pressure to the ends of the dumbbell, whereas *Demonstrate* (*mechanical slippage*) learned not to touch the dumbbell.

Woops! versus There!

Carpenter *et al.* found that 14–18-month-old infants were more likely to copy

transitive actions if the adult model said '*There!*', rather than '*Woops!*' as she completed the action[b]. These vocalizations are interpreted by adult speakers of English as indicators that the foregoing action was deliberate and accidental, respectively, but their modulation of infants' imitative performance does not establish that infants interpret them in the same way. It is plausible that, before they understand desire or intention, toddlers learn that imitation of actions accompanied by the sound '*Woops!*' is less likely to have rewarding consequences (e.g. interesting sensory stimulation, adult approval) than imitation of actions that are followed by '*There!*'.

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age matched controls (i.e. that there is an autism-specific deficit) only on imitation of symbolic movements[30]. By contrast, Rogers and Pennington's survey[31] in 1991 found autism-specific deficits in imitation of meaningless gestures and emotional expressions, as well as symbolic movements. Subsequent, well-controlled experiments[32–36] have tended to confirm the latter view.

The only study to date of imitation in autistic infants (at 20 months old) showed that, relative to controls with developmental delay, they were impaired on spontaneous imitation (and/or emulation) of actions on novel objects[32]. Hobson and Lee's study of autistic children and adults (9–18 years) suggested that, in this age group, the

deficit is in imitation not emulation[33]. Compared with language-delay and age-matched controls, their autistic individuals were equally likely to move objects spontaneously in the way they had seen them moved by a model, but were less likely to imitate features of the force, rate and/or topography of the model's body movements. Also studying a group of autistic children and adults (11–21 years), Rogers *et al.*[35] found that, relative to age and verbal IQ matched controls, those with autism were equally impaired in instructed imitation of meaningful/symbolic and meaningless hand and face movements, and more impaired on instructed imitation of hand movement sequences than of single hand movements. The latter finding contrasts with Smith and Bryson's report that,

relative to controls with receptive language delay, 6–18-year-old autistic individuals were impaired when asked to imitate single meaningless manual postures, but not when required to imitate simple sequences of the same stimuli[36]. It is likely that failures to find autism-specific deficits in imitation[37,38] have been due to ceiling effects.

Thus, there is evidence that, from infancy to adulthood, autistic individuals are impaired on a broad range of imitation tasks, and that these deficits are not purely a consequence of problems in visual recognition memory or motor control[34,35]. However, several studies conflate imitation with emulation[32,37,38], and it is not yet clear which imitation tasks are most challenging for individuals with autism, or the degree to which their imitation impairments are motivational[38].

Mature characteristics

Recent research on the 'chameleon effect' in social psychology has confirmed that human adults, especially those with high cognitive empathy scores, engage in unintentional, 'nonconscious' imitation of interactants' facial expressions, gestures and mannerisms (e.g. face rubbing), and that this inclines the model to like the imitator and to perceive the interaction as smooth[39,40].

Studies of 'observational learning' typically fail to distinguish the contributions of body movement observation and of manipulandum movement observation to skill acquisition, i.e. they confound imitation and emulation[41–44]. Both confounded studies and those that examine imitation specifically[45,46] suggest functional equivalence between observation of skilled performance and overt practice. Observation can be as effective as practice in promoting skill learning[42,47,48], and some independent variables, such as training schedule[42] and stimulus-response compatibility[45], have the same effects on observation and practice. Examining more directly whether common cognitive mechanisms underlie observation-based and practice-based skill learning, one study suggests that both observation and practice give rise to effector-specific motor learning in a serial reaction time task[46].

Neurobiology

Research on neural mechanisms of imitation (see Box 3), is focussed on the hypothesis that areas 44 and 45 of the left inferior frontal gyrus (IFG) are specialized for imitation. This region subsumes Broca's area, and is thought to be the human homologue of monkey F5 (Refs 49,50). F5 contains 'mirror neurons', which are activated by observation of, and by execution of grasping actions[51].

Causes and consequences

Perceptual–motor translation

Many of the psychological requirements for imitation (e.g. detection and analysis of others' movements, memory, motor control) are also prerequisites for other types of behaviour. The requirement that is unique to imitation, and therefore the distinctive explanatory challenge for theories of imitation, is a mechanism that can translate visual information about the body movements of others into matching motor output. However, many theories of imitation either do not address this perceptual–motor translation problem, or propose mechanisms that could produce imitation of perceptually transparent movements, those that yield similar sensory input when observed and executed (e.g. hand movements), but not of perceptually opaque movements, which give rise to sensory input in different modalities or coordinate frames when observed and executed (e.g. facial expressions)[2,52]. Recent theories that are not concerned with perceptual–motor translation include the 'response facilitation' hypothesis[53] and 'string parsing' theory[54].

Computational/robotic theories suggest that perceptual–motor translation is achieved via selection processes in which input from the model is compared with the observer's motor output ('reverse model'[55]), and/or with predictions of what that output would be if each of a set of motor primitives were activated ('forward model'[56,57]). These theories are plausible for perceptually transparent movements because the input and output could be matched on sensory coordinates, but neither these nor other proposed coordinate frames (e.g. the via point method[58]) have been demonstrated to be adequate for imitation of perceptually opaque movements such as facial gestures[55].

Two theories that address the translation problem for opaque as well as transparent movements are 'Active Intermodal Mapping' theory (AIM)[18], and 'Associative Sequence Learning' theory (ASL)[2].

Active intermodal matching

AIM was formulated to account for infants' imitation of facial expressions but has been applied to imitation generally[52,55] (see Fig. 1). It proposes that there is a dedicated, innate imitation mechanism that transforms visual input from a model into a 'supramodal' representation encoding the modelled movement as a set of 'organ relations'. Then, in a 'goal-directed' selection process, this supramodal representation is compared with proprioceptive feedback from the observer's motor output, also encoded as a set of organ relations, and motor variants that match the representation of the modelled movement are favoured for future production. AIM does not specify the form in which organ relations are encoded, or the mechanisms through which organ relations are derived from observed body movement.

AIM has played an important heuristic role in research on imitation, focussing attention on the problem of perceptual opacity and directly

Box 3. What is the role of the left inferior frontal gyrus in imitation?

Evidence of a link between the left inferior frontal gyrus (IFG) and imitation has come from functional magnetic resonance imaging (fMRI)[a], and magneto-encephalography (MEG)[b]. The fMRI study found more activity in left BA 44 when participants lifted one of two fingers cued by a video of the corresponding finger movement, than when choice of finger movement was cued by a static hand with a dot on the to-be-moved finger, or by a dot in one of two positions on a blank rectangle. Similarly, the MEG study reported that when participants performed a finger and thumb pinching movement paced by observation of the same movement executed by an experimenter, peak activation in BA 44 was twice as high as when participants' pinching movements were self-paced, or they passively observed the pinching movement. MEG also showed that, in all conditions, peak activation in left BA 44 preceded, and therefore could not be a product of, peak activation in the left primary motor area (BA 4).

Imitation versus recognition

Assuming that the observed activation of the left IFG was specific to concurrent observation and execution of matching, rather than non-matching, movements, these results are susceptible to at least two interpretations:

(1) *Imitation hypothesis:* imitation typically or invariably occurs via activation of the left IFG which plays an important role in translating perceptual input from observation of a model's movement into matching motor output[a,b].

(2) *Recognition hypothesis:* the left IFG mediates body movement recognition (e.g. naming), which is achieved via activation of premotor and motor areas, and it is involved in imitation only on those occasions, or to the extent, that imitation is accompanied or mediated by movement recognition[c–e].

Two findings favour the recognition hypothesis: first, the observed and executed actions that activate mirror neurons in monkey F5 are the same in terms of their 'goals' or outcomes, but not at the level of body movement[c]. Second, PET studies show that BA 44/45 is more active when people are passively watching meaningful arm movements (e.g. mime of opening a bottle) than when they are passively watching static hands, and that BA 44/45 is *not* more active during passive observation of meaningless arm movements, or of meaningful or meaningless arm movements under instructions to imitate[e] (see Fig. I).

Direct route(s)

Most of the areas that show greater regional cerebral blood flow (rCBF) when participants are observing arm movements in order to imitate than during passive observation are cortical and subcortical regions known to be active during verbally instructed motor preparation and mental practice[d] (see Fig. II). Activation of these areas during observation for imitation suggests that there is a direct (not mediated by left IFG) link between movement perception and movement execution. However, it does not explain either the origins of this link, or how it translates visual information into motor commands[e].

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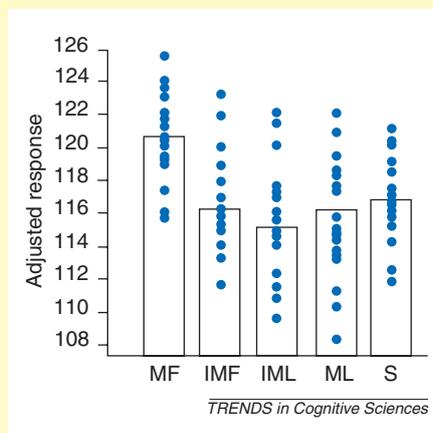
Fig. I. Activation of the left IFG. Histogram bars represent rCBF in the inferior frontal gyrus (BA 44/45) when adult human participants were observing: meaningful movements without any purpose (MF), meaningful movements under instructions to imitate (IMF), meaningless movements under instructions to imitate (IML), meaningless movements without any purpose (ML), and stationary hands (S). The blue circles represent the distribution of scans across the 10 participants in each experimental condition. These data support the view that activation of the left IFG is associated, not with imitation specifically, but with observation of meaningful movements. Reproduced, with permission, from Ref. e.
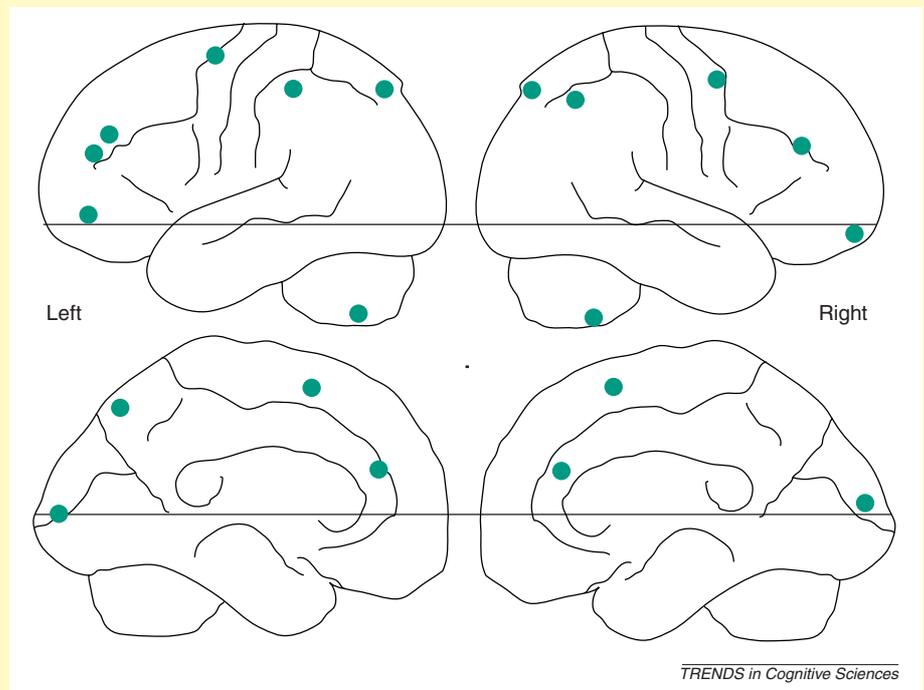
Fig. II. Cortical regions associated with imitation. Lateral (top) and medial (bottom) views of the left and right hemispheres. Green dots indicate regions where rCBF was higher during observation of sequences of arm movements under instruction to imitate than during passive observation of the same movements, regardless of whether the movements were meaningful or meaningless. Reproduced, with permission, from Ref. e.

Fig. 1. Theories of imitation that address the problem of perceptual opacity. Schematic representations of (a) Active Intermodal Mapping (AIM) theory[18], and (b) Associative Sequence Learning (ASL) theory[2]. (See text for further details.)
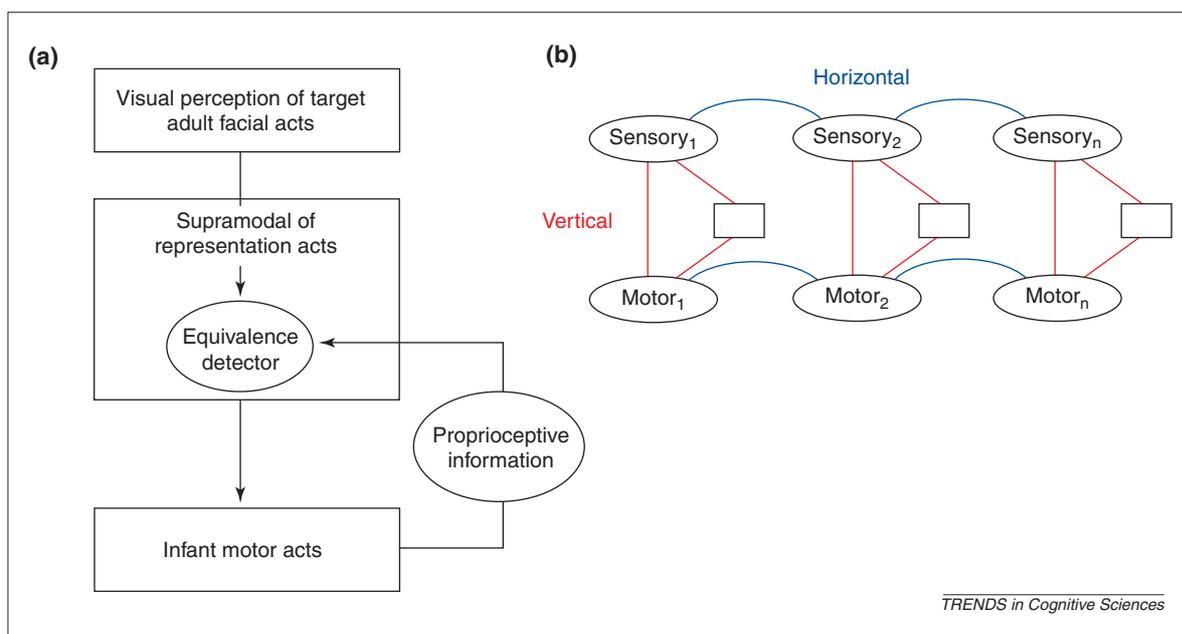
addressing this explanatory challenge. However, there is a poor fit between AIM and recent data on imitation (summarized in Box 4). Evidence is accumulating that neonatal facial imitation, the primary evidence in support of AIM, is based on an innate releasing mechanism. AIM can be understood either to make no predictions about imitation in nonhuman animals, or, in view of its claim that there is an *innate* imitation mechanism, to be inconsistent with evidence that imitation is experience-dependent in our closest primate relatives. AIM is not inconsistent with evidence of functional equivalence between skill observation and overt practice, and it is compatible with generalized imitation deficits in autism[59]. However, insofar as AIM emphasizes that imitation is intrinsically goal-directed or intentional, it is incompatible with the 'chameleon effect', and with the equivocality of the evidence that toddlers attribute intention in order to imitate. Finally, although recent reports that the left inferior frontal gyrus is specialized for imitation have been interpreted in the light of AIM (Ref. 60), they do not lend specific support to this theory. Current data favour the hypothesis that the left IFG plays a key role in movement recognition, rather than imitation (see Box 3), and, even if a stronger link with imitation had been established (i.e. if it had been shown that, for meaningful *and* meaningless movements, the left IFG is more active during observation plus execution of matching, rather than non-matching, movements), it would remain an open question whether the left IFA mediates non-verbal, supramodal representation of observed action.

Associative sequence learning
In contrast with AIM, ASL suggests that development of the imitation mechanism is highly experience-dependent, and that it consists of a set of bidirectional excitatory links between sensory and motor representations of movement units, rather than an innate device that actively, internally transforms visual input into motor output via supramodal representations[2] (see Fig. 1).

The links or 'vertical associations' are of two kinds: direct vertical associations connect sensory and motor representations of a movement unit without intermediate representation in a distinctive code or of distinctive content. Whereas some are innate (e.g. smiling, yawning, tongue protrusion in humans) the majority are formed by co-activation arising from correlated experience of observing and executing the movement unit. Co-activation of sensory and motor representations of the same perceptually transparent movement occurs whenever the individual observes, unaided, their own motor output, and, in the case of perceptually opaque movements, through experience with mirrors, of being imitated, and of socially synchronous movement in response to a common stimulus. Indirect vertical associations between sensory and motor representations of a movement unit are mediated by another sensory representation, typically in humans of a word or phrase, and are established when the verbal stimulus co-occurs on some occasions with sight of the movement, and on other occasions with its execution.

ASL is little more than a sketch of a theory, which needs testing and elaboration, but it is compatible with recent empirical findings (see Box 4). Because ASL emphasizes the role of experience in the development of imitative capacity, and predicts that humans and animals will be capable of imitation to the extent that they have had the opportunity to form vertical associations, it is consistent with the

absence of significant imitative ability in human neonates, the experience-dependence of chimpanzee imitation, and the finding that avian species can imitate foraging behaviours they have performed in flocks. ASL is compatible with the chameleon effect, functional equivalence of skill observation and overt practice, and innervation of corresponding muscle groups during action observation[49,61], because it assumes that activation of motor representations via vertical associations provides input to task-general processes of motor learning, and results in imitative performance unless inhibited by mechanisms regulating intentional action[62]. It is these mechanisms, which are not imitation-specific, that harness the output of vertical associations to specific goals, including on some occasions (in adults, if not in 18-month-old infants) reproduction of the model's intended act. ASL does not have any direct implications regarding the source of generalized imitation deficits in autism. However, it raises the possibility that they represent impoverished development of a repertoire of vertical associations resulting from early inattention to social stimuli (including adults imitating the autistic infant), and deficits in joint attention reducing the frequency of synchronous movement in

response to a common stimulus. Finally, ASL is consistent with recent data on neural mechanisms of imitation, and provides testable hypotheses about their origin. It suggests that direct activation of motor preparation areas via the dorsal visual route represents direct vertical associations, and, more tentatively, that activation of the left IFG during imitation may represent indirect vertical associations.

Imitation and theory of mind
Three kinds of relationship between imitation and theory of mind have been proposed. First, imitation has been defined as body movement copying guided by ascription of goals or intentions to the model[63]. Second, it has been suggested that imitation and theory of mind both draw on a capacity for metarepresentation; for example, representation of the intentions of others[30,38], or executive function, including working memory and inhibition[31,34,35]. As an empirical claim, rather than a definition, the hypothesis that imitation is typically based on attribution of intention is incompatible with the occurrence of nonintentional imitation in adult humans, and with the range of imitation deficits associated with autism[34,35]. The executive function hypothesis is consistent with evidence of generalized imitation deficits in autism but, given that working memory and inhibition are required for a multitude of behavioural tasks, the relationship between imitation and theory of mind is not close if all they have in common are these cognitive requirements.

Finally, it has been proposed that imitation contributes to the development of theory of mind[31,59,64–66]. According to Barresi and Moore[64], during imitative performance of transitive actions, the infant simultaneously has first-person and third-person experience of a relationship between an action and an object, and experience of this kind is necessary, but not sufficient, for learning to distinguish first- and third-person perspectives, a crucial component of

theory of mind. Presumably, simultaneous experience of first- and third-person perspectives could also be obtained from nonimitative synchronous action, and therefore this hypothesis assigns a modest, nonspecific role to imitation in the generation of theory of mind. By contrast, Meltzoff and Moore[66] have proposed a specific, generative relationship, in which the imitating infant: (1) intends to copy the model's movement; (2) represents this intention; (3) recognizes the physical similarity between his or her own movement and that of the model; and (4) infers from 1–3 that the model's movement was

intentional. This hypothesis is admirably clear and internally coherent, but it does not have strong empirical support. The assumption that imitating infants have a first-order intention to copy is in doubt along with other evidence of neonatal imitation, and there is no evidence that such intentions, if they occur in infants, are themselves represented.

Thus, although it is plausible that the experience of imitating and being imitated contributes to the development of theory of mind, there is not currently a well-supported theory specifying the nature of the contribution.

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The shape of ears to come: dynamic coding of auditory space

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In order to pinpoint the location of a sound source, we make use of a variety of spatial cues that arise from the direction-dependent manner in which sounds interact with the head, torso and external ears. Accurate sound localization relies on the neural discrimination of tiny differences in the values of these cues and requires that the brain circuits involved be calibrated to the cues experienced by each individual. There is growing evidence that the capacity for recalibrating auditory localization continues well into adult life. Many details of how the brain represents auditory space and of how those representations are shaped by learning and experience remain elusive. However, it is becoming increasingly clear that the task of processing auditory spatial information is distributed over different regions of the brain, some working hierarchically, others independently and in parallel, and each apparently using different strategies for encoding sound source location.

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Although vision might be our dominant sense, we rely on hearing as our only panoramic, long-range sensory system. The ability not only to detect and identify a sound, but also to pinpoint swiftly and accurately the location of its source can bring substantial advantages. This applies equally to a predator stalking its prey in the wild and to the modern day pedestrian negotiating a busy crossroads. But although determining the location of a visual or tactile stimulus is relatively trivial (it can be read off directly from the receptor array in the retina or skin), localizing a sound source is a highly complex computational task. The brain has to infer sound source locations from acoustical cues generated by the physical properties of the head and external ears (see Box 1). Some of these cues vary over ranges that tax the resolution of our sensory system to the limits. For example, humans can discriminate between two nearby sound sources by detecting differences as small as 10 μs in the time it takes each sound to reach each ear. Moreover, each set of auditory localization cues is, to some extent, ambiguous, and might have to be processed in an environment full of distracting noises and echoes. To arrive at consistent, and usually highly accurate, estimates of sound source location, the brain has to pool information from different auditory processing channels. Matters are further complicated by the fact that the association between sound locations and their corresponding cue values must be learned and then recalibrated if these spatial relationships change. This applies especially, though not exclusively, during development, as the head grows.

Although auditory distance perception in humans and other primates has been the subject of recent studies[1–3], most psychophysical and neurophysiological research on sound localization has focused on the basis for determining the horizontal and vertical direction of a sound source. Much is now known about the sensitivity of neurones in the central auditory system to individual localization cues. Nevertheless, many details of the neural circuitry involved in processing auditory spatial information remain obscure. Indeed, the