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Human infant imitation as a social survival circuit

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Human infants rapidly and effortlessly learn from other people. Imitation provides a direct avenue for transmitting information across generations, before language. Infants learn about people, objects, and themselves through imitation. A large body of behavioral experiments has provided insights about the development, functions, and psychological mechanisms underlying human infant imitation. Infants not only imitate other people, but also recognize when they are being imitated. Reciprocal imitation between infants and caregivers promotes interpersonal affiliation and bonding. New cognitive neuroscience research complements the behavioral work by providing evidence about infant cortical body maps. These body maps help explain how infants match the behaviors they see with their own corresponding bodily acts. Imitation is a distinctive channel for early human learning. It links human infants to their caregivers who are conduits of cultural information. Infant imitation serves as a social survival circuit with evolutionary roots and socio-cultural consequences.

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Introduction

Human children are imitative generalists. They imitate diverse classes of behaviors, including vocalizations, body postures, and actions on objects, and have the capacity to do so both immediately and from memory. Imitation is quicker than operant conditioning, more flexible than the maturation of fixed motor programs, and less cognitively demanding than independent discovery and innovation.

The imitative capacity of human infants is unmatched in other species [1••], is disrupted in children with autism spectrum disorder [2•,3], and sets a goal for roboticists who seek to design machines that can learn via observation as infants do [4•,5]. Imitation is a primary mechanism for the transmission of culturally diverse practices, skills, and customs to the human young [1••,6,7,8••], and it promotes caretaker–infant affiliation and bonding. Recent neuroscience experiments are beginning to shed light on the neural processes associated with human infant imitation [9,10••].

Human infants are born helpless, completely dependent on adult caretaking for survival. Human adults not only nourish and protect children, but also introduce them to a culture filled with adaptive tools and practices that would be impossible for infants to invent by themselves. Before language, infant imitation complements the hard-wired survival circuits described by LeDoux [11] with a behavioral 'social survival circuit' that enables infants to flexibly acquire novel behaviors by imitating other members of their culture. The adoption of LeDoux's term is not meant to convey that infant imitation is a hard-wired module, but rather that it is a social behavior that serves an adaptive function for the young, which enhances learning and survival.

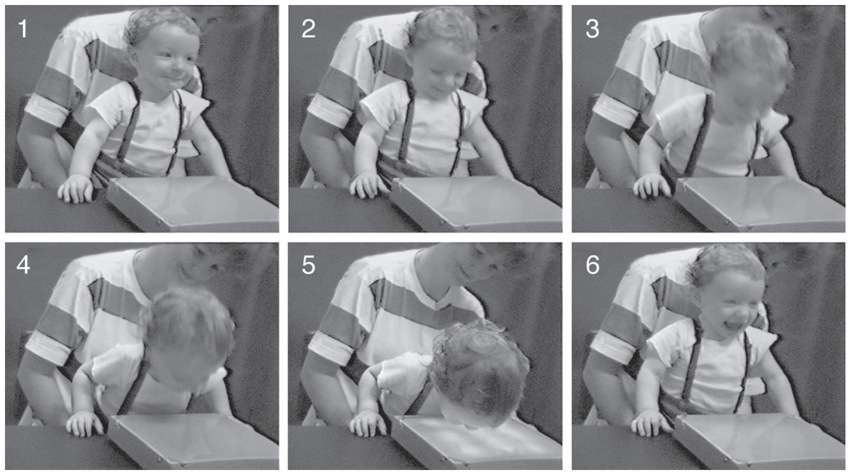
Behavioral imitation

Infants use imitation to learn about the actions and proclivities of other people and the functions and causal properties of physical objects. Imitation is also a way for infants to learn about themselves, in terms of their own characteristics, abilities, and similarity to others.

Novel acts, memory, context, and culture

For imitation to be an effective channel for cultural transmission, two cognitive competencies are required to extend learning across time and space: deferred imitation (which goes beyond immediate 'resonance') and imitation across changes in context (generalization). Both have been demonstrated in infants (for a review see Ref. [8••]). In one study of deferred imitation, 14-month-old infants saw a novel act and were required to imitate after a significant delay. An adult used his head to turn on a light panel. This novel act was performed by 0% of the infants in baseline control conditions. Infants simply observed the adult demonstration; they were not allowed to touch the panel so there was no possibility of operant conditioning or motor practice. When re-presented with the panel after a 1-week delay, 67% of the infants imitated the novel head-touch act, based on recall memory [12] (Figure 1). Infant imitation of novel acts [13,14] and sequences [15] has been replicated across cultures, with some studies suggesting that infants are more likely to imitate if the acts are demonstrated in a pedagogical

Figure 1



Infant imitation of a novel act. Photos of a 14-month-old infant imitating head touch, which he witnessed 1-week prior. Infants simply watched the novel act on the first visit to the laboratory. They were not allowed to touch or handle the object. Infants returned to the laboratory after the 1-week retention interval and were presented with the object. Infants performed the novel act and often exhibited positive emotion when they did so, panel 6.
Source: Meltzoff [75].

manner [16]. Human infants also show the ability to generalize. For instance, they show deferred imitation across changes in environmental context, even when the object used in the demonstration differs in size and color from the one the presented to the infant [8••,17].

The ability of infants to imitate completely novel acts across temporal delays and contextual changes lies at the heart of cultural learning. If imitation was more restricted in time and space, it could not serve as an efficient mechanism for cultural transmission. Instead, learning would be place bound, temporally restricted, and object specific. On the contrary, infants' capacity to learn a novel act by observation, and to imitate it at a later time in a new context, is robustly present in human infants. This powerful set of abilities places imitation in a class of behaviors that has far-reaching effects for human development.

Causal learning

Infants also learn about cause and effect by watching the behavior of others. In a two-choice procedure, infants and toddlers saw an adult perform the same act on two different objects, but only one object caused an effect. From observation alone, infants learned which object to select and what to do with it to bring about the effect [18]. Infants and young children also take statistical information into account when imitating [19–21]. For cases in which two similar acts lead to the same result, infants selectively imitate the act that is observed to have a relatively higher rather than lower probability of producing the result. Infants pay special attention to and preferentially re-enact causal chains that are instigated by intentional human acts (versus having the objects move via invisible magnets or attached wires) [18,22,23]. This ability promotes infants' learning of specific causal relations that are important in their culture or social milieu.

Related research has examined imitation of tool-use and persistence in trying to cause an effect. Various species learn to use tools via trial-and-error. Human infants and young children have the capacity to learn tool-use simply from observing the trial-and-error of others. Children can thus profit from the efforts and innovations of others by watching their struggles, before acting themselves. Indeed, 15-month-old infants who watch adults repeatedly trying to achieve a goal show increased persistence on a novel causal task [24], indicating that the scope of infant imitation extends beyond specific muscle movements to higher-order behavioral strategies and approaches to problem-solving, sometimes termed 'abstract imitation' [8••].

Emotions and the modulation of imitation

Emotions also regulate imitation. For example, if an infant sees an adult respond with a negative emotion to a certain behavior, this changes the likelihood that the infant will imitate that behavior. An experimenter showed 15-month-old infants a new way of using an object, and a second adult (the 'Emoter') was randomly assigned to become angry (or not) when the experimenter performed the act [25]. The Emoter then adopted a neutral facial expression, and the infant was allowed to imitate. The study systematically manipulated whether or not the previously angry person watched the infant's imitation. Infants were more likely to imitate when the Emoter did not watch them (when the Emoter's back was turned, or she had her eyes closed, or was reading a magazine). Because infants did not want to become the target of the Emoter's anger, they chose not to imitate when she was watching them. This underscores that infant imitation is not an automatic or compulsory response. It also places infant imitation further within a larger web of social cognition that involves multiple social influences, including emotional reactions of others, eye-gaze, and inferences about the consequences of imitation.

Imitation is also modulated by other social factors. Infants and young children preferentially imitate more friendly and trustworthy models [26], intentional rather than accidental acts [27,28], ingroup versus outgroup members [29], and models who receive favored versus prejudiced treatment by others [30]. Infants flexibly choose what, when, and who to imitate. Well before spoken language, imitative acts are selective and deliberate, rather than being fixed, automatically triggered reactions.

Newborns

A primitive form of imitation exists at birth, including the matching of basic facial and manual acts [31–33]. Early imitation has been replicated and extended in more than two dozen experiments across multiple laboratories and cultures (reviewed in Refs. [34•,35]), but careful eliciting conditions are needed for documenting the behavior (see for example Ref. [36]). The phenomenon has sparked vigorous discussion about underlying mechanisms. The typical alternative explanation is that it is a general arousal effect activated by seeing moving faces or fingers. However, experiments using dynamic body movements as controls have demonstrated that early imitation is not reducible to arousal [37,38].

We favor the 'active intermodal mapping' (AIM) [39•] account of early imitation. This theory holds that imitation, even in early infancy, is a matching-to-target process. Consider the simple case of imitating hand opening and closing. Here, the behavioral target for imitation is perceived in the same modality for self and other. Infants can compare the sight of the adult's hand actions to the sight of their own hand actions and can use visual guidance to home in on the match (across changes in size and orientation). AIM proposes that a similar process can occur across modalities, as in facial imitation. In this case, the behavioral endpoint is perceived visually (e.g. tongue beyond lips) and infants can use proprioceptive feedback from their own motor movements to steer their response. AIM proposes that intermodal comparison is possible because the perception and production of human acts are represented within a common framework.

The AIM model also proposes that motor activity plays a role in shaping early imitative abilities. Bodily movements of the fetus and young infant may contribute to early imitation via 'body babbling' [39•]. Analogous to vocal babbling in the linguistic domain, body babbling provides motor practice for how to move one's effectors to reach certain bodily and postural targets. According to AIM theory, infants capitalize on this prior experience when aiming to achieve the target in imitative contexts.

Infant imitation and neuroscience

Developmental scientists are now applying neuroscience techniques to further investigate the mechanisms of human infant imitation. One possibility is that mirror neurons, as discovered in rhesus monkeys, underlie human infant imitation. However, the 'direct resonance' of canonical mirror neurons cannot account for the full scope and complexity of the infant behavioral phenomena described above. A neurobiologically informed, ontogenetic perspective on infant imitation is now being formulated. To date, this work has mainly focused on the imitation of goal-directed acts, and is shedding light on the neural bases of connections between the bodily acts of self and other.

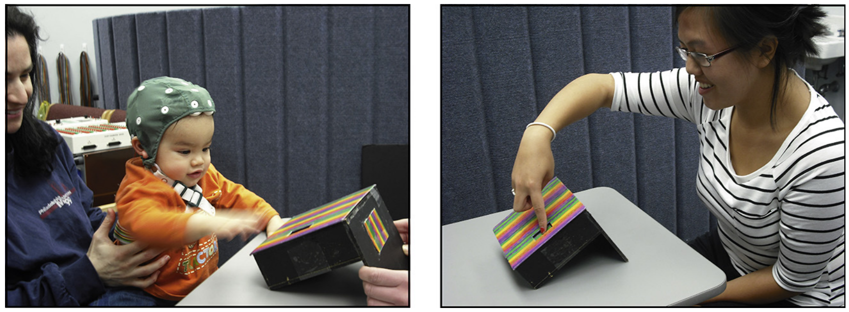
Sensorimotor brain rhythms

One line of neuroscience studies uses measures derived from the electroencephalogram (EEG) to investigate linkages between action perception and action production in infants (Figure 2). These studies have leveraged the properties of the sensorimotor mu rhythm, an alpha-range rhythm prominent in the infant EEG [40,41•,42,43]. Experiments show a desynchronization (reduction in amplitude) of the mu rhythm both when infants carry out goal-directed acts and when they observe the same act executed by an adult [44,45].

The infant mu rhythm has been used to further investigate social perception and imitation [46,47]. One study tested responses of the infant mu rhythm to being imitated [48••]. This work builds upon behavioral experiments showing that infants express positive emotions and prosocial behavior toward adults who mimic them [49,50], and they exhibit special patterns of visual attention when seeing reciprocal imitation [51,52]. There was significantly greater desynchronization of the infant sensorimotor mu rhythm when an adult imitated the infants' acts compared to when an adult mismatched them, providing neuroscientific evidence that infants recognize behavioral matches between self and other [48••].

Taking the brain and behavioral data together, one speculation is that when caregiver–infant dyads engage in bouts of reciprocal imitation, positive emotional states and affiliative tendencies are induced not only in the participating adults [53] but also in the infants, promoting interpersonal bonding. Moreover, when adults imitate

Figure 2



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Infant social-cognitive neuroscience. EEG was recorded from 14-month-old infants as they observed and executed the act of pressing a button. Results indicated similar patterns of EEG activity in both cases, a desynchronization of the mu rhythm (6–9 Hz in infants) at central electrode sites. Source: Marshall and Meltzoff [40].

infants, the infants may tap the same processes as used to produce imitation, but in reverse. Instead of using the perception of the other person to drive motor production (as in productive imitation), the infant begins by producing a behavior and then perceptually recognizes that the adult is acting 'like-me' (when being imitated). One theory of infant social development holds that the experience of others acting 'like-me' is a building block for developing more complex forms of social cognition [49]. On this view, both the production of imitation and the recognition of being imitated play crucial roles in infant psycho-social development.

Infant body representations

Another novel neuroscience finding with implications for infant imitation is that infant mu rhythm responses to observed actions are somatotopically organized [54]. In one study, 14-month-old infants saw an adult press a button to activate an object, which lit up and made a sound. This same effect was achieved by the same experimenter either by pressing the button with the hand or pressing the button with the foot. The infant mu rhythm showed greater desynchronization over lateral central sites (overlying the hand region of somatosensory cortex) during the observation of hand acts, and greater desynchronization over the midline central site (overlying the foot region) during observation of foot acts. This suggests that goal-directed acts by an adult's hands can be mapped onto the infant's own hand representation, and likewise for feet. This finding is compatible with the AIM theory of imitation, which hypothesizes that a first step in imitation is the identification of the body part used to carry out an observed act [39•].

Continued investigation of how the body, both one's own and that of others, is represented in the developing brain will help sharpen accounts of infant imitation. Indeed, novel applications of methods for recording brain activity are revealing relevant information about the development of infant cortical body maps [55–57]. One line of work involves examining brain responses to punctate touches to different parts of the infant's body. A somatotopic response pattern to tactile stimulation of infants' lips, hands, and feet was documented in infants as young as 60 days old [58]. The findings concerning lip stimulation are novel and invite further study, because of the special importance of lips for infant nourishment, emotional expressions, facial imitation, and speech. It is also of interest that the 60-day-old infants exhibited a particularly prominent response to lip touch, perhaps due to cortical magnification of this crucial body part, which may also be relevant to infants' precocious ability to imitate lip and tongue behaviors.

Multimodal body maps connect self and other

A further advance has come with the application of magnetoencephalography (MEG) brain-imaging techniques to infant populations [59]. MEG work with 7-month-olds showed that tactile stimulation of infants' hands and feet registered a somatotopic response pattern in primary somatosensory cortex [10••]. More interestingly, the mere observation of another person's hand or foot being touched also produced detectable activation in the infants *own* somatosensory cortices, albeit at a much weaker level than felt touch [10••]. Such neural responses to vicarious touch are compatible with other infant studies [60•] and with cognitive neuroscience experiments with adults showing that the perceivers' own somatosensory system is activated by observing others being touched [61••,62,63]. The temporal precision and source localization methods afforded by infant MEG, combined with behavioral data, can further illuminate the multimodal nature of infant body representations and their contribution to imitation.

The neuroscience findings raise questions about the origins and neuroplasticity of body representations in the developing brain. Somatotopic body maps likely emerge prenatally through an intertwining of intrinsic and activity-dependent processes. In a study of nonhuman primates, somatotopic maps developed in somatosensory cortex even in the context of disordered sensory inputs [64•]; other studies point to a role for fetal activity in forming and tuning early body maps [65,66].

Future studies should examine postnatal neuroplasticity in neural body maps — particularly how these maps change with motor experience. Does grasping experience alter the neural representations of hands? Does the onset of babbling or spoken language change the neural representation of the lips? Social experience may also play a role. In reciprocal imitation, parents act as social mirrors reflecting infants' behavior back to them. This experience may sharpen or change pre-existing body maps as infants gain experience in seeing what felt actions look like, as discussed in Ref. [39•].

Conclusions

Brains evolved from simpler nerve nets alongside the evolution of sensory systems enabling the coordination of directed locomotion, predator evasion, and food seeking. In the mammalian brain, the brain circuits mediating these basic survival needs have been supplemented by circuits enabling kin recognition and bonding [67]. In the human case, the additional importance of transmitting acquired skills across generations has contributed to a ratcheting effect that harnesses multiple brain systems to enable social learning [68]. The empirical research on infant imitation, including both brain and behavioral studies, advances our understanding of these processes and how infants meet the need for socially connecting to and learning from social others.

The cultural diversity exhibited by human social groups is a noteworthy quality of *Homo sapiens*, and anthropologists and evolutionary biologists have long discussed how human cultures emerge and are maintained [69,70••]. One likely contribution is the fact that human young are born relatively 'immature' with a high degree of neuroplasticity, which combined with the capacity for imitative learning, engenders diverse cultural outcomes [6,71].

Although other species imitate, a distinctive characteristic of humans is that we are imitative generalists. For example, our closest living relatives, chimpanzees, can copy object use, but have a limited capacity to imitate body movements [1••,72•] and little or no ability to imitate vocally [73]. Human infants imitate all these types of behaviors with great facility [8••,74]. Copying of actions by chimpanzees is usually in the context of obtaining food. Human children have a strong social motivation to 'be like' the other. The very act of imitating and being imitated seems to provide its own reward.

Imitation is a distinctive and powerful channel for learning. It links human infants to their caregivers who are conduits of cultural information. Infant imitation is where biology meets culture. Through imitation infants become like us.

Conflict of interest statement

Nothing declared.

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Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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The author describes a theory of social-cognitive development that puts prosocial behavior center stage. He marshals evidence from both cross-cultural studies and comparative experiments comparing the capacities of human infants to those of chimpanzees and bonobos. The book squarely addresses the longstanding debate of what makes us uniquely human. In many cases, the author has performed the same controlled experiments with human children and great apes, enabling him to quantify with unparalleled precision cross-species similarities and differences in imitation and other forms of social learning.

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By reviewing 53 empirical studies of individuals with autism, this paper provides an informative analysis of imitation deficits in children and adults. Meta-analytic findings reveal that individuals with autism perform below controls on tests of imitation. Severity of autism symptoms is significantly correlated with imitation deficits. The review reveals that children with autism show prominent deficits on specific types of imitation, notably those measuring high-fidelity matching of the form of behavior (i.e. matching the details of the bodily acts of the model), which fits with the ideas advanced in our current paper.

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Turing's vision was to design computer programs that learned like a child. This book takes up this challenge by discussing the field of 'developmental robotics.' The authors used child development principles to design robots that change with experience and can engage in primitive social learning. Topics relevant to infant imitation include Chapter 6 on robotic imitation, gaze following, cooperation, and theory of mind.

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This is a comprehensive review of the infant imitation literature. The cognitive basis of imitation is considered alongside four proposed functions that infant imitation serves in human development. Current issues in infant and child imitation are critically examined, including mirror neurons, rational imitation, overimitation, neonatal imitation, and abstract imitation. Both the cognitive and social aspects of imitation are reviewed. Also discussed is the evidence that infants perceive the actions of others as being 'like-me,' with implications for theories of social cognition.

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This paper uses MEG brain-imaging techniques to investigate infant social perception. In two experiments 'felt touch' (touch of the infant's body) and 'observed touch' (observing another person being touched) were examined in 7-month-old infants. Results show significant activation in somatosensory cortex following felt touch and also in response to observed touch of another person. Moreover, in the observed touch condition, activation occurred in cortical regions which in adults are involved in the visual processing of bodies. The authors discuss neuroplasticity for body maps and how neural body representations contribute to infant imitation.

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