Dissecting the imitation faculty: The multiple imitation mechanisms (MIM) hypothesis

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ABSTRACT

Is the imitation faculty one self-contained domain-general mechanism or an amalgamation of multiple content-specific systems? The multiple imitation mechanisms (MIM) hypothesis posits that the imitation faculty consists of distinct content-specific psychological systems that are dissociable both structurally and functionally. This hypothesis is supported by research in the developmental, cognitive, comparative and neural sciences. This body of work suggests that there are dissociable imitation systems that may be distinguished by unique behavioral and neurobiological profiles. The distribution of these different imitation skills in the animal kingdom further suggests a phylogenetic dissociation, whereby some animals specialized in some (but not all possible) imitation types; a reflection of specific selection pressures favoring certain imitation systems. The MIM hypothesis attempts to bring together these different areas of research into one theoretical framework that defines imitation both functionally and structurally.

1. Introduction

Imitation has both fascinated and frustrated scientists for over 100 years. One of the greatest frustrations has to do with the definition and conceptualization of imitation; A problem that is as real today as it was over a 100 years ago when Morgan complained that, "In the face of such apparently diverse usage it is necessary to show within what limits and with what qualifications the word [imitation] may profitably here be used to individuate a factor in social evolution" (Morgan, 1900, p. 180). In the past 50 years, the comparative sciences have moved in the direction of describing different hypothetical mechanisms[1] that may contribute to social learning, including attentional and motivational mechanisms triggered by the presence of conspecifics that accelerate individual, trial-and-error learning and, ultimately, behavior matching. These 'lower-level' mechanisms include stimulus (Spence, 1937), local (Thorpe, 1956), and social (Clayton, 1978) enhancement (see Zentall, 2006 for a review). More recently, researchers have postulated 'higher level' social learning mechanisms that result in behavior matching. One of these social learning mechanisms

include, mimicry, which involves copying specific actions, while remaining ignorant of the model's goals or intentions. For example, the use of "hello" or "good-bye" by domesticated parrots. In this case, parrots are reproducing a vocal action learned from their keepers without an understanding of the significance of these actions (Zentall, 2006). Another social learning mechanism is emulation, which involves copying the results, causal structure or goals of actions while ignoring the precise actions used by the model to achieve that result (Tomasello and Call, 1997; Whiten and Ham, 1992; Whiten et al., 2009). These social learning mechanisms are seen as being distinct from imitation, which has been defined by some as the copying the actions and goals of a model to achieve a specific action (Carpenter and Call, 2002; Tomasello and Call, 1997).

Carpenter and Call (2002) have proposed a clever framework, the chemistry of social learning (CSL), that attempts to capture the heterogeneity of social learning. The Call and Carpenter model breaks down these social learning mechanisms onto three basic elements: actions, goals, and results. According to Carpenter and Call (2002), these elements map unto existing conceptual mechanisms. For example, the copying of actions only is akin to the concept of mimicry. The copying of results only is akin to the concept of affordance learning or emulation. And, the copying of goals only is akin to the concept of goal emulation. Additionally, the copying of actions and results is akin to "blind imitation," while the copying of actions, goals and results is akin to "insightful" or "true imitation." However, this model does not distinguish between sensory modalities. Or whether what is to be imitated is familiar or novel. As such,

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[1] Throughout the text the word mechanism and system are used interchangeably to mean a cognitive module that makes certain computations over specific content-types.
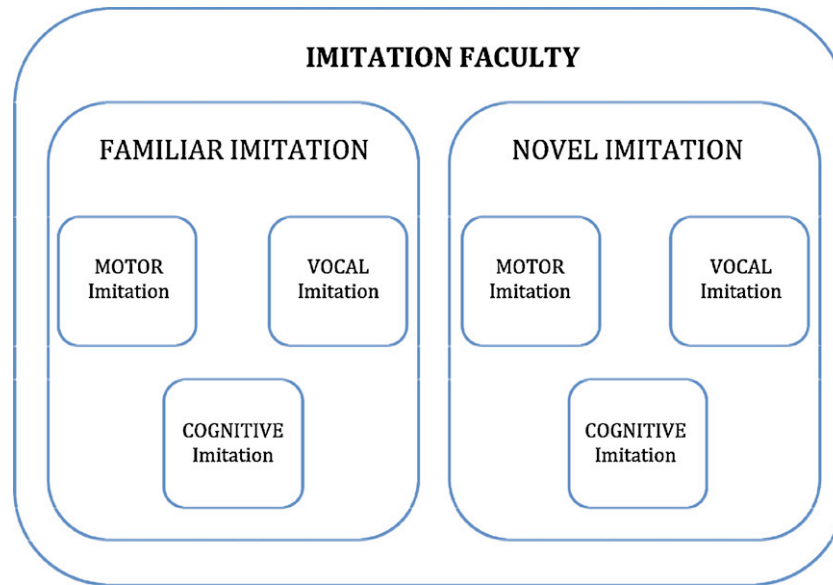
Fig. 1. Diagram of the multiple imitation mechanisms (MIM) hypothesis. The MIM Hypothesis posits that the imitation faculty consists of multiple, dissociable imitation systems that specialize in copying specific types of information. Some of these systems process broad content types (e.g., familiar vs. novel imitation), while other systems process narrower content types (e.g., motor, vocal, and cognitive imitation). But as can be seen in Fig. 2, each of these more specialized imitation systems are likely to consist of more narrow and more specialized subsystems.

it leaves unanswered a number of questions: Are the mechanisms involved in copying abstract cognitive rules (such as serial order) the same mechanisms involved in copying specific motor actions? Does it matter if the actions are 'transparent' (such as when one reaches for something) as opposed to actions that are opaque (such as oral-facial imitation)?

Some of these important distinctions are captured by another influential model proposed by Piaget (1929, 1951). Piaget's model is based on observations of his own children's development. In particular, Piaget believed (as do all contemporary developmental psychologists) that imitation development was contingent upon broader changes in cognitive development. Nonetheless, Piaget believed that imitation developed in stages and, in this sense, imitation was not a unitary skill but rather a whole suit of skills that involved copying different types of responses at greater levels of abstraction. Most fundamentally, Piaget (1929, 1951) distinguished between simple and complex imitation. Specifically, between the copying of single, familiar actions as opposed to the copying of multiple, serial actions or unique, novel actions. He also made an important distinction between the copying of transparent responses, such as manual actions on objects, and the copying of opaque responses, such as oral-facial imitation (involving a body part that one does not have direct visual access to).

Here I will outline a novel imitation model, the multiple imitation mechanisms (MIM) hypothesis (Fig. 1), that combines some of the elements of the Carpenter and Call (2002) model among other popular conceptualizations of social learning mechanisms (e.g., Shettleworth, 1998; Tomasello and Call, 1997; Whiten et al., 2004a,b, 2009; Zentall, 2006), including those of Piaget (1951). The MIM model shares the desire of comparative psychologists to identify mechanisms of social learning. However, the MIM model seeks to link these mechanisms to multiple sources of evidence including neurobiological and developmental data in addition to comparative evidence, to better define the cognitive and neural architecture of the imitation faculty. The MIM model also rejects the notion that the imitation faculty is an all-purpose, domain-general psychological faculty (Buller, 2006); a type of 'general intelligence' that is the product of selection for 'social intelligence' (Boyd and Silk, 2006; Byrne, 2005; Byrne and Whiten, 1988; Jolly, 1966; Whiten and Byrne, 1997). To the contrary, the MIM hypothesis proposes

that imitation, like the memory and language faculties, is a mosaic cognitive faculty whose evolution was not the result of a general selective force favoring social or technical intelligence, but rather it's evolution is the product of a confluence of factors some that are 'social' others that are 'ecological' and still others that are 'technical' (Parker and Gibson, 1977; Parker and McKinney, 1999). These different pressures from these different domains produced different imitation mechanisms, specialized in the representation of specific classes of stimuli (novel, familiar, motor, vocal, social, cognitive) for the express purpose of reproducing them (i.e., copying).

2. The multiple imitation mechanisms (MIM) hypothesis

2.1. The many faces of imitation

To imitate is to copy. The reason being that you cannot imitate something without also copying something. As such, the MIM hypothesis views imitation as consisting of various imitation mechanisms or imitation systems each involved in copying specific types of information. Together, these various systems comprise the imitation faculty. This framework is not unlike the dominant framework in memory which contrasts episodic with semantic as well as between short/working- and long-term memory (all quite different types of memory mechanisms). But despite these differences, they are memory systems, nonetheless, as they are all involved in encoding and retrieving certain information types that require special forms of processing. In this model, the imitation faculty is conceptualized as consisting of various subsystems, each specializing in the copying of a specific class of stimuli. These subsystems are in some cases independent of other subsystems (as may be the case with cognitive and motor-spatial imitation). But in other instances subsystems are likely to be inter-dependent, taking as input the output of other subsystems. For example, the observational learning system likely provides necessary input to the novel imitation subsystems.

This view of imitation fundamentally differs from the widely held domain-and content-general view of imitation (e.g., Heyes, 2002, 2004). In fact, most view the imitation faculty as a domain-

and content-general mechanism that operates across different problem domains and content types, allowing individuals to learn everything from motor rules such as how to use chop sticks, to vocal rules such as *aguacate* ('avocado' in Spanish), to abstract rules such as how to cook your favorite pasta dish. Given what is known about the imitation skills of human children and other primates, it appears that the environment of early hominids favored individuals who were flexible imitators, capable of copying a wide range of behaviors and responses: from using chop sticks, among other tools, to saying *aguacate*, among other novel sounds, to cooking pasta among other procedural rules. However, the representation of auditory stimuli (such as *aguacate*) for the purposes of reproducing that sound must be fundamentally different than the representation of a motor action (such as using chop sticks) for the purposes of copying that action. A general-purpose mechanism capable of performing these different tasks seems unlikely if not improbable. What is more likely is that selection sifted through individuals with varying imitation skills and a unique cognitive-neural imitation profile capable of identifying, representing and copying these different types of information. This process would have produced distinct imitation skills mediated by specific imitation mechanisms dedicated to representing and copying specific types of stimuli. From this it follows that humans are good imitators relative to other primates not because we have an imitation mechanism that primates lack but because our species has evolved a whole suite of distinct imitation mechanisms or 'imitation instincts' that together result in an impressive ability to copy all sorts of responses in a flexible and adaptive fashion.

Specifically, the MIM Hypothesis proposes that the imitation faculty is similar to other vertical cognitive faculties (Fodor, 1983), such as language and memory, that are modular, specialized and consist of multiple components with discrete functions (cf. Fig. 1). However, it's unlikely that the imitation faculty is as encapsulated as Fodor (1983) proposed for visual systems, for example (cf. Marr, 1982). It's more likely that the imitation faculty consists of rather open or loosely encapsulated modules (see Carruthers, 2006 for a description of these types of modules). In this conceptualization, the imitation faculty represents a specialized psychological system with input from a number of domain-general or 'central' systems like attention and reasoning as well as domain-specific 'core knowledge' that include 'theory of mind,' 'naïve physics' and 'naïve biology' (Carey, 2008; Spelke, 2000). Through this kind of domain-specificity, the imitation faculty can copy responses across different domains in a flexible and adaptive fashion (Fig. 2).

Like other faculties, the imitation faculty can be divided by its various functions. These functions are best captured by super-ordinate and subordinate imitation mechanisms associated with the processing of specific types of stimuli. The super-ordinate imitation mechanisms include, (a) 'familiar imitation,' or the copying of familiar rules or responses and (b) 'novel imitation,' or the copying of novel rules or responses; often referred to as 'imitation learning,' which is distinguished from 'familiar imitation' in that it requires observational learning. That is, the ability to learn through vicarious (rather than direct) reinforcement (Bandura, 1977). Various researchers have made similar class distinctions, recognizing that different mechanisms likely mediate the learning and copying of a novel behavior(s) and the copying of behaviors that already exist in an individual's repertoire (Byrne and Russon, 1998; Heyes, 2001; Visalberghi and Fragaszy, 2002). However, these investigators have tended to argue that these skills are not related and consequently have tended to give these skills different names. The likely reason being that many of these researchers believe that imitation is a single unitary cognitive process that animals either have or lack entirely; a notion that in psychology dates back to Thorndike (1898). In the MIM framework, familiar and novel imitation mechanisms are brought together as part of the same cognitive faculty that mediates the ability to flexibly copy rules or responses across contexts. Moreover, subsumed within those two broad functional concepts are subordinate mechanisms of imitation that specify the type of stimuli that is reproduced by either novel or familiar imitation (cf. Fig. 1).

As has been noted, all the proposed imitation mechanisms are characterized by flexibility *and* specificity. The flexibility requirement means that the behavioral rule that is copied is deliberate or replicable. That is, it can be elicited in multiple contexts on multiple occasions; not the result of happenstance or trial-and-error learning or the product of narrow contextual cues. The specificity requirement emphasizes that individuals must copy a specific 'rule' or response. The term 'rule' is broadly defined as a response involving more than two steps (e.g., with a distinct 'beginning-middle-end' structure) that are hierarchically organized and structured to achieve a matching response. The requirement that any type of imitation be rule-governed and flexible is necessary in order to differentiate imitation from either perceptual or motivational mechanisms that in association with rapid trial-and-error learning may represent an ancestral learning mechanism that predates (and may, perhaps, co-exist) with the imitation faculty, providing critical input to the mechanism mediating familiar imitation, for example. The same is true of narrow species-specific skills such as copying mate preferences that while impressive, learning does not extend beyond a very narrow context (i.e., mating) and is dependent on specific stimuli (i.e., females) (Bshary and Grutter, 2006; Paz-y-Miño et al., 2004). Nevertheless, such studies provide important clues into the origins of the imitation faculty; highlighting for instance, how selection for multiple content-specific observational learning skills could be aggregated by natural selection resulting in a more robust domain-specific imitation faculty like the one described here.

2.2. Super-ordinate mechanisms of imitation: Novel imitation

Part of the confusion in the imitation literature is that 'imitation' has been largely conceptualized as 'novel imitation' or the imitation of novel behaviors. For example, in 1898, Thorndike defined imitation as "learning to do an act from seeing it done" (p. 79). Nearly a half-century later, Thorpe defined imitation more narrowly and in purely behavioral terms: "copying a novel or otherwise improbable act" (p. 122). These definitions are often viewed as synonymous, but they are quite different. One core difference between these two definitions is the requirement that individuals *copy* another's behavior. Copying is, arguably, the essence of imitation. After all, what is imitation if it is not copying something? Yet, Thorndike's definition does not mention or imply copying but rather observational learning. The distinction between observational learning and imitation is critical. It is possible to learn something from another, yet not overtly express the acquired knowledge; for example, learning what *not* to do. In such instances, one can learn from a model without imitating the model. Thorpe's definition, unlike Thorndike's, stresses both (observational) learning and copying. Learning is implied in the criteria that what is copied is 'novel' rather than something that already exists in the observer's behavioral or cognitive repertoire. Despite a number of qualifications and revisions (e.g., Galef, 1988; Tomasello and Call, 1997; Whiten and Ham, 1992), Thorndike (1898, 1911) and Thorpe's (1956) definition of imitation remain influential because of their simplicity and the ease with which they lend themselves to experimentation. Nevertheless, these definitions, which conceptualize imitation as the copying of specific and novel motor responses, have largely ignored an equally important function of the imitation faculty, familiar imitation.
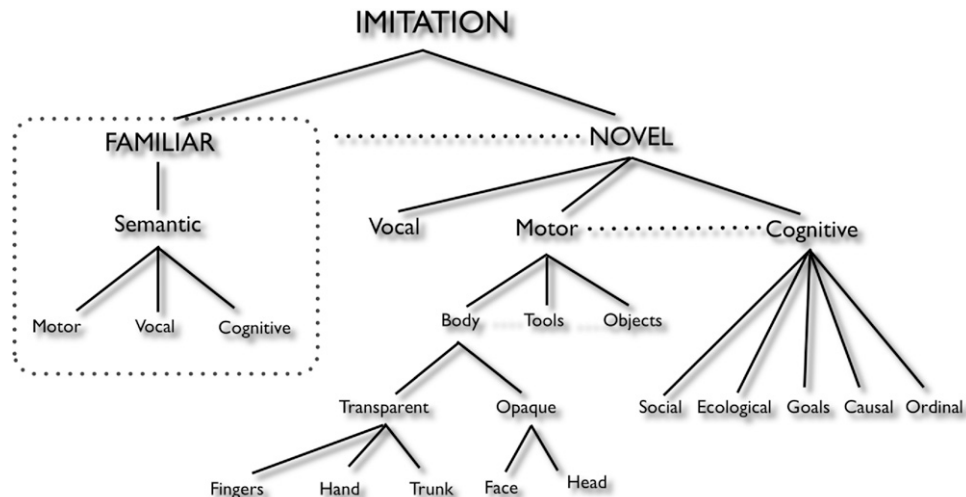
Fig. 2. Multiple imitation systems. There are likely to be multiple imitation subsystems that process different content types within domains. Here is a partial representation of what are likely to be some of the most likely subsystems that make up the human imitation faculty. These subsystems specialize in the copying of specific rules and responses. Dashed lines correspond to hypothesized connections between larger systems (e.g., novel and motor and motor and cognitive). These systems are likely to take as input the output of other imitation systems.

2.3. Super-ordinate mechanisms of imitation: Familiar imitation

Familiar imitation involves the ability to flexibly and adaptively copy common or recognizable rules/responses that exist within an individual's behavioral repertoire. In the motor domain, everyday actions fall into two distinct and conceptually significant categories: transparent versus opaque. Transparent responses are those responses that are immediately available to the senses such as transitive actions that involve reaching for and interacting with objects and, as a result, may be executed via a visual–visual match (i.e., my hand on an object looks like your hand on an object). However, opaque responses cannot be executed in the same fashion, as they are not available to the senses in the same way as transparent actions. Consider the act of imitating someone scratching their head. What you perceive when you see someone scratch their head is very different from what you perceive when you scratch your own head. The phenomenological experiences are very different. This problem of translating a visual experience into a corresponding proprioceptive response has been termed the "correspondence problem" (Dautenhahn and Nehaniv, 2002).

While to some, the distinction between 'novel' and 'familiar' imitation may be obvious, there is significant debate as to what should count as a 'novel' response. Does 'novel' imply an entirely new behavior? By the most strict of standards this would exclude all species-typical behaviors; a constraint that significantly limits research questions. One way around such a constraint is to require animals to execute a series of familiar behaviors in arrangements that are never (or rarely) observed. This technique—of stringing familiar actions in an arbitrary sequence—has been employed by a number of animal researchers (apes: Whiten, 1998; birds: Nguyen et al., 2005; monkeys: Caldwell and Whiten, 2002) and represents one way of operationalizing 'novelty' in imitation research. Another technique has been to use a tool in novel problem-solving tasks (e.g., Visalberghi and Fragaszy, 1990; Visalberghi and Fragaszy, 1995; Visalberghi and Trinca, 1989; Horner and Whiten, 2007a,b). Perhaps these studies, more than any other, represent the most strict standards of novelty, as subjects must often learn how to handle the tool and then learn how to use the tool *in relation to* another object. However, this poses a unique problem when comparing human and non-human ape imitation studies that involve tool-use because humans may have unique causal conceptual mechanisms and by extension, species-specific skills pertaining to objects in general and tools in particular that non-human primates may lack (Johnson-Frey, 2003; Povinelli, 2000). But there are other ways to operationalize 'novelty' without using tools or specific motor responses. One such paradigm was developed by Subiaul et al. (2004, 2007). Subiaul and colleagues tested novel cognitive imitation in monkeys as well as children, using the simultaneous chaining paradigm (Terrace, 2005). In this paradigm participants are given the opportunity to copy novel serial rules independently of copying novel motor actions. The cognitive imitation paradigm requires that participants learn something new in order to be reinforced (i.e., a novel ordinal rule of the form: A → B → C), and exclude the possibility that subjects already know how to execute the target response because the picture items are new to the participant and are arbitrarily related to one another. At the same time, this paradigm controls for the possibility that the ability to execute the motor response interferes with the expression of knowledge gained during observation.

Others have tried to operationalize 'novelty' using single and familiar actions on objects (e.g., apes: Hopper et al., 2007; monkeys: Bugnyar and Huber, 1997; Voelkl and Huber, 2000, 2007; Children: Meltzoff, 1995). In many instances, a baseline measure if used, where individuals freely interact with an object(s) prior to a demonstration that involves a specific interaction with the object(s). However, familiarity is a continuous variable where some actions are more familiar than others. When presented with an object or tool, individuals are most likely to exhibit the actions that are the most typical or common. It is unlikely that all the possible actions known to the participant will be applied to the given object within a narrow window of time in a laboratory setting. Consider all the different ways to interact with a ball: we can kick it, bounce it, throw it, roll it, squeeze it, rub it, sit on it, etc. Consider the study by Meltzoff (1995). Sure, turning on a light with one's head is unusual, but is it novel? Hardly. We use our heads to do all sorts of instrumental actions, particularly when our hands are occupied. Young children in the confines of their cribs and while crawling use their heads more often than most. So while using one's head to do an instrumental act is by anyone's definition unusual, it's not novel in a strict empirical sense as (a) this is an action that the individual has done in other contexts in the past and (b) clearly this action schema exists in the individual's behavioral repertoire.

Consider the comparative study with monkeys by Voelkl and Huber (2000). In these studies, the rationale is that while a behavior such as mouthing is species-typical, mouthing an object in order to open it is novel. The problem is that animals often explore objects using their mouths and certainly use their mouths on objects associated with food. So, while a particular behavior directed toward a specific object may be unique, the actual behavior is not. In this regard, it's more likely that familiar imitation of the familiar action (e.g., mouthing) rather than novel imitation is the primary mechanism underlying the behavioral response in single action paradigms. Such paradigms also make it difficult to distinguish between various mechanisms of the imitation faculty and the products of perceptual and motivational mechanisms in which, for example, an animal's interaction with an object may direct an observer's attention to that object (stimulus enhancement) or a part of that object (local enhancement), motivating the observer to interact with it (social enhancement). In such instances, these two individual's responses may be very similar, yet the similarities are likely to be the products of stimulus and social enhancement as well as rapid trial-and-error learning, rather than by any imitation mechanism.

2.4. Subordinate mechanisms of imitation: cognitive, motor and vocal imitation

As can be seen in Fig. 2, in addition to distinguishing between familiar and novel imitation, the MIM hypothesis also distinguishes between various subordinate imitation mechanisms that form part of the imitation faculty. These mechanisms involve copying different classes of stimuli: auditory, motor, and cognitive. The reproduction of these different types of stimuli compromise three broad classes of imitation: vocal imitation (the imitation of vocal/auditory responses), motor imitation (the imitation of motor actions), and cognitive imitation (the imitation of cognitive rules, including rules governing serial order, social conventions and spatial relationships, for example). The distinction between super-ordinate mechanisms of imitation (e.g., novel vs. familiar) and subordinate mechanisms of imitation (e.g., vocal, motor and cognitive) are important because it allows researchers to specify what type of imitation they are capable of. For example, an individual may be able to reproduce *familiar* vocal rules (e.g., words), but may not be able to copy *novel* vocal rules (e.g., novel words). Moreover, individuals may be able to copy novel *cognitive* rules (e.g., serial order), but not novel *motor* rules (e.g., specific action sequences). Some of these dissociations appear to be true in monkeys for instance, which seem unable to copy novel motor rules, but can copy novel cognitive rules (Subiaul et al., 2004, 2007). Interestingly, similar dissociations exist within humans. For example, children with autism, are unable to copy novel motor rules, but can copy familiar motor rules (Williams et al., 2004). There's also a dissociation in novel imitation performance among individuals with autism that parallels the dissociation in monkeys; in particular a dissociation between novel motor and novel cognitive imitation (Subiaul et al., 2007).

The MIM framework calls to question familiar terms that have become an integral part of the imitation literature such as emulation—where individuals copy the outcomes or 'affordances' of actions—or goal emulation—where individuals copy the 'intended' action of others using idiosyncratic means. Specifically, the MIM model questions the logic that terms such as emulation are alternatives to imitation or more precisely, that 'emulation' is a mechanism that exists outside the imitation faculty as described here. Rather, the MIM model advances the contrarian's view that terms such as mimicry, affordance learning or emulation and goal emulation describe the imitation of different types of rules or responses; specifically, copying rules—novel or familiar—about specific actions or responses, environmental affordances or goals, respectively.

3. The neurobiological evidence

3.1. Neurobiology of familiar and novel imitation

Recently, a number of advances have supported the MIM Hypothesis. A functional dissociation between novel and familiar motor imitation is supported by neuropsychological and neurophysiological research. In a series of studies, Rumiati and Tessari (2002) and Rumiati and Bekkering (2003) presented two groups of subjects with two different tasks: one involved copying familiar "meaningful" actions; the other involved copying novel "meaningless" actions. Meaningful (i.e., familiar) actions consisted of common actions such as brushing one's teeth. Meaningless actions (i.e., novel, arbitrary actions) consisted of performing common actions in an arbitrary fashion, for example, a brushing action performed with the right arm extended outwards and the hand held upright. Predictably, subjects copied "meaningful" actions with fewer errors than meaningless actions. Rumiati and Tessari interpreted these results to mean that different systems mediate the imitation of "meaningful" and "meaningless" actions. In their model, the perception of familiar actions are recalled from long-term memory then moved into working-short-term memory in order to generate a matching motor output. The perception of novel "meaningless" actions, however, is processed in working-short-term memory as there's no memory trace to recall from semantic long-term memory.

Neuroimaging studies conducted by the authors have provided additional support for a dual-processing route. Rumiati et al. (2005), reported that the left inferior temporal gyrus was associated with a significant increase in blood flow when subjects copied meaningful actions. Whereas, greater blood flow to the parieto-occipital junction was associated with copying meaningless actions. When comparing neural activation during the imitation of familiar relative to unfamiliar actions there were differential increases in neural activity in the left inferior temporal gyrus, the left parahippocampal gyrus, and the left angular gyrus, structures associated with long-term memory processes. Whereas, the superior parietal cortex (bilaterally), the right parieto-occipital junction, the right occipital–temporal junction (MT, V5), and the left superior temporal gyrus were differentially active when subjects copied novel actions relative to familiar actions. The primary sensorimotor cortex, the supplementary motor area, and the ventral premotor cortex showed increased neural activity when subjects copied both types of actions (familiar and novel).

It's important to point out, however, that novel actions could be perceived as meaningful, yet, not exist in the observer's behavioral reportoire. For example, we may observe two American Sign Language (ASL) speakers communicate with one another. Though the actions are novel to us because we are unfamiliar with ASL, the signs are, nevertheless, recognized as being "meaningful." That is, they are recognized by naive observers as having a communicative function. Consequently, individuals may imitate meaningful novel actions differently from meaningless novel actions. Future experiments may wish to more directly assess the role of "meaning" in imitation independently of the familiarity of actions.

There are other neurophysiological studies that are consistent with the MIM Hypothesis (Buccino et al., 2001; Cochin et al., 1999; Fadiga et al., 1995; Decety and Chaminade, 2005; Heyes, 2002, 2004; Stevens et al., 2000). For instance, various neurophysiological studies using transcranial magnetic stimulation (TMS), magnetoencephoalography (MEG), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI) have found that when subjects observe an individual executing an action using a
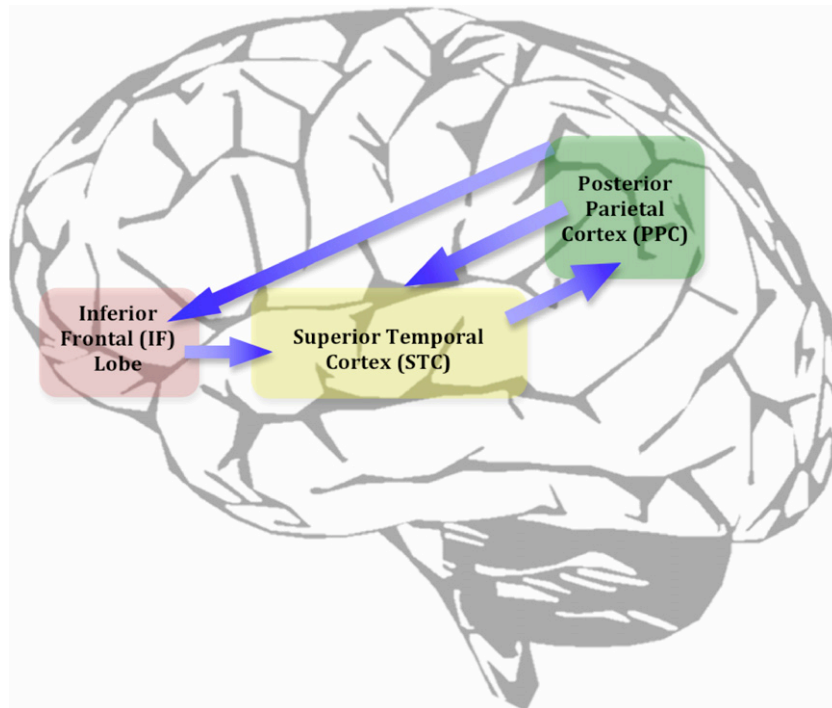
Fig. 3. Familiar motor imitation circuit. According to Carr et al. (2003) information flows as follows: (1) the STC codes early visual descriptions of actions and projects these representations to the PPC mirror neurons; (2) the PPC integrates representations of kinesthetic aspects of actions and projects this information to IF mirror neurons; (3) IF codes the outcome or the 'goal' of the target action; (4) IF and PPC send efferent copies of the action plan back to the STC, creating a matching 'resonance' mechanism between visual and motor representations of the same action event; (5) motor execution of imitation is initiated.

specific muscle group, corresponding areas of the observer's motor strip is activated, as if the observer was executing the action themselves rather than passively observing someone else performing the same action (Buccino et al., 2001; Cochin et al., 1999; Fadiga et al., 1995). Consequently, when one sees a conspecific execute actions that are familiar and form a part of one's own motor repertoire, neural regions such as the supplementary motor area (SMA), the premotor cortex, and the superior and inferior parietal cortices—the action preparation system—are activated. This "motor resonance" phenomenon is not triggered by novel actions because they are not present in the motor repertoire of an observer and are yet to be learned. When individuals observe novel actions they have no existing representations of the motor component of these actions. At best, they can call upon related or similar rules or responses. As implicated by the dual-route model (Rumiati and Tessari, 2002; Rumiati and Bekkering, 2003; Tessari and Rumiati, 2004), the match between what is seen and what is ultimately executed must be done online (in working memory) with little or no help from existing cognitive representations of the target action.

The apparent motion paradigm (Shiffrar and Freyd, 1990) has further highlighted the functional and structural differences associated with copying novel as opposed to familiar actions. Using PET technology, Stevens et al. (2000) presented participants with a human model engaged in possible (i.e., familiar) and impossible (i.e., novel) biomechanical paths of apparent motion. When the subjects perceived 'possible' paths of human movement, the left primary motor cortex and the parietal lobule in both hemispheres were found to be selectively activated. These areas were not activated when participants observed impossible biomechanical movement paths.

The results reported by Rumiati and Tessari as well as those by Shiffrar and Freyd make clear that different neural mechanisms mediate the imitation of novel as opposed to familiar responses. They further demonstrate that the distinction between familiar and novel imitation may best be characterized as a difference between

recall and learning. In the case of familiar imitation, individuals recollect past (learned) experiences. Whereas in the case of novel imitation, individuals are encoding novel experiences and knowledge through observation or vicarious learning. In any event, these distinct imitation systems may feed into a more general motor imitation circuit such as that proposed by Carr et al. (2003) and summarized in Fig. 3.

Additionally, neurobiological studies have demonstrated that observational learning—the core feature of novel imitation—has independent neurobiological circuits. Again, it must be stressed that in the MIM framework, observational learning is not synonymous with imitation, particularly, familiar imitation. There are two main differences between observational learning and novel imitation: First, novel imitation requires observational learning, but familiar imitation does not. Second, novel imitation requires observational learning in addition to copying. Observation learning requires only learning, not copying. The rationale here is that one may learn many things from observation (dispositional traits, the worth of things, what *not* to do or how *not* to behave) without copying.

A number of lesion and single-cell recording studies suggest that observational learning is largely mediated by the right cerebellum. For example, Petrosini and colleagues (1999, 2000, 2007) demonstrated that rats tested in a Morris water maze task learn to locate a hidden platform in a pool one of two ways: by individual, trial-and-error learning or by observing an experienced conspecific. To explore the cerebellum's role in this skill, Petrosini and colleagues removed the right hemicerebellum of naïve rats either after they had been given the opportunity to observe expert rats navigate through the pool and settle on a hidden platform (post-observation surgery treatment) or ablated the same part of the cerebellum before naïve subjects had been given the opportunity to observe the expert rat find the hidden platform (pre-observation surgery treatment). Results revealed that rats that received the post-observation surgery treatment learned how to find the hidden
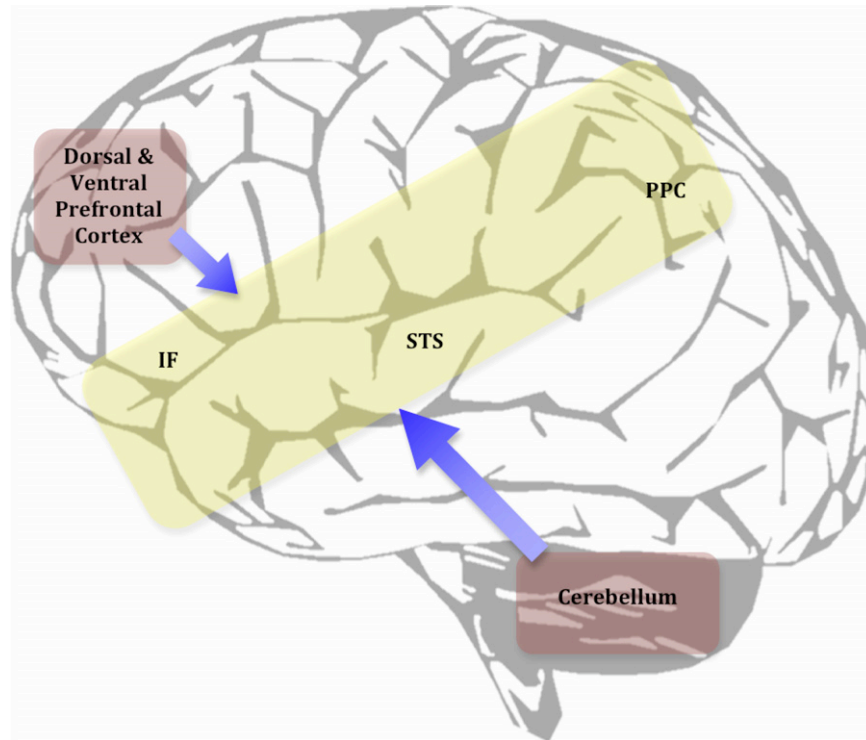
Fig. 4. Novel motor imitation circuit. A number of authors have pointed to the left posterior cerebellum as well as the dorsal and ventral prefrontal cortex as critical for (i) the intention to imitate (e.g., Chaminade et al., 2002) and (ii) observational learning (e.g., Petrosini, 2007). Leslie et al. (2004) have suggested that these cerebellar and frontal circuits that appear critical for novel motor imitation, likely interact with circuits that appear responsible for familiar motor imitation (cf. Fig. 3).

platform significantly faster than they would by trial-and-error. However, rats in the pre-observation surgery treatment failed to learn where the hidden platform was located. As a result, these rats performed randomly, eventually learning where the platform was located by trial-and-error learning.

Though these experiments do not exclude learning by perceptual/motivational mechanisms such as local enhancement, the results reported by Petrosini and colleagues (1999, 2000, 2007) have a number of significant implications. First, the removal of the right hemicerebellum in rats does not extinguish spatial or navigational abilities because all subjects are capable of learning where the hidden platform is located. Moreover, the ablation of this part of the cerebellum did not affect motor movements and/or coordination. Second, the difference between the performance of individuals in the pre- and post-observation surgery treatment demonstrates that the right cerebellum plays a significant role in learning. Third, the cerebellum's potential role in observational learning strongly suggests that a distinct circuit (independent of neural circuits mediating familiar imitation) is at work in social learning tasks in general and novel imitation in particular. This last point is corroborated by at least one other study with human subjects. Grezes et al. (1998) showed that the left posterior cerebellum is uniquely active when subjects have the intent to imitate a novel response. Results demonstrated that the cerebellum becomes active when subjects are confronted with new rules that must be learned by observation (rather than by trial-and-error). In humans, as in rats, this cerebellar circuit (Grezes et al., 1998; Petrosini et al., 2000; Petrosini, 2007) appears to be independent of a separate frontal (e.g., BA 6, 9, 10, 46) and parietal (e.g., BA 40 and 7) circuit that have been linked specifically to familiar imitation (Carr et al., 2003; Lingnau et al., 2009; Rizzolatti et al., 2002). Nevertheless, while these cerebellar circuits appear to mediate observational learning, Leslie et al. (2004), suggest that information from the left posterior cerebellum as well as the dorsolateral and ventral prefrontal cortex interact with the circuit (i.e., inferior frontal, STS and posterior parietal) associated with

familiar motor imitation (Carr et al., 2003) in order to achieve novel motor imitation, for example (cf. Fig. 4).

3.2. Neurobiology of cognitive and motor imitation

Theoretically, the brain may imitate in one of two ways: either via a single imitation network involving hippocampal networks for familiar imitation (e.g., Rumiati et al., 2005) and a cortical-striatal network for novel imitation or through distinct networks corresponding to the imitation of different types of stimuli such as motor, vocal, cognitive. At present the evidence is mixed. At least one imaging study on the "song system of the human brain" (Brown et al., 2004) suggests that familiar motor imitation and certain aspects of novel vocal imitation may have overlapping neural structures or be mediated by the same neural systems. While certain aspects of the human song system were unique, such as activation in the superior part of the temporal pole (BA 38), others either overlap or are adjacent to the 'mirror neuron system' in the inferior frontal operculum (BA 44) that the work of Lingnau et al. (2009) and others have shown to play a role in familiar motor imitation (cf. Fig. 3). However, the overlap in the present study may have been due to subvocal rehearsal or the recall of lyrics from songs with a similar melody. Importantly, Brown et al. (2004) report that this system is only active when subjects are actively matching the pitch and rhythm of novel sequences but not when participants are recalling familiar melodies. Another neuroimaging study supports a dissociation between motor and cognitive imitation systems. Chaminade et al. (2002) presented subjects with a model executing one of three different aspects of an event: (a) the complete action arc from start to finish, (b) only the means used to achieve the action, and (c) only the result of the action. Subjects made one of three different responses: (a) passive observation, (b) imitated what was observed, or (c) acted freely. Because the task involved the intentional copying of actions, neural regions associated with higher order motor representations and sensorimotor transformations in addition to the

posterior Superior Temporal Sulcus (STS) were active across conditions. However, different neural regions were active when subjects observed and copied an entire event as opposed to when subjects observed and copied only the means or only the goals of that same event. Specifically, there was significant activation in the cerebellum (bilaterally) and the dorsolateral prefrontal cortex (DLPFC) when subjects copied both the means and the goals of an action. Yet, there was hypo- or no activation in these same regions when subjects copied the entire event. Moreover, despite the fact that some of the same regions were active when copying goals and means, regions of activation within DLPFC were not entirely overlapping. Furthermore, the medial prefrontal cortex was active only when subjects copied the means used to execute the action, whereas the left premotor cortex was active only when subjects copied the goals of the action. The fact that premotor cortex was differentially active in the course of copying goals versus means is of some significance as premotor cortex is associated with "mirror properties" in monkeys and humans (Buccino et al., 2001) and associated with the preparation and execution of goal-directed actions. Chaminade et al. (2002) argue that premotor cortex is only active when subjects copy goals because this is the only condition in which the means of the actions must be inferred from the observation event.

Taken together, these results suggest the possibility for imitation-specific circuits that correspond to different content-types. However, it cannot be overlooked that the studies by Chaminade et al. (2002) investigated goals, means, and actions in the context of a motor imitation task rather than a task that involved copying non-motor or cognitive rules (independently of the execution of specific motor actions) as was done by Subiaul et al. (2004, 2007), for example. Moreover, this study did not distinguish between copying familiar (familiar imitation) versus unfamiliar (novel imitation) goals and means, as was done by Tessari and Rumiati (2004). So, on the one hand, the mechanism that mediates the copying of novel goals may differ from the mechanism that mediates the copying of familiar goals. On the other hand, the mechanism that mediate the copying of motor goals may differ from the mechanism that mediates the copying of serial or temporal goals.

4. The comparative evidence

4.1. Do primates ape?

Certainly, social learning is common in the animal kingdom (Zentall, 2006) and sophisticated local traditions exist in apes (Whiten et al., 1999; Van Schaik et al., 2003a,b) and to a lesser degree in monkeys (Panger et al., 2002; Perry et al., 2003), which has been taken as evidence of imitation learning (see Subiaul, 2007 for a review). But, there has been a long-lasting controversy over whether or not humans are unique in the ability to learn from others. In fact, Aristotle argued in the *Poetics* that humans are "the most imitative creatures in the world and learn first by imitation." Yet despite this long-held assumption, only twelve studies have directly compared imitation learning (i.e., novel imitation) in human and non-human [adult] apes using analogous procedures (Call et al., 2005; Call and Tomasello, 1995; Herrmann et al., 2007; Horner and Whiten, 2005, 2007a,b; Horner et al., 2006; Horowitz, 2003; Nagell et al., 1993; Tomasello et al., 1993a,b; Whiten et al., 1996). Only one study has compared novel imitation in monkeys and children (Subiaul et al., 2007).

Six studies have reported that on an operational task, where a tool or object had to be manipulated in a certain manner to achieve a specific result (or reward), humans reproduce the demonstrator's actions with greater fidelity (i.e., imitation) than did mother-reared apes (Call et al., 2005; Herrmann et al., 2007; Horner and Whiten,

2007a,b; Call and Tomasello, 1995; Nagell et al., 1993; Tomasello et al., 1993a,b). The other studies reported both similarities and differences between humans and peer-reared apes when executing specific actions on an object following a demonstration (Horner and Whiten, 2005; Horner et al., 2006; Whiten et al., 1996). And two other studies, one that involved an operational, tool task (Horowitz, 2003) and another that used a cognitive imitation paradigm (Subiaul et al., 2007), found no differences between the performance of human participants and non-human primates. Thus, when copying novel motor responses, there appears to be significant differences as well as important similarities between humans and other primates.

Given these results, it is obvious that there's no simple answer to the question, 'Do [primates], ape?' How might one explain these seemingly conflicting reports of similarities and differences, particularly if imitation is viewed as one unitary faculty that animals either have or lack entirely? If the MIM Hypothesis is correct, then these differences in performance stem from the fact that the studies described above are measuring *different* imitation mechanisms, rather than one mechanism. When viewed this way it appears that human and non-human primates share some imitation mechanisms, as expected by common descent, but do not share all. Using the MIM framework outlined above, studies such as, Horner and Whiten (2005) and Horner et al. (2006) are likely to be tasks of familiar motor imitation, whereas studies such as Horner and Whiten, 2007a,b are tasks of novel motor imitation. For example, Horner et al. (2006) used a 'foraging' task that asked the chimpanzee to direct a behavior (i.e., poking an apparatus with a stick) to a single location in order to retrieve a reward. These actions are both familiar and species-typical. For these reasons, these tasks are considered familiar, rather than, novel motor imitation tasks. However, in another task, Horner and Whiten, 2007a,b had chimpanzees use some of these same actions (poking with a stick) in a trap-tube paradigm, where chimpanzees have to insert a stick into a tube with a reward and a trap in the middle. The task, then, is to insert the stick in the tube *and* push the reward *away* from the trap. There are at least three different rules that must be copied in this task some of which are familiar, others are novel: [rule 1 (familiar): *insert the stick in the tube*], [rule 2 (familiar): *push the reward with the stick*], [rule 3 (novel): *push reward away from trap*]. The MIM model envisions three distinct motor imitation systems mediating the copying of each of these rules. It also envisions the activation of distinct cognitive imitation systems that mediate the copying of the ordinal structure of the task, for example, copying the above mentioned motor rules in the following order: Rule 1 → Rule 2 → Rule 3. When viewed this way, a relatively simple task becomes a complex negotiation between imitation systems and the need to activate and coordinate one imitation mechanism may make the difference between success and failure.

Without question, novel motor imitation tasks are harder than familiar motor imitation tasks; the reason for this being that novel motor imitation tasks require subjects to engage many more imitation systems as well as non-imitation (central) systems in a coordinated fashion. To succeed, the participant must first attend to the relevant information (hand or body part, tool or object), activating specific motor imitation systems, create a *new* action or goal representation for the purposes of reproducing these representations, activating specific cognitive imitation systems and then match these representations (motor and cognitive), generating a unique action plan. The same is not true for familiar imitation tasks because the observation of a familiar action likely primes that same action in memory (i.e., recognition memory). In this case, the construction of a novel action plan is not necessary as it is recalled from memory.

There are likely to be other differences that contribute to differences in motor imitation performance among apes. Perhaps the

most significant has to do with tool-knowledge and tool-use. Most studies that require animals to use tools in ways that they do not do naturally in the wild tend to find differences between human and non-human subjects (e.g., Herrmann et al., 2007; Horner and Whiten, 2007a,b). When the imitation task involves using tools in ways that are more 'naturalistic' (i.e., behaviors that typically appear in the wild such as probing with a stick or pushing objects out of the way), more similarities are reported between humans and other apes (e.g., Horner et al., 2006; Hopper et al., 2007). However, there are some studies where apes are required to execute 'familiar' actions—such as pulling or pushing—on unfamiliar objects or in novel experimental circumstances (Call and Tomasello, 1995; Herrmann et al., 2007). These studies, too, tend to report more differences than similarities between humans and other apes.

Johnson-Frey (2003, 2004) and Povinelli (2000) have suggested that there may be in some cases subtle and in other cases dramatic differences between humans and other animal's orientation to objects with tool properties. For instances, some of the differences in imitation performance may be due to differences in the "Grasp" and "Manipulation" motor system that are mediated, in part, by circuits in the parietal and frontal lobe. While Johnson-Frey suggests that differences in these two motor systems may be negligible, how these systems interact with conceptual systems mediating causal action likely produces significant species differences, as borne out by a number of comparative studies on chimpanzee tool-use (e.g., Povinelli, 2000). Novel motor imitation likely depends on input from these various systems, without which it cannot operate. The same is likely to be less true for familiar motor imitation, as experience allows individuals to recall existing motor representations and rehearsed motor action plans.

4.2. Evidence of multiple imitation mechanisms in non-human primates

Chimpanzees differentially imitate novel vs. familiar actions (Myowa-Yamakoshi and Matsuzawa, 1999). In one study, Myowa-Yamakoshi and colleagues presented chimpanzees with a number of object-based actions that they characterized as general actions (familiar actions on objects that were commonly observed) and non-general actions (relatively novel actions on objects that were not commonly observed). This corresponds roughly to the proposed distinction of familiar vs. novel imitation. They applied this scheme to different actions on objects that ranged from copying single but specific actions on objects such as banging the bottom of a bowl, to copying actions that involved directing objects to specific body parts such as putting the bowl on the head, to copying object–object interactions such as putting a ball in a bowl. Results revealed that performance was best for familiar actions and relatively poor for novel actions. Chimpanzees in these studies performed best in the object–object condition and worst in the single action condition. However, these results are derived from multiple trials and do not represent first trial performance. Unfortunately, no data is presented on 'familiar' vs. 'novel' actions in these different conditions. But, Myowa-Yamakoshi and colleagues note that chimpanzees rarely copied any type of action (familiar or novel) on the very first trial. A strong indication that all or any subsequent copying behavior was likely mediated by familiar rather than novel imitation. Yet, given the hypotheses of the MIM model it's surprising that object–object actions were ultimately easier to reproduce than single actions on objects. There may be two explanations for this result. One possibility is that the objects used in the study constrained or limited the range of object–object responses as compared with the single action on object condition, where many more responses may have been possible. So, for instance, the object–object action most accurately copied by chimpanzees was the familiar action of putting a ball in a bowl;

an object–object interaction with clear causal affordances. Given that the chimpanzees tested in these studies have a lot of experience putting things in bowls, the fact that this action was copied with the highest fidelity should not be surprising even when compared to a relatively simple but arbitrary (and, perhaps, novel) single action like rubbing the bottom of the bowl. A second explanation may have had to do with the fact that when subjects failed to reproduce the action, they received explicit instruction. During the 'Teaching Phase' the demonstrator trained the subject to produce the target action through "verbal and gestural guidance, molding, shaping with verbal praise and food reinforcements, or a combination of these methods" (Myowa-Yamakoshi and Matsuzawa, 1999, p. 130). One or both of these factors may explain the difference reported between copying a single action on objects and copying object–object actions.

Recently, a number of studies have focused on a special type of familiar imitation: oral-facial imitation. Comparative developmental psychologists have shown no significant differences between a human and a chimpanzee infant's ability to copy the oral-facial expressions of a model. Chimpanzees, like human infants (e.g., Meltzoff and Moore, 1977), reproduce tongue protrusions, lip protrusions, and mouth openings in response to a model displaying the same expression (Myowa-Yamakoshi et al., 2004). There are also parallels in the developmental trajectory of oral-facial imitation in both of these species. Myowa-Yamakoshi and colleagues report that after 9 weeks of age, the incidence of oral-facial imitation in chimpanzees slowly disappears. A similar phenomenon has been reported for human infants (Abravanel and Sigafoos, 1984). In short this study found no qualitative differences between human infants and infant chimpanzees in oral-facial imitation. Recently, Ferrari et al. (2006) have reported oral-facial imitation in infant rhesus macaques. However, researchers have cast doubt on the notion that matching oral-facial responses is best characterized as imitation (as defined here or elsewhere). First, an extensive review of the literature revealed that only tongue protrusions are matched by human infants (Anisfeld, 1996, 1991; Anisfeld et al., 2001). Second, and perhaps most surprisingly, a number of studies have demonstrated that a moving pen (Jacobson, 1979), blinking light(s) (Jones, 1996) and music (Jones, 2006) are all as likely to elicit tongue protrusions in neonates as is watching a model display the same behavior. However, the study by Ferrari and colleagues on neonatal imitation in macaques is unique in that the experimental design included non-social controls such a spinning disk in addition to the typical social stimuli in such experiments (i.e., mouth opening, tongue protrusions, etc.). Ferrari and colleagues reported that lipsmacking and tongue protrusions occurred significantly more often in response to displays of those same actions than they did to other types of stimuli. However, lipsmacking occurred the most often in response to different types of stimuli, much like tongue protrusions in human infants (Jones, 1996). Ferrari et al. (2006) noting the amount of inter-individual variation and the sensitivity to specific oral-facial movements (e.g., mouth openings and tongue protrusions) in both human and monkey neonatal imitation pointedly caution that "the capacity to respond to the model may not reflect a general imitative skill but rather a sensorimotor sensitivity tuned to specific facial gestures" (p. 1506). At this point it is impossible to say with any certainty whether these results are mediated by a mechanism independent of the imitation faculty (for a more complete review see Subiaul, 2007).

Taken together, the research reviewed here and elsewhere (Subiaul, 2007) suggests that the imitation faculty of primates is a mosaic, consisting of many different imitation mechanisms mediating the copying of different types of responses. From this it follows that paradigms that conceptualize imitation as one unitary faculty that an individual either has or lacks entirely is problematic. As has been already noted, humans and other primates appear to

share some imitation mechanism such as the ability to copy familiar motor actions and even novel cognitive rules (Subiaul, 2007; Subiaul et al., 2004, 2007) explaining the similarities reported by some comparative researchers. However, it's also clear that apes do not possess all the imitation mechanisms of a human 2.5-year old. This conclusion appears to be particularly true for novel motor imitation, a mechanism that may rely on many higher level conceptual mechanisms. The fact that humans possess more imitation mechanisms sensitive to different types of stimuli, rather than a domain- and content-general imitation mechanism, may explain our species ability to copy a broad range of behaviors and responses relative to other primates.

5. Testing the MIM hypothesis

The MIM hypothesis makes a number of predictions about the architecture of the imitation faculty and its relationship to other cognitive systems. These predictions contrast with existing concepts of imitation, which generally view imitation a amodal or domain-general. In contrast, the MIM hypothesis argues that if the imitation faculty is massively modular, then one should expect a whole suite of functional (and, perhaps, structural) dissociations where none are expected. Below are three general predictions made by the MIM model and some ideas on how to test these predictions.

5.1. Prediction 1: Imitation is content-dependent

One's ability to copy in one domain should not predict imitation success in other domains; Specifically, the MIM hypothesis predicts that imitation performance should be discontinuous and vary by content type (e.g., excellent vocal mimics may not necessarily be exceptional motor mimics, all things being equal). But dissociations in imitation performance are also expected within domains. For example, a character actor may be excellent at copying a historical figure's bodily, facial and emotional expressions, but the same actor may be poor at copying simple dance moves. The reason being that just as there are distinct mechanisms mediating the copying of vocal and motor actions, there are also many motor imitation systems mediating the copying of distinct motor content (e.g., opaque body actions such as facial expressions vs. transparent body actions such as dance moves).

5.2. Prediction 2: Imitation performance is discontinuous

Given Prediction 1: *Imitation performance is content-specific*, one should expect imitation to be both developmentally and phylogenetically discontinuous. (a) *Development*. If imitation is mediated by multiple, content-specific imitation systems, it's unlikely that all these systems develop simultaneously and contingently with one another. Consequently, one should expect that different imitation systems, responsible for copying specific content types, will develop at different rates within individuals, creating within-subject dissociations in performance. (b) *Phylogeny*. The same reasons that predict developmental discontinuities predict phylogenetic discontinuities. Different imitation systems are the product of selection pressures favoring specific solutions to recurring species-typical problems. Because those problems vary, so should the selection pressures favoring specific imitation systems. As such, it is extremely unlikely that all imitation systems are present in all animals. What is more likely is that animals should have aspects of the imitation faculty that are shared and other aspects that are unique to that species making each species imitation faculty unique.

An alternative to Predictions 1 and 2 is that discontinuities in imitation performance stem from a failure to integrate information from other cognitive systems with the domain-general operations of the imitation faculty. The most likely reason being that either the central skill in question, such as representing opaque motor actions (cf. Fig. 2), has either not developed or is absent from the cognitive repertoire of the participant (as may be the case in comparative studies). Developmental discontinuities in imitation performance was most prominently described by Jean Piaget and much of this view is held to date by virtually all contemporary developmental psychologists. According to this view, as individuals acquire certain skills and discover how to process information within certain content-domains, they automatically acquire the ability to imitate in this domain, as no special change in cognitive architecture is required once knowledge of the central content-domain has been acquired.

A similar view exists in the comparative literature. Tomasello and Call (1997), for example, have argued that a failure to appreciate intentions and goals (i.e., a theory of mind deficit) explains why non-human primates typically have such difficulty with imitation learning problems. In Tomasello and Call's view, as in Piaget's, imitation performance is contingent upon the ability to reason about unobservable psychological states such as goals and intentions. The predictions made by these alternative frameworks are fairly straight-forward: if you lack a given 'central' cognitive skill (e.g., symbolic representation of actions or Theory of Mind) imitation deficits should ensue, specifically, as they relate to the central skills in question.

5.3. Prediction 3: Imitation systems vary in their encapsulation

The typical view of a module is one that is highly encapsulate and its output is obligatory given specific input (Fodor, 1983). The classic examples of a Fodor module are vision modules that detect lines and edges (Marr, 1982). However, since Fodor (1983), many cognitive scientists and philosophers of mind have argued for a more expansive and heterogeneous view of modularity (e.g., Carruthers, 2006; Pinker, 1997; Tooby and Cosmides, 1992). These authors agree that Fodor modules exist, but that there are many cognitive systems with modular properties that are neither entirely encapsulated nor is their response to certain stimuli obligatory (e.g., Carruthers, 2006).

Some of the imitation systems in the MIM model are relatively encapsulated. That is, they do not take as input the output of other imitation or cognitive systems, while other imitation systems are less encapsulated and regularly take as input the output of other cognitive systems. This range of modularity explains Predictions 1 and 2. But if imitation is modular, it should have clear neural representations that are structurally dissociable. As such, functional neural imaging should be able to isolate the different hypothesized imitation systems described in the MIM framework.

The alternative to this prediction is that all imitation systems share a basic neural architecture. This basic architecture should become active whenever any imitation system as articulated by the MIM hypothesis is engaged. The mirror neuron systems has been proposed as such a system, particularly, since it's been implied in motor, vocal and cognitive imitation. However, mirror neurons play no role when copying meaningless or novel actions; they appear to become active in human participants only when copying meaningful or familiar actions (Lingnau et al., 2009). Moreover, mirror neurons in non-human primates have only been demonstrated for transparent actions and most fMRI studies with humans have involved copying similar transparent actions (e.g., Iacoboni et al., 1999). Nonetheless, while mirror neurons may not underlie all imitation systems, some as yet to be identified neural circuit may have such domain-general functions that are imitation-specific.

5.4. Testing the predictions of the MIM hypothesis

Testing Predictions 1–3 requires making a number of changes to existing paradigms as well as entrenched conceptualizations of imitation that have been around for more than 100 years (cf. Thorndike, 1898, 1911; Watson, 1908; see Subiaul, 2007 for a historical review). As described here and elsewhere (e.g., Subiaul, 2007), existing imitation paradigms that use objects such as problem or puzzle boxes or use tools are problematic for many reasons. These paradigm are a problem because they confound (a) vicarious and imitation learning, and (b) the copying of new vs. familiar rules and responses, (c) the copying of different types of rules [goals, causal, outcomes, actions], (d) the relationship between imitation and non-imitation cognitive systems [e.g., memory and attention]. So, while imitation tasks that use tools and objects are very ecologically valid, they are experimentally problematic. Worse, existing paradigms and concepts in the social learning literature make it impossible to assess not only *what* but also *how* certain aspects of an observed event are copied, a crucial question in both the cognitive and neural sciences.

Subiaul et al. (2004; in review) have attempted to address these confounds by using touch-screen computers and tasks such as the simultaneous chaining paradigm (Terrace, 2005) that clearly defines the aspects of the task that are familiar (e.g., touching pictures on the screen) and those that are novel (ordinal rule), for example. Using this approach one can hold central cognitive demands such as memory, visual load, and motor responses constant, while varying the types of rules that must be copied by the participant. For example, copying a novel ordinal (cognitive) rule such as [*first*, *second*, *third*], vs. copying a novel motor-spatial rule such as [*up → down → right*]. To test the MIM paradigm we must be able to articulate exactly what it is that participants are copying and be able to control for the operations of non-imitative systems. The reason being that for any given task, even those as relatively simple as copying a simple cognitive or motor-spatial rule, co-occur with other cognitive processes that must be experimentally controlled. Only by isolating the rule(s) that is to be copied this way, will we be able to better understand the architecture of the imitation faculty, including how it develops and how it evolved.

6. Conclusions

The MIM hypothesis is an empirical model that differs in a number of ways from existing models of social learning. First and foremost the MIM model is unique in its ability to capture the heterogeneity of imitation and social learning performance reported in human and non-human primates as well as neuro-typical and neuro-atypical human populations. If there are distinct systems, mechanisms or modules that mediate the copying of novel vs. familiar information and subsystems within each of these dedicated to copying different classes of rules and responses (e.g., motor, spatial, cognitive, social, etc.) then an individual may be able to imitate *familiar* vocal rules (e.g., words), but may not be able to imitate *novel* vocal rules (e.g., non-words) as is the case in autism. The MIM model also explains why monkeys, for example, are able to copy novel *cognitive* rules such as serial order, but not novel *motor* rules such as novel actions on objects (Herrmann et al., 2007; Subiaul, 2007; Tomasello and Call, 1997). This feature of the MIM model, shifts focus away from debates about whether something is emulation or 'true imitation' to one that focuses exclusively on the type of information that is being copied *and* the underlying system(s) that makes such copying possible (e.g., Heyes, 2004; Rumiati and Tessari, 2002; Tessari and Rumiati, 2004; Subiaul, 2007).

Though many aspects of the MIM model are new, the differentiation of types of imitations is not, as scientists have long distinguished between vocal and motor imitation (Shettleworth, 1998), for example. And, others such as Piaget distinguished between novel vs. familiar actions as well as transparent (visually-guided) and opaque (symbolically-mediated) imitation. The MIM Hypothesis builds on this tradition by adding a novel class of imitation, cognitive imitation, which involves copying information that is neither motor nor vocal in nature. These are *abstract rules* that include ordinality, conventions, goals, etc. Now, it must be emphasized, that the term cognitive imitation, like motor and vocal imitation, does not describe underlying processes but rather the stimuli that is being copied. As such, cognitive imitation describes the copying of cognitive stimuli (that are not directly perceived, but inferred) and does *not* imply that motor or vocal imitation are non-cognitive.

Arguably, the most unique feature of the MIM Hypothesis is that it's a domain-specific theory of imitation. This view has been influenced in part by the work of Carruthers (2006) who argues, for example, that all cognition is modular because natural selection tends to carve out specific abilities from existing skills. He, like evolutionary psychologists (Tooby and Cosmides, 1992; Pinker, 1997), argues that the more specialized the problem-solving mechanism in question, the more successful and adaptive that mechanism will be at solving a given problem; certainly more successful than a general-purpose mechanism that is only broadly attuned to the problem in question. As a result, Carruthers (2006) believes that evolution tends to produce massively modular cognitive architectures. The MIM hypothesis shares this massively modular view and argues that as there are learning problems there are potential imitation mechanisms specifically dedicated to solving them. Because these problems vary by species, each species' imitation faculty should vary accordingly.

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