**The evolution of skilled imitative learning: A social attention hypothesis**

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Humans possess many skills that others animals do not (and vice versa). Among our distinctively and perhaps uniquely human skills are the uses of a range of sophisticated motor tools (such as tools that modify or extend the control of biological effectors, like hand or legs), sensorial tools (that enhance the capacities of sensory organs) and cognitive and communicative tools (including the natural number system, and syntactically structured natural languages). Given the unique nature of our skillset, questions arise about its origins. Are these human specific skills biologically inherited, or are they learned? And if they are learned, what explains our capacity for learning them?

Some authors have argued that some of our uniquely human skills arise partly on the back of our possession of another more fundamental skill: a uniquely human form of social learning – imitation[[1]](#footnote-1). Imitation is a form of action copying in which an agent is concerned to replicate the precise strategy of an observed demonstration (Fridland & Moore, 2015; after Tomasello, 2010). This concern allows imitative learners to reproduce with faithfulness the actions that they watch others perform, and to accumulate knowledge from observing and reproducing the actions of their peers.

In recent accounts that emphasise the role of social learning in the development of the human skillset, imitation has been thought to play a foundational role, because its mastery allows for the rapid acquisition of a large number of further skills (Richerson and Boyd, 2008; Moore 2013; Fridland 2018). Since imitation is available even to cognitively undeveloped individuals (including, for example, pre-verbal infants), it constitutes a simple mechanism through which further cognitive, manual, and sensory tools can be developed. To illustrate with examples, the acquisition of spoken language seems to require (among other things) high-fidelity vocal imitation. The words and sentences of a natural language are usable only to the extent that they are copied with a high degree of accuracy. Poorly imitated utterances might be incomprehensible to the members of one’s speech community. Imitation therefore seems necessary for the development of natural languages in ontogeny and phylogeny (Fridland & Moore, 2015; Moore, 2013a; Tomasello, 2010; Tramacere & Moore, 2018).

Imitation has also been argued to be important for the production and mastery of many manual tools, such as the spears and long bows needed for hunting large prey (Boyd, Richerson, & Henrich, 2011; see also Moore 2016). Many tools could in be principle produced by individuals in isolation through trial and error. Indeed, recent findings support the view that hominids invented and re-invented tools many time during hominid evolution (Tennie et al. 2017; Braun et al. 2019). However, as the number and complexity of tools used by a given population increased, copying technological solutions from others would have become an adaptive strategy. Agents who were able to copy an expert demonstrator’s tool-making techniques could have quickly produced a stock of high calibre equipment, and by using the same skills to copy demonstrations of tool use could train themselves to use those tools. Meanwhile, agents who copied poorly would have been more likely to produce poor quality tools, and to use them without skill. Alternatively, they might have been forced to spend time and effort reinventing adaptive technological solutions for themselves. Thus, imitation is hypothesised to have been central to explaining our human ancestors’ ability to adapt to and survive in a variety of climates since their migration out of Africa sometime between 130k and 60k years ago.[[2]](#footnote-2)

Since imitation contributes to the accumulation of human specific knowledge and cultural products and is shared by other species only in limited respects, it seems well placed to contribute to an explanation of why the aforementioned elements of human cognition are uniquely human. Comparative studies show that humans use imitative learning strategies to acquire certain cultural practices, by copying precisely the actions they watch others perform (e.g., (Henrich, 2015; Tennie, Call, & Tomasello, 2009; Tomasello, 2010). In contrast, neither monkeys nor apes seem to imitate – although they use other forms of social learning – like emulation (see Whiten & Ham 1995; Moore 2013b for discussion). These typically result in less faithful forms of cultural learning. A chimpanzee, for example, might learn that a certain tool can be used to retrieve a piece of food, but typically won’t pay close attention to the techniques with which others use it. Thus chimpanzees will fail to learn behaviours that can be learned only with high fidelity copying (e.g., Tennie, Call & Tomasello, 2009). Tennie and collaborators demonstrated this by showing that chimpanzees were unable to produce a rope lasso to retrieve food even after watching others use one. Meanwhile four-year-old children learned the same skill with relative ease (ibid.). For this reason, chimpanzee communities seem unable to support processes of cultural evolution where high fidelity copying is required.

The scarcity of imitative behaviours in non-human species, and its ubiquity in human activities, such as linguistic, musical, technical and mathematical skills, has the potential to explain why other primate species fail to learn skills humans learn easily. Thus, imitative learning in humans seems to be important for understanding the origins of human cognition and culture, because it facilitates the learning of other valuable skills. It makes the acquisition of imitative abilities by humans a crucial cognitive achievement in human evolution. For this reason, in recent years cognitive scientists have wondered where our imitative abilities come from. Is imitation itself an adaptation, or has it been learned through cultural processes?

In the chapter to come, we address an ongoing debate about the origins of human imitation. Specifically, we will discuss whether the observation and execution of fine-grained manual and vocal actions associated with imitative learning is the result of biological or cultural changes in the hominin lineage, with particular reference to the Mirror Neuron System hypothesis.

There are currently two central hypotheses about the origins of human imitation. According to one influential view, defended by Michael Arbib among others, the Mirror Neurons System (MNS) in humans is a candidate for being the neural substrate of action copying behaviours. According to Arbib, the MNS that humans possess emerged in the hominin lineage under the selection pressure for the skilled copying of manual behaviour, likely in the service of better tool use and gestural communication (Arbib, 2005; Arbib, 2012; Arbib, 2017). The emergence of a complex imitation system for manual actions supported by an evolved MNS distinguished the hominin lines from the great apes; and enabled us to acquire new skills through imitative learning. During phylogeny this manual imitation system extended to the vocal domain when our ancestors, who communicated using gestural languages, switched to the vocal domain in order to free their hands for other tasks. Thus, according to Arbib’s view, we possess domain-specific adaptations for manual and vocal imitation: a bodily mapping schema for matching others’ actions to one’s own. It is because selection for this system occurred after humans split from our last common ancestor with great apes that we alone are imitators *par excellence*. While our ancestors underwent selection to be imitative learners, the more recent ancestors of our chimpanzee and bonobo cousins did not.

Against this view, a group of psychologists led by Celia Heyes argues that imitation is a product of cultural and not biological evolution; and that the MNS is composed of only domain general cognitive processes that are shared with other species, and trained in human ontogeny (e.g. (Heyes, 2018). According to this view, if humans are good imitators, it is because we have learned to be so – possibly with the assistance of cultural practices developed to cultivate imitative success. On this view, what makes humans but not great apes good at imitative learning is not a matter of our biological inheritance, but our having participated in the right sorts of cultural entrainment.

In the chapter to follow, we suggest a third account of the origins of human imitation. It borrows elements from both the nativist and non-nativist hypotheses, while offering a parsimonious explanation of the cognitive and neurobiological differences between humans and other species. Consistent with Arbib’s view, we argue that hominini underwent biological changes that supported the development of fine imitative skills. However, contra Arbib, we will propose that these changes may not have been triggered by selective pressure for imitation *per se*; and they do not result in a MNS specialised for complex imitation in humans. In agreement with Heyes, we argue that high-fidelity imitative skills are learned, and depend on changes in the social environment. Contra Heyes, though, we posit that humans have been adapted for social learning – by undergoing selection for better social attention combined with selection for enhanced fine motor (i.e., manual, facial and vocal) control. On the view that we adopt, the emergence in humans of sophisticated and multimodal social learning strategies exploited a combination of biological and socio-environmental resources.

This story has implications for, among other things, the characteristics of the cortical MNS (i.e., the temporo-fronto-parietal network of the human brain supporting observation and execution of skilled actions) and the mechanisms for social attention connected to it. It explains why humans alone are exceptional imitators, and so why our acquired cultural skillset so exceeds that of other species.

(**1) Uniquely human skills: manual, vocal and orofacial imitation**

Imitation is a form of action copying in which the agent is concerned to replicate the precise observed strategy of a demonstration. In light of this concern, an imitator pays attention to the way the copied agent acts, and subsequently tries to recreate her actions as carefully as possible (Fridland & Moore, 2015). Where an imitator can identify the goals of others, and carefully copy the actions they are pursuing in order to achieve those goals – either by uttering words, or performing manual actions – an imitating individual can acquire new resources (e.g., a natural language, or mastery of a new manual tool) with which to navigate her environment.

At the cognitive level, imitation involves a perceptual representation of an *observed* *sequence of behaviours* that are matched to a pattern of motor activation that can produce the same sequence of behaviours. Consequently, imitative learning requires that agents recognize intentional actions, and can match their own voluntary bodily actions to those of an observed agent. This involves abilities for recognizing the goals performed by others, selecting appropriate goal-directed movements for performing a task, controlling motor output based on predictions about the actions needed to realise that task, and being guided by perceptual feedback in order to make adjustments to improve one’s chances of success. Attention to others’ actions and fine motor control of the biological effectors (e.g., hand, mouth or larynx) used to copy observed actions are therefore fundamental for imitative behaviour.

While infants from one year of age are able to reproduce complex action sequences, both in the manual and the vocal domain (Jones and Herbert 2008), great apes do not. Chimpanzees are capable of what has been called *simple imitation* (Arbib, 2002), or *emulation* (Tennie et al., 2009). This allows actions to be acquired through a focus on the end product of the observed activities. However, a number of experiments suggest that while chimpanzees are capable of recognising the goals with which others are acting through observations of their behaviour, they do not spontaneously perform high-fidelity action copying (Arbib, 2005; Tennie, Call, & Tomasello, 2006; Tennie et al., 2009; Tennie, Call, & Tomasello, 2012; Tomasello, 1994). Rather than copying the others’ manual and vocal behaviours, they recreate their own ways of achieving the goal they have watched others pursue. In the more restrictive characterisation of imitation useful for cultural evolution research (see (Fridland & Moore, 2015) for discussion), this makes chimpanzees capable of *emulation*, but poor at *imitation*.

**(2) The Mirror Neuron System as a possible neural substrate of imitative learning**

Recent work in cognitive neuroscience suggests that imitative learning is connected to activity in the temporo-fronto-parietal (TFP) network, a network of cortical regions associated with the execution of a broad range of biological actions, such as hand gestures, tool actions and vocalizations. Specific parts of the TFP network activate during the *observation* of the same or similar actions performed by others. This network is therefore collectively defined as the Action Observation Network (AON) or the Mirror Neuron System (MNS).

In this section, we review evidence suggesting that the execution of goal-directed manual and vocal actions involves activations of the TFP network computing individual sensorimotor coordination. Moreover, the perception of these actions performed by others activates parts of the TFP network (the MNS) and facilitates their reproduction and learning (for reviews and meta-analysis see Caspers et al. 2010; Van Overwalle and Baetens 2009; Molenberghs, Cunnington, and Mattingley 2012).

A review of existing findings on the neural substrates of the MNS shows that, while the MNS associated with the observation and execution of goal-directed manual and vocal actions are all present in humans, a MNS for the matching of vocal perception and reproduction is not present in non-human primates (Tramacere, Pievani, & Ferrari, 2017, Tramacere et al. 2019). Further, the MNS associated with hand and tool perception and execution present interesting neurophysiological differences between humans and apes. Consequently, the comparative analysis of these networks supports the hypothesis that action copying in humans and apes is governed by different neural mechanisms. This may give important insights into an understanding of how humans evolved to become good imitators, and how imitation supported the historical emergence of a number of associated cultural tools, like the use of natural languages and technology.

In human and non-human primates, a subclass of sensorimotor neurons - called *mirror neurons* (MNs), fires both when an individual performs an action and observes that same or similar action performed by another (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). MNs are embedded in the MNS (Keysers & Perrett, 2004; Rizzolatti & Craighero, 2004) comprising specific sectors of the frontal (i.e., premotor and motor) and parietal cortices that contain MNs, plus the superior temporal sulcus (STS) that contains only sensorial neurons. In recent years, additional neurophysiological and neuroanatomical studies have led some scholars to propose an “extended MNS”, which includes not only these regions of the brains but also the primary motor, the secondary somatosensory and the ventrolateral prefrontal cortex, together with specific limbic and subcortical structures (Bonini, 2016; Bruni et al., 2018). Since we are here interested in the high-level multimodal representations associated with the voluntary/intentional reproduction of perceived actions, we will consider only the cortical TFP regions of the MNS, which is activated during the perception and execution of goal-directed actions.

MNS can be classified in different sub-systems, using two unambiguous physiological criteria: the modalities of sensory input triggering the response, and the effectors involved in the motor output (Tramacere et al., 2017). Consequently, we treat the hand visuomotor and the audio–vocal MNS as independent mirror systems. In this way, we can analyse independently how hand and vocal actions are represented in the brain, and identify the neurobiological correlates of different sensorimotor skills and their behavioural implementations in different animals. We will refer to the *hand visuomotor MNS* (hereafter hand MNS) as the network of neuronal cells activated by the observation of others’ hand gestures that are also involved in the control of own hand actions. We use the term *audio-vocal MNS* to refer to the network of neurons that discharge during both listening and vocalizing.

The recruitment of the human *hand MNS* is associated with imitative tasks performed in a social context (Cross & Iacoboni, 2014a; Iacoboni, 2005; Kessler et al., 2006). For instance, the execution of manual actions after observation of the same action performed by another leads to an increased activation of the MNS compared to when the same manual action is performed in response to a symbolic cue, suggesting that the hand MNS works by mapping sensory information to motor knowledge (Iacoboni et al., 1999). Further, a number of Transcranial Magnetic Stimulation and kinematic experiments show that the observation of some manual actions prime (and thereby facilitate) the execution of similar actions. This shows that the observation and execution of specific movements relies on the same neural mechanisms (Cross & Iacoboni, 2014b).

Using imaging studies the activation of the chimpanzee and human hand MNS has been compared during observation of goal-directed and non-goal-directed grasping actions. Results show the human parietal and occipitotemporal regions of the MNS activated significantly more, especially during non-goal-directed actions (Hecht et al., 2012). This finding correlates with those showing that in chimpanzees there is a greater discrepancy between the *ventral* (frontal with superior temporal lobe) and the *dorsal streams* (frontal with parietal lobe), with the ventral components larger than and strengthened relative to the dorsal ones (Hecht et al., 2013). In humans this difference is not present. Further, in humans but not in chimpanzees an additional dorsal pathway passes through the parietal opercular white matter to the anterior supramarginal gyrus, with the latter univocally implicated in tool-use (Orban, 2016; Peeters et al., 2009). Finally, the link between the mirror parietal region (enlarged in human and associated with spatial coding) and the inferior temporal sulcus, where objects and tools are recognized, is more developed in humans than in chimpanzees (Hecht et al., 2013).

Functionally speaking, the ventral stream is considered the *What route*, devoted to identifying objects and events and to computing what has been defined as “vision for perception”. The ventral stream may be used in processing the end–results of observed actions, because it works “to select the goal object from the visual array” (Goodale & Milner, 2013) p.100). On the contrary, the dorsal stream (known as the *Where-How route*) supports the kinds of visuomotor transformation in which visual input leads to manual actions such as reaching, grasping and manipulating objects (Goodale, Westwood, & Milner, 2004). The dorsal stream can be considered a “vision for action” pathway that processes the spatial mapping of movements and allows the extraction of a finer level of action kinematics (Goldenberg & Spatt, 2009; Johnson-Frey et al., 2003).

The findings of the selectively greater activation in the ventro-parietal cortex during observation of goal and especially non goal-directed actions in humans compared to chimpanzees can be interpreted in the light of this evidence. A greater portion of the human parietal cortex is dedicated to finer level action processing. These areas are recruited during the observations of others’ actions, potentially for inferring the proximate goals of these actions, and for translating observed actions for the performance of similar actions (Kilner, Friston, & Frith, 2007).

In support of this hypothesis, studies in patients with specific impairments in the parietal cortex further show that the dorsal stream is implicated in processing the causal relation of objects that are commonly used in sequence (e.g., a hammer and nails), a phenomenon called paired-object affordance. Moreover, selective lesions in uniquely human represented sectors of the parietal cortex indicate a dissociation between the neural mechanisms that support the simple grasping of an object and those that support using an object following specific action plans (Binkofski & Buxbaum, 2013; Johnson-Frey, 2004). This provides evidence that the human-specific expansion of sectors of the parietal cortex is implicated in understanding the general principles of tool use and causal interactions between objects.

The role of the frontoparietal pathway in visuorimotor transformation has also been generalized to the auditory-vocal domain. Concerning the auditory domain, both human and non-human primates seem to possess a similar kind of auditory processing (Rauschecker & Scott, 2009), while a dramatic difference between human and non-human primates lies in their respective abilities for vocal production. Classically, vocal communication in non-human primates has been attributed to mesial and subcortical structures and thought to be involuntary, due to mainly emotional and motivational control (Jurgens, 2002). Consequently, non-human primates have been typically described as lacking the discrete and voluntary vocalization that can be detected in humans and that can ascribed to the somatosensory motor control found in the frontoparietal pathways of the human cortex.

However, several sources of evidence now speak in favour of a greater control of voluntary vocalization in non-human primates. Recent experiments showed that the monkey homologue of Broca's area, as well as the premotor and/or primary motor cortices, are all involved in the initiation of volitional calls that have been uttered in response to visual or auditory stimuli (Coude et al., 2011; Hage & Nieder, 2013). Further, a fraction of neurons in these areas exhibit responses to auditory stimulation with species-specific calls (Hage & Nieder, 2015). Since the auditory responses do not temporally match the pattern of vocal output, these neurons cannot be considered audio-vocal MNs (by definition). However, the findings suggest that the frontal cortex in primates is involved in the multisensory control of oro-facial cues, and may constitute a precursor of cortical control in the evolution of vocal learning (Hage & Nieder, 2016). Interestingly, studies in songbirds show that vocal learning is grounded in a continuous matching process between vocal output and auditory feedback (both in a social and a first-person perspective), which involves, at the sub-personal level, neurons that show a precise temporal matching between auditory and vocal stimuli (Prather, Peters, Nowicki, & Mooney, 2008).

We interpret this evidence as showing that the more the performance of a specific action requires a fine level of kinematics and complex causal control, the more it involves regions of the TFP network and temporally precise matching between sensorial and motor stimuli (Tramacere et al. 2019). The stronger activation of the MNS in humans with respect to manual and vocal perception in a social context can be thus interpreted in terms of humans’ possessing more developed capacities for manual and vocal fine-grained and sequential (i.e., skilled) motor control. In sum, the neurobiological evidence described so far suggests that there are substantial neurological differences between humans and primates with respect to the areas of the brain that have been identified as playing a role in imitative learning. It is a further question whether these differences are a product of our evolutionary history, or whether they are learned in ontogeny.

**(3) The evolution of the MNS**

In recent years a debate has arisen concerning the origins of the MNS, and its status as an important neurobiological candidate for explaining imitative learning. It is a matter of ongoing debate whether the neurobiological differences described above are biologically inherited through natural selection mechanisms, or whether they might themselves arise as a product of cultural learning. Two rival hypotheses have been proposed: (3.1) the associative hypothesis (Cook, Bird, Catmur, Press, & Heyes, 2014; Heyes, 2014) and (3.2) the adaptive hypothesis (Arbib, 2005; Rizzolatti & Arbib, 1998; for a review see also Ferrari et al. 2013). Proponents of the associative hypothesis argue that the ability of humans to imitate (and thereby acquire advanced linguistic and technological skills) is a product of cultural and not biological evolution. On the contrary, proponents of the adaptive hypothesis argue that human beings possess adaptations for imitation, and that these enable their skilled learning of cultural practices and products.

**(3.1) Mirror neurons and imitation are not in our genes**

According to the *associative learning (ASL) hypothesis*, MNs are forged through associative learning, which connects observing and executing the same actions. Associative learning offers a parsimonious explanation for how neurons acquire mirroring properties: contingent and repeated activation of the sensory and motor representation of an action cause sensorimotor associations. Sensorimotor associations at the behavioral level produce Hebbian learning at the subpersonal level: sensory and motor “neurons that fire together, wire together” (Hebb, 2005). Sensorimotor neurons are firstly associated through the observed experience of our own bodies in action. A subpart of these neurons also activate during the observation of others’ body in action. Clusters of neurons thus acquire differential observation-execution matching properties through a domain-general process of sensorimotor associative learning.

As a by-product of individual sensorimotor learning, MNs *may* play a functional role in social learning, but they need not have a specific adaptive function (Cook et al., 2014). According to the associative hypothesis, biological evolution has played a non-specific background role in the evolution of MNs and associated cognitive skills, including imitation. The general abilities for associative learning and connectivity between the sensory and motor cortices, but not the MNs, are genetic adaptations, while the characteristic matching properties of MNs are forged by sensorimotor learning.

In particular, the associative hypothesis states that (i) neither human nor non-human primates have a specific genetic predisposition to develop MNs; these animals do not inherit a set of MNs, or even a domain specific learning mechanism that promotes the development of MNs. (ii) Human and non-human primates have genetic predispositions to develop (a) connections between particular sensory and motor areas of the cortex, which evolved because it promotes precise visual control of action, and (b) a domain-general capacity for associative learning. (iii) When individuals with these predispositions receive correlated experience of observing and executing the same actions, they develop MNs for those actions. (iv) MNs are primarily a collateral result of individual sensorimotor learning and social interactions and, although MNs may contribute to behaviour in a number of important ways once they have been developed, they are not an adaptation for any specific social learning function (Cook et al., 2014; Heyes, 2014).

On this associative view, MNs and imitation are not products of biological evolution. They both result from a process of the generalization of individual sensorimotor learning. We learn to imitate through culture-specific forms of social interaction. These include culturally trained processes of socialized attention, and activities like perceiving one’s own and others’ oro-facial and manual actions. Experiences of our own and others’ bodies in every day life are further trained by cultural practices like looking at ourselves in mirrors and watching videos – practices that are predicted to contribute substantially to the maturation of the MNS in ontogeny. The same neural and behavioral mechanisms mediate individual motor learning and social cognitive skills, such as imitation. Body movements are represented in the same way during individual visual feedback in the course of motor coordination and during observations of other’s actions. In the case of imitation for example, the domain-general mechanisms of motor learning process social input – i.e. the observed actions of others – rather than executed individual body movements. Processing of this input is made possible by a set of bidirectional excitatory links or vertical associations, each of which connects sensory (usually visual) and motor representations of the same movement. MNS and thus imitation are not genetically programmed. What makes us good imitators lies in the social environment in which we are raised and in general processes of cultural evolution (Heyes, 2011; Heyes, 2016a)

* 1. **Evolving imitation for a language ready brain**

In contrast to the associative hypothesis some scholars have formulated an *adaptive hypothesis*. They propose that macaque and human MNS are an evolutionarily conserved neural mechanism that has been selected during phylogeny for accomplishing high-level cognitive functions, such as action understanding, imitation, mind-reading and language (Arbib, 2005; Gallese & Goldman, 1998; Gentilucci & Corballis, 2006; Rizzolatti & Craighero, 2004). One function of this system is (paraphrasing (Heyes, 2018)) to map the felt-but-not-seen movements of our own bodies to the seen-but-not-felt movements of others’ bodies. (Heyes calls this process ‘solving the correspondence problem’). Once observers have mapped others’ actions to their own bodily movements, they can use first personal abilities to infer the goals that others’ actions were intended to realise. Thus, this mapping system generates knowledge of the goals’ underlying others’ bodily actions.

Michael Arbib has defended one variant of this adaptive proposal. We focus on his account, because he has clearly explained the cognitive functions (imitation and language) that are hypothesised to drive the evolutionary changes underlying the human MNS. Arbib’s *mirror system hypothesis* claims that the MNS for grasping present in macaque and chimpanzee evolved into a key component of the mechanisms that rendered the brain of recent humans ancestors ready for learning imitatively a proto-language consisting of manual gestures, and subsequently a language consisting in syntactical organized vocal symbols (Arbib, 2005). Specifically:

[I]mitation is seen as evolving via a so-called simple [mirror] system such as that found in chimpanzees (which allows imitation of complex “object-oriented” sequences) to a so-called complex [mirror] system found in humans (which allows rapid imitation even of complex sequences, under appropriate conditions) which supports pantomime. This is hypothesized to have provided the substrate for the development of … protosign and protospeech then developing in an expanding spiral. … [T]hese stages involve *biological evolution* of both brain and body. (Arbib, 2005) p. 105)

Arbib specifies that possessing a MNS for grasping like that of macaque monkey does not guarantee the development of any imitative or linguistic abilities. The MNS associated with hand action shared with common ancestors of human and monkey is simply the first necessary step for developing imitative skills both in the manual and subsequently in the vocal domain. The hand MNS shared with the common ancestor of monkeys and humans enabled only the voluntary control of hand actions and the understanding of manual gestures for communicative purposes. On the other hand, the common ancestor of chimpanzees and humans shared a hand MNS not only for the voluntary control of hand actions in individual and social perspective, but also for emulation – the form of action copying that apes are able to perform.

According to Arbib, only in the recent hominin lineage (that is, in hominini who were ancestors of humans but not of chimpanzees and bonobos) did a further biological step enable the MNS to support what Arbib calls “true imitation” in the vocal domain, following selection pressure for the mastery of a protolanguage based on the use of ritualized manual gestures. The development of this manual-based protolanguage imitation in the manual domain was crucial: prior to the emergence of sophisticated vocal communication, our ancestors communicated using protolanguage consisting largely of manual gestures, the learning of which was supported by manual imitation. It was only at a later stage of evolution that communication migrated into the vocal domain (see (Tramacere & Moore, 2018) for discussion).

This evolutionary step is hypothesised to have brought a series of biological changes. Starting from the connections between the premotor, parietal and temporal areas in macaque monkeys (which we shall call the ‘monkey MNS’), changes “lifted” the premotor homologue of the common ancestor of human and monkey to yield the human (premotor and frontal) Broca’s area, and also “lifted” the other regions to yield (the parietal) Wernicke’s area and other areas that support imitation and subsequently language development in the human brain (Arbib, 2005, p. 106).

Setting aside Arbib’s metaphorical and somewhat opaque talk of “lifting”, the view that emerges here is that human imitation is a product of evolutionary changes that occurred during our accession to language. These changes equipped us with an inborn ability to map others’ actions to our own, and thereby interpret the intentions underlying them. This in turn gave us new abilities for imitative learning.

**(3.3) The evolution of the MNS: The social attention hypothesis**

Proponents of both the adaptationist and associative accounts of the function of the MNS have offered sustained critical responses to each other’s arguments. Heyes (2018) has argued, for example, that imitative tongue-protrusion apart, there is no evidence that children are born with general imitative learning abilities (see (Heyes, 2016b; Oostenbroek et al., 2016). Consequently she argues that there is “no good reason to believe that the capacity for imitation is genetically inherited” (Heyes, 2018) p.129). Heyes also points to evidence that imitative abilities improve following sensorimotor experience (see (Catmur, Walsh, & Heyes, 2009) and (Cook et al., 2014) reviews) as evidence that imitation is learned.

Meanwhile, proponents of the adaptationist view argue that the proponents of the associative view have constructed a straw-man argument against the adaptive view, because they work with a concept of adaption that is unnecessarily rigid. They claim that even though the proponents of the associative view convincingly proved that the MNS is modulated by sensorimotor experience, this does not rule out the possibility that the capacity to match sensorial and motor representations of actions was under selection pressure during evolution (Lingnau & Caramazza, 2014).

We would further add that Heyes’s hypothesis that the human skill for social learning is itself learned fails to explain why our species so uniquely good at social learning. On current formulation it says very little about the neurological differences between humans and other primates in brain development – differences that seemingly support our differential abilities for skilled action copying in the technological and linguistic domain. Yet it is consensus – as Heyes herself acknowledges (2018) – that apes are not capable of learning to imitate as skilfully as humans do. This may be because the differences between human and ape social learning are correlated with fundamental – and potentially unlearned – neurobiological differences.[[3]](#footnote-3)

For reasons of space, we will not evaluate in full the arguments for and against the adaptationist and associative views here. However, we want to suggest that a third option is also consistent with existing data. It takes elements from both views and gives a plausible account not only of the complex abilities for imitation that humans possess, and the extensive and uniquely human neural circuitry that supports these abilities, but also of the role of social learning in the development of social learning in human ontogeny.

The starting point of our hybrid account is that both the associative and adaptive accounts are to some extent plausible and heuristically fruitful. The associative hypothesis is a parsimonious and testable account of how any brain possessing connectivity between sensory and motor cortices and capable of associative learning could give rise to something like a MNS as a side effect of sensorimotor coordination. Meanwhile the adaptive hypothesis provides a valuable working hypothesis for identifying and explaining the changes associated with species-specific differences in cognitive functions based on brain properties, and non-equivalent social learning abilities.

At the same time, both accounts are also somewhat limited. The associative hypothesis does not explain why chimpanzees seem to be so poor at social learning. One plausible explanation of this difference is that species that imitate well have undergone selection pressure for imitation relevant abilities, if not imitation *per se*.

We suggest that a variety of cerebral and cognitive mechanisms – e.g., hierarchical coding and control of own movements, coarse-grained sensorimotor connectivity, selective attention for others’ actions and specific input representation – are necessary for the development of a MNS that is consistently activated during perception of others actions, and for social cognition in general (Bonaiuto, 2014) In other words, connections between sensorial and motor regions plus associative learning are necessary but not sufficient for MNS involvement in social and eventual imitative learning. Specifically, we propose that the MNS can be better understood as a neural system connecting expanded cortical areas evolved for facilitating sensorimotor development in an individual and social perspective. Such systems likely evolved in environments where the monitoring and continuous comparison of one’s own and others’ actions was fundamental for developmental steps in cognitive maturation.

Following Heyes, our account endorses the proposition that sensorimotor experience plays a constitutive role in the development of MNs through associative learning, but adds that without special-purpose social learning mechanisms (such as an adaptation that predisposes agents to be attentive to others, and to the actions that they perform) the development of imitative learning as we observe it in humans would not have arisen. According to this account, extant ancestors of macaques and humans developed flexible mechanisms of sensorimotor control, such as the MNS, by relying on specific connectivity between sensorial and motor areas of the brain. During phylogeny, developing MNS started to play a key role in social cognition, as a result of increased social demands (e.g., monitoring and copying own and others actions). Consequently, selection pressures emerged that lead to the development of flexible sensorimotor mechanisms sensitive to and modulated by social conditions, so that the properties and distribution of the MNS reflected not only sensorimotor experiences, but also the socio-cognitive evolution of species (Ferrari, Tramacere, Simpson, & Iriki, 2013; Tramacere, Ferrari, & Iriki, 2015; Tramacere et al., 2017).

**(4) The evolution of skilled imitative learning**

The central content of our proposal here is that humans are not biologically adapted for imitation *per se*. Rather, we have undergone selection to be more attentive to the actions of our peers.[[4]](#footnote-4) Additionally we have undergone selection for fine-grained motor control and sequential learning of complex actions. Because humans are biologically prepared to attend to others’ motor actions, and to physically perform these kinds of actions, we are particularly good associative learners of behavioural sequences performed by others. As a result, imitation is learned, and it is learned on the back of evolved skills for attending to and performing fine-grained motor actions, thus making the type of social attention that hominids are endowed with sensorimotor in nature. Our imitative skills are a by-product of natural selection for both skilled motor control (particularly in the manual and oro-facial domains) and social attention – specifically towards the motor actions performed by others (again, particularly oro-facial and manual actions).

While the study of attentional patterns of humans and great apes is in its infancy, some differences between our species have become apparent already (see Hirata & Myowa, 2018, for a review). These are consistent with our hypothesis that there are evolved differences in the way that humans and great apes attend to actions.

No studies that we know of have yet looked at whether there are differences in the ways that humans and adults attend to skilful actions. However, we predict that differences would be apparent. In particular, we hypothesise that humans would spend longer than non-human great apes attending to the hands and faces of agents engaged in manual imitation tasks. In contrast, we would expect chimpanzee attention to be more oriented to the objects on which an agent acted. These attentional differences would be reflected in differences in ways that chimpanzees and humans reproduced the actions they had observed – with the humans’ manual actions being more faithful to those of the actor. In other words, attentional differences would reflect the fact that while humans imitate, great apes emulate.

It follows from our view that imitation must be learned – potentially, as Heyes argues, through domain general associative learning process. (This would be true even if attentional differences are unlearned.) Given that imitation must be learned, it’s highly likely that developed skills for imitation have been honed by human cultural practices like those described by Heyes, and that there would be changes in both imitation (and perhaps also changes to attention) in ontogeny. Nonetheless, we hypothesise that under selection pressure for abilities that would boost our capacities for social living, human (but not great ape) ancestors underwent selection for better social attention and motor control. If this is right, our cultural practices build on a biological preparedness to learn behaviours from others. In other words, chimpanzees raised in a human environment might become better imitators than if they were raised in the wild, but they will still not be as adept at motor execution and observation as we are, simply because they are not capable of the same flexible control, and because their attentional resources are comparatively poor.

The social attention hypothesis, as it might be called, has yet to be tested directly. However, it is consistent with a number of lines of evidence form comparative studies of primate and human cognition. For example, great apes seem to be less attentive to one another, and to human caregivers, than are humans to their peers (Moore, personal observation). This difference likely stems from a number of sources. These include the greater need for humans to communicate in order to solve coordination problems, and thereby secure food (see (Moore, 2017; Moore, Call, & Tomasello, 2015) and the greater reliance of humans on social learning (see (Fridland & Moore, 2015; Henrich, 2015; Moore, 2013a, 2013b). The hybrid view that we propose is also attractively parsimonious, since small tweaks to social attention could have improved both our ancestors’ communicative abilities (Moore, 2017) and their social learning skills. It may be, for example, that a chimp-like tendency in our ancestors to look to the world for solutions to their problems was replaced by a human-like tendency to look to peers for solutions. We think this proposal is worthy of further investigation, in both empirical and conceptual domains.

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1. Whether or not imitation is itself a skill will, of course, depend on what we take skills to be. But – as the following article will argue – it seems to possess at least one key feature of many skills: it is learned and perfected through practice. [↑](#footnote-ref-1)
2. For discussion of the importance of social learning to hominin and (later) human survival, see Boyd, Richerson & Henrich (2011), Sterenly (2012) and Moore (2016). For an argument that the importance of imitation for tool mastery has at least sometimes been overstated in phylogeny, see Tennie et al. (2017). For recent discussion of ancestral migrations out of Africa, see Malaspinas et al. (2016), (Mallick et al. 2016), Pagani et al. (2016), and Timmerman and Friedrich (2016).  [↑](#footnote-ref-2)
3. Another possibility is that great apes have not been enculturated and trained in imitation in ways that would make comparisons with human imitators legitimate. This concern is not without merit, but given the dubious ethics of raising chimpanzees in human environments, it is not likely to be tested any time soon. For a relevant discussion see (Leavens, Bard, and Hopkins 2019). [↑](#footnote-ref-3)
4. For an application of our social attention hypothesis to the interpretation of differences in human and chimpanzee understanding of referential communication see Kano et al. (2018). [↑](#footnote-ref-4)