Action-Perception Matching in Human Cultural Evolution: Updates from the Cognitive Science Debate

Antonella Tramacere[*] *and Fabrizio Mafessoni*[**]

[*] *University of Bologna*
[**] *Weizmann Institute of Science*

Abstract

Analyses of action-perception matching mechanisms, such as the Mirror Neuron System (MNS), have been prominent in evolutionary accounts of human cognition. Some scholars have interpreted data on the MNS to suggest that the human capacity to acquire and transmit cultural information is a learned product of cultural evolution (the Culture not Biology Account of cultural learning). Others have interpreted results related to the MNS to suggest that cultural learning in humans result from both cultural *and* biological evolution (the Culture per biology Account of cultural learning).

In this paper, we analyse action-perception matching mechanisms considering evolutionary models *and* novel experimental findings about the MNS. We review the Culture not biology account plausibility within evolutionary theory and argue that as it stands this account is theoretically unsound. We finally argue for the plausibility of the Biology per culture account and discuss how it paves the way to further neurobiological investigations about the evolution of our capacity to learn, understand and transmit cultural information.

Keywords: Human cognition, Cognitive evolution, Brain evolution, Mirror neuron system, Action-perception matching.

1. Introduction

There is wide agreement that culture had a driving role in human evolution, and that human intelligence depends on the capacity to acquire, understand, and transmit cultural information in development and across generations. The evolution of culture in hominids regards the acquisition, innovation and transmission of tools, communicative gestures and language, cooperative actions and rituals. Based on these assumptions, cultural learning is investigated in a comparative and

Argumenta 10, 2 (2025): 687–704 DOI 10.14275/2465-2334/202200.tra
ISSN 2465-2334 First published: 5 July 2022
© 2022 Antonella Tramacere and Fabrizio Mafessoni

developmental perspective to explore the neurocognitive requirements for the evolutionary origin of the human mind (Parker and Gibson 1994; Boesch 2007; van Schaik and Burkart 2011).

Because of the importance of cultural learning in the analyses of the human mind, several cognitive science accounts have investigated human cultural evolution by focusing on the role of action-perception matching mechanisms in the brain (Gentilucci & Corballis 2006; Heyes 2018; Preston & de Waal 2002; Rizzolatti & Arbib 1998; Whiten 2013; Whiten & van de Waal 2017). Many aspects of cultural learning rely on the capacity of mapping perceived behaviour with one's own motor repertoire and respond to it with opportune action, be it imitative or not. Therefore, the dynamics of action-perception matching in imitation, communication and social understanding has been a central interest for studies of cognitive evolution.

In line with these previous proposals, we stress the importance of analysing the Mirror Neuron System as a proxy for the role of action-perception matching mechanisms in the evolution of cultural learning, and focus specifically on imitation, behavioural (including facial) mimicry, and social understanding. Through discussion of evolutionary models and novel experimental findings, we will contribute to the debate about human evolution by evaluating contrasting accounts of cultural learning. We will consider accounts that support or dismiss a direct role of natural selection and genetic evolution for cultural learning and the MNS (Arbib 2017; Heyes 2016, 2018; Rizzolatti & Arbib 1998; Whiten 2013).

Our analysis maintains that, while biological changes in the MNS are crucial for explaining the emergence of cultural learning in humans, the evolution of this system cannot be analysed by exclusively focusing on single populations of mirror neurons. Therefore, we propose to overcome the atomism intrinsic in previous accounts by focusing on the network properties of the MNS. We will conclude by discussing the plausibility and fruitfulness of inquiring into biological changes involved in human action-perception matching mechanisms due to the evolution of culture.

We start by reviewing relevant evidence about the role of the MNS in cultural capacities, and specifically in mimicry, imitation, and social understanding (Section 2). In section 3, we briefly present the two opposite accounts on the evolution of the MNS, and namely the Culture not biology account, which claimed that cultural learning is a learned product of cultural evolution and general process of learning, and the Culture per biology account, which claims that human cultural learning is a learned product of both cultural and biological evolution. We then discuss evolutionary models exploring the adaptive value of the MNS (Section 4). In Section 5, we evaluate the Culture not biology account from an evolutionary perspective, and in Section 6 we review empirical evidence in support of the Culture per biology account. We conclude with discussing why is heuristically fruitful to pursue the line of research opened by the Culture per biology account to understand the evolution of human intelligence through a focus on action-perception matching mechanisms.

2. The Role of the MNS in Cultural Cognition

The MNS owe its name to the discovery of mirror neurons (MNs), neurons activating both when an individual performs a specific behaviour and observes that same or similar behaviour performed by another. From their first description in

the ventral premotor cortex and inferior parietal lobule of the macaque monkey (di Pellegrino et al. 1992; Gallese et al. 1996), these neurons received great attention, because the matching between perception and action at the level of single neurons is relevant to a mechanistic understanding of social and cultural cognition.

In this section, we discuss evidence highlighting the connections between mirroring mechanisms and cultural learning, with a specific focus on imitation (including facial mimicry) and social understanding, also called mentalizing. Because imitation and mentalizing are pivotal mechanisms of human cultural evolution, including the evolution of language (Woensdregt et al. 2021), the analysis of the role of action-perception matching in these mechanisms can help us investigating their evolutionary origins.

The MNS is crucially involved in a variety of imitation capacities. The execution of bodily movements after the observation of the same act performed by another, leads to an increased activation in the MNS, compared to when the same movement is performed in response to a symbolic cue (Iacoboni et al. 1999). This suggests that the MNS works by mapping sensory to motor information in the brain. In studies using Transcranial Magnetic Stimulation (TMS), the observation of some actions facilitates the execution of the same actions, supporting the view that the observation of bodily movements modulate the reactivity of the individual toward similar behavioural responses (see for example Cross and Iacoboni 2014). Several fMRI studies (for reviews and meta-analysis see Van Overwalle and Baetens 2009; Caspers et al. 2010; Molenberghs, Cunnington, and Mattingley 2012) shows that, the observation and execution of a similar action rely on the activity of the MNS.

Support for the idea that the MNS is implicated in multimodal forms of imitation also derives from experiments with non-human animals. One of these studies regard manual actions copying in chimpanzee (Pope et al. 2018). Further, numerous studies in songbirds (Giret et al. 2017; Hanuschkin et al. 2013; Roberts & Mooney 2013) show that neurons matching vocal execution and listening are functionally embedded in a sensorimotor nucleus, whose lesion impair vocal recognition and imitative learning (for a discussion see Tramacere et al. 2019). In macaques which are experimentally trained to vocalize, neurons matching both the listening and execution of calls emerge in regions that are homologous to the human Broca's area (Hage 2018; Hage & Nieder 2015), suggesting that imitative learning recruits neural mechanisms of vocal and auditory matching.

MNS are also involved in facial mimicry, a fast and automatic form of imitation based on the activation of facial muscles. Experiments simultaneously combining various investigative techniques have shown that viewing emotional faces is associated with the activation of the motor and somatosensory areas involved in the execution of the observed facial expressions (Arnstein et al. 2011; Hogeveen et al. 2015; Likowski et al. 2012; Schilbach et al. 2008). For example, experiencing disgust and witnessing the same emotion expressed by someone else, activate the same neural structure—the anterior insula—in an overlapping location (Wicker et al. 2003) and thus similar facial muscles involved in the expression of disgust. This shows that at least in some cases, facial mimicry is associated with emotional contagion, that is the phenomenon in which an observer manifests the same emotion observed in another.

Together these studies support the view that the MNS is an important network for imitative learning (Binder et al. 2017; Tramacere et al. 2017), and lesions

to the MNS core regions affected—critically and to a similar extent—not only the copying, but also the recognition of actions and gestures (Binder et al. 2017). Furthermore, mimicking and imitating others are not simply a matter of re-enacting or copying the sequence of others' movements. They also regard the emotional resonance with the person who executes the action and, in case of complex actions, the understanding of the observed goal. During mimicry, the MNS concurrently activates with the non-mirror fast route of the brain for emotional processing. In addition, during the reproduction of complex actions and understanding of other's behavior, the MNS interacts with the mentalizing system, comprising sectors of the dorsolateral prefrontal cortex, and the temporo-parietal junction (Sperduti et al. 2014; Tramacere & Ferrari 2016). Several studies have investigated the role of both the mirror and mentalizing systems when individuals are asked to infer others' emotions and intentions and to imitate novel actions (Vogeley 2017).

According to a widely accepted view, the MNS is involved in sensorimotor and somatosensory processing of action and emotion, while the mentalizing system is involved in the interpretation and understanding of others' behavior, and the identity of the individuals executing it (Catmur 2015; Michael et al. 2014). Although the disambiguation of the functional role of both systems is still object of investigations, evidence converges on the view that the MNS and the mentalizing system have a complementary and reciprocal role in various forms of copying and action understanding (Cole & Barraclough 2018) and that the interplay between activation and inhibition in the MNS is necessary for both imitation and mentalization (Basavaraju et al. 2020) in social situations.

It is important to noting that mechanisms of neural inhibition are likely to contribute to the probabilistic computation involved, at the network level, in the process of perception, copying of (or responding to) others' behavior. Single-cell studies in monkeys show in fact that during action observation, output of premotor neurons in the pyramidal tract are subjected to an overall suppression of their activity (Kraskov et al. 2009). Vigneswaran et al. (2013) demonstrated the existence of suppression of MNs activities also in the primary motor area. Mechanisms of neuronal inhibition have been interpreted as being instrumental to the observer to prevent automatic movements as the result of perceiving others' actions (Bonini 2016).

Further, new studies (Caggiano 2016; Albertini et al. 2021) highlight that MNs activate and interact in a more significant way than previously thought with non-agentive actions, supporting a more extensive involvement of the MNS in action-perception matching with non-social causality. The activation of the MNS for sensory-motor transformations that work at the interplay between social and mechanical causality, make action-perception matching mechanisms in the frontoparietal system even more interactive and relevant for understanding the evolution of imitative, communicative and technological skills in the human lineage (Stout & Hecht 2017).

For these reasons, we think it is important to contextualize the properties of MNs in broader network of action-perception matching mechanisms. As single neurons involved in the perception of the motor and somatosensory components of others' behavior, in the responding to others' action and object causal properties, MNs should be better considered a proxy of the degree of integration between brain areas involved in social perception, object motor properties and action. This is in line with network-level analyses in comparative and system neuroscience,

showing that the size of associative areas activated for social coordination tasks (with and without objects) increases as a function of social complexity, and that it targets the expansion of putative areas of the MNS in interaction with the mentalizing system (Yokoyama et al. 2021). These studies suggest that social and ecological factors impacted different but interacting circuits during human phylogeny, and that the comparative analyses of MNS activation and integration with other circuits can help highlighting evolutionary patterns of brain change (DeCasien et al. 2022).

3. Contrastive Accounts of the MNS Evolution

Because of the role of the MNS in imitation, mimicry, and social understanding, various scholars have analysed the developmental and evolutionary origin of MNs. Some theories have proposed that the MNS evolve in the hominin lineage, because it played a key role in how individuals process and apply information acquired through the interactions with others, both socially and culturally (Arbib 2017; Preston & de Waal 2002; Rizzolatti & Arbib 1998; Whiten 2013).

These proposals however never specified how exactly the MNS could have contributed to the evolution of cultural learning in humans, while perhaps implying that mechanisms of action-perception matching evolved (also) by natural selection and genetic evolution (Heyes 2010). Furthermore, while many suggestions have been done in the literature regarding the role of the MNS in human cognitive evolution, no account whatsoever have discussed the plausibility of the evolution of action-perception matching mechanisms in terms of theoretical models, genetics, and neurobiological evidence. We will therefore evaluate evidence about action-perception mechanisms and the MNS within a Culture per Biology account of cultural learning, which claims that human socio-cultural cognition is a learned product of both cultural *and* biological evolution.

We contrast the Culture per biology account with an opposite view, namely the Culture *not* biology account of cultural learning. The culture not biology account has been more specific on developmental and evolutionary causes affecting the properties of the MNS. It claims that crucial mechanisms implied in human cultural learning are not the result of genetic evolution, but a learned product of cultural evolution and general processed of learning (Heyes 2014, 2016, 2018). Consequently, according to this account, the specific brain processes involved in imitation, mimicry and mentalizing are cultural tools inherited by social and cultural learning and are not in our genes (Heyes 2016, 2018). The neurobiological repertoire that we utilize for imitating others, for thinking about others' minds, and for learning language is acquired through socio-cultural learning in childhood rather than being dependent upon genetically inherited structures.

Note that the Cultural not biology account is *not* engaged in claiming that biology is unimportant in the evolution of human cognition, nor the Culture not biology account denies that humans' brain and cognitive capacities are genetically different from other animal species. The culture not biology account predicts that various aspects of human cognition have evolved under the pressure of natural selection in hominins, producing enhanced social motivation, facial preference and tolerance in the hominin lineage (Heyes 2018). Further, on this account, various general-purpose mechanisms have evolved during human phylogeny, and genetic evolution had a role in enhancing human associative learning capacities, mechanisms of inhibition and memory.

The claim that we associate with the Culture not biology account of cultural learning (and that we will critically evaluate) is only that natural selection and genetic evolution did not play a specific, direct role in the evolution of cultural learning skills, such as imitation, mimicry and social understanding. Because of the relevance of cultural learning in shaping human intelligence in development and evolution, it is important that the evaluation of existing accounts of the MNS considers its plausibility in the context of evolutionary theory and in relation of available neuroscientific evidence.

4. Evolutionary Models of the MNS

Because cultural learning is thought to be of fundamental importance in human evolution, evolutionary theory would predict that cognitive mechanisms for cultural learning could have been shaped by natural selection. Under this assumption, evolutionary biologists explore the potential effects of natural selection on cultural learning, and its associated neurocognitive mechanisms, such as the MNS (Arbib 2017; Preston & de Waal 2002; Whiten & van de Waal 2017).

A question that evolutionary models can answer is: "when do we expect to observe these mirroring phenomena in nature?". Some evolutionary models focus on the role of MNs in imitation. Neurons activating during the execution and the observation of an action evolve in autonomous neural networks, where an observer learns to execute an action from observing another individual doing the same. The authors thus suggest that a selective pressure for imitation could have a key role in the evolution of the MNS (Borenstein & Ruppin 2005). Note that these evolutionary simulations only require their neurons to emerge via Hebbian learning, while the structure of the network evolves. Learning and evolution mutually contribute to the emergence of the MNS and have complementary roles: the overall structure and connectivity of the neural network is shaped by natural selection and facilitate the development of MNs in ontogeny through learning[1].

One may object that we don't know whether a selective pressure for imitation was present and sufficient to shape neural systems with mirror properties, considering that in the animals where MNs have been primarily investigated (such as macaques), copying an action from a demonstrator does not seem to be a pervasive behavioral strategy (Tennie et al. n.d.; Whiten 2013). Moreover, the activation of the MNS has also been observed in non-imitative contexts, and for other functions. This objection however loses force if considered through an evolutionary lens. While it is true that imitation is not the only function of the MNS, this does not rule out the possibility that more complex socio-cultural challenges put pressure on the neurobiological mechanisms of imitation during hominids' phylogeny (authors' forthcoming article; Barrett 2015; Jablonka, Ginsburg, and Dor 2019).

Another model shows that the MNS is expected to evolve in a variety of social interactions (Mafessoni & Lachmann 2019), and specifically both in cooperative (imitative) and non-cooperative (non-imitative) actions. According to this model, the MNS is expected to evolve not only when individuals need to activate

[1] The authors implemented an Hebbian model of associative learning because of its simplicity and biological realism at the level of single neuron. Additional studies using evolutionary autonomous neural networks could however be useful to explore the effects of other forms of associative learning (e.g. Rescorla-Wagner) and non-associative learning (reinforcement learning) which could alternatively play a role in the development of MNs.

underlining mechanisms of observed actions, but also when activating the same action or emotion of another can be disadvantageous. Using evolutionary game theory and computational simulations, the model compares two different learning strategies, differing in their underlying architecture and in the type of information used for learning.

Firstly, the model demonstrates that mimicking perceived actions and emotions can provide important advantages in increasing complex socio-cultural contexts. The advantage of activating mirroring mechanisms here stems from the fact that in complex social environment, individuals have to take into account many variables to predict others' behaviors and discriminate it rapidly. Thus, strategies exclusively based on observing other individuals may provide an insufficient amount of information, compared to strategies based on the activation of mirroring mechanisms. Furthermore, in Mafessoni and Lachmann's model, the recruitment of the own cognitive machinery is evolutionary advantageous also when individuals possess different—or even competing—goals. In this way, the model can explain the observation that MNs are integrated in neural networks supporting a functional interplay between activation and inhibition (see Section 2 above), to prevent the automatic activation of the observed behavior.

Initial evolutionary models only focused on cases in which doing what others do and feeling what they feel is beneficial. This is the case of the model of Borenstein and Ruppin 2005 regarding the role of the MNS in the evolution of imitation, but also of other models (see (Akçay et al. 2009; Nakahashi & Ohtsuki 2015) which exemplified the role of action-perception mechanisms in the evolution of emotional contagion, empathy and cooperation. These models are useful because they show how more complex socio-cultural environments, requiring cooperation, communication and copying of others' actions put pressure on the developmental properties of the MNS. Furthermore, it is with the model Mafessoni and Lachmann 2019 that we can appreciate how the MNS is activated and is expected to develop even when the agent responds to the actor by executing a different behavior. All together these models suggest that natural selection would operate on the developmental properties of the MNS as a function of socio-cultural complexity.

In sum, evolutionary models suggest that, under complex socio-cultural interactions, natural selection creates the scaffold upon which individual experience shapes neural connections *via learning*, and support that view the mechanisms of action-perception matching can evolve in the brain to sub-serving a wide spectrum of flexible cognitive processes, from social to cultural cognition, and from cooperative to competitive interactions. Finally, neurophysiological evidence discussed above, and evolutionary models suggest broadening the target of evolutionary analyses to the properties of action-perception matching network, instead of only focusing on single neurons, such as MNs. The evolution of cultural cognition as based on action-perception matching mechanisms, such as the MNS, must necessarily consider the properties of interacting brain mechanisms in socio-cultural learning.

This is in stark contrast with the two main, opposite accounts of the evolution of cultural learning presented above. On the culture per biology account, cultural learning in humans is enhanced because of a process of direct selection pressure on its neural basis, the MNS. In contrast, on the culture not biology account, cultural learning and a fortiori the MNS are exclusively side-effects of the increased learning and cognitive potentiality inherited by hominins during phylogeny. Both

accounts analyse the evolutionary properties of the MNS in isolation and disregard the retroactive feedback between culture and biological evolution on the developmental and evolutionary properties of the brain networks where the MNS is embedded.

5. Is the Culture Not Biology Account Compatible with Evolutionary Theory?

While evolutionary models suggest that both natural selection and learning had a role in the evolution of the MNS, the Culture not biology account claims that only learning is responsible for the emergence of the MNS (Cook et al. 2014; Heyes 2010). An assumption of this account is that learning and biological evolution have been mutually exclusive in the emergence of cultural learning. In contrast, evolutionary models do not neglect the role of learning in favour of a process of natural selection. Natural selection is seen as promoting the most efficient learning mechanisms suited for cultural interactions, rather than determining the exact behaviours to be learned.

However, an important caveat of evolutionary models is that they cannot prove conclusively that biological traits, such as the MNS, evolved in response to a specific selection pressure, but only show whether certain explanations are plausible. In addition, and in line with the assumption of the Culture not biology account, not every biological phenotype trait contributing to the survival and reproduction of an individual is shaped by natural selection. Considering that not every trait contributing to the individual fitness is shaped by natural selection, the Culture not biology account, in which biological evolution did not shape the MNS, could be reconciled with evolutionary theory on the basis of two main arguments.

First, one could argue that the MNS has no functional role; therefore, natural selection would not exert any effect on these neural mechanisms: we call it the "no function, no selection hypothesis". This hypothesis can be recognized in the arguments of authors raising doubts on the role of MNs in social cognition (Hickok 2010, 2014). However, there is increasing evidence that mirroring mechanisms are functionally recruited in a variety of contexts during social perception, imitation and mentalizing (see section 2). Further, we have seen that evolutionary models predict that mirroring mechanisms are expected to evolve as a function of the complexity of social interactions.

A second argument against a role of natural selection in shaping the MNS could state that the MNS does have a functional role, but it emerges in ontogeny as an epiphenomenon of associative learning, which have wide functional roles in a variety of different contexts besides social cognition. We call it the "function, no selection hypothesis". According to this hypothesis, although MNs have a functional role in social cognition, natural selection does not exert any effect on their developmental dynamics. How the "function, no selection hypothesis" can explain that the MNS is not affected by natural selection, while it does have a social cognitive function? One explanation offered by evolutionary theory is that the effects of natural selection are hindered by learning. If associative learning is sufficient to develop efficiently a given trait, natural selection will be ineffective, because all individuals will be able to develop the phenotype regardless of the presence of the biological trait.

In line with this idea, the Culture not biology account has suggested that domain-general associative learning is both necessary and sufficient for the

development of the MNS (Heyes 2010; Cook et al. 2014): If MNS could develop easily during ontogeny as a consequence of general processes of learning, no selective pressure is required to evolve biological structures facilitating its development (Heyes 2018).

This view has been defended through two main arguments. Firstly, because the activation of the MNS is largely affected by learning and plasticity, this system has not evolved by natural selection and genetic evolution to support cultural learning during hominin phylogeny (Catmur and Heyes 2021). Second, no specific heritable variation exists among individuals in their action-perception matching mechanisms because domain-general learning processes are sufficient for the development of MNS and its social functions (Heyes 2018). We discuss the first argument here, and the second argument in the next section.

Consider studies related to the plasticity of MNs after incongruent imitative training. These studies measure the activation of the MNS and associated muscular components, during the observation of bodily movements involving the use of incongruent muscles (Catmur et al. 2008, 2011). During action observation, the activation of somatotopic sectors of the MNS areas, and of the same muscles involved in the observed movement, is recorded (Buccino et al. 2001; Fadiga et al. 2005). In contrast, training an individual to perform a specific bodily movement during the observation of an incongruent movement, seems to lead to the emergence of "countermirror" responses, i.e., the activation of congruent areas of the MNS during the observation of incongruent actions (Catmur et al. 2011). This plasticity has been taken to support the view of an exclusive role of associative learning in the development of the MNS. Crucially, the possibility that training could reverse the functioning of the MNS would exclude any role of natural selection in shaping action-perception matching mechanisms.

However, no studies so far have proved the existence of countermirror responses at the level of single neurons. Because studies on the reversibility of mirror responses have been exclusively conducted in humans, only indirect evidence of countermirror responses is available. Furthermore, debates are ongoing on how to best interpret countermirror experiments. Some scholars have suggested and provided interesting evidence for counter imitative responses depending on descending inhibitory projections from prefrontal cortex (Barchiesi & Cattaneo 2013; Ticini et al. 2017; Ubaldi et al. 2015) thus dismissing the possibility that non-mirroring imitative training can affect the properties of MNs on the fly.

It is important to add that, even if countermirror responses will be proved at the level of single neurons, this would speak against a role of biological evolution only if one acquires an idea of genetic evolution determining fix, and unchangeable properties of single neurons, rather than facilitating the development of neural networks with various functional properties (Ferrari et al. 2013; Barrett 2015, plus see Tramacere 2022). Yet, as research on the plastic, contextual properties of cortical neurons advance, it shows that this conclusion is not realistic.

For example, visual neurons in the different cortex layers possess coding properties that specify their excitability to various characteristics of the visual receptive field. However, under experimental conditions, these properties can be modulated and enriched with new types of responses (Tolias et al. 2005), suggesting that the plasticity of visual neurons does not exclude that biological factor contribute to the evolution of their (visual) coding properties.

To conclude, while a Culture not biology account of cultural learning is in principle compatible with evolutionary theory, the argument of developmental

plasticity of the MNS and cultural learning is inconclusive to dismiss a role of natural selection during hominin phylogeny.

In the next section, we will discuss evidence related to presence of specific heritable variations in cultural learning and the MNS (as a discussion of the second argument above), to suggest that the Culture per biology account of cultural learning is not only plausible, but it also deserves more attention in future research.

6. Empirical Evidence for the Culture per Biology Account

In this section, we discuss empirical evidence that are against the arguments brought from the Culture not biology account of cultural learning, and that are compatible with the Culture per biology account of cultural learning. Specifically, we show that specific heritable variations exist for action-perception matching mechanisms and that therefore the learning mechanisms at the basis of the MNS could have evolve *also* through genetic evolution and not *only* for cultural evolution, in a wider frontoparietal network supporting inhibitory and mentalizing functions.

Evidence for a role of genetic factors in shaping the recruitment of the MNS in social tasks regards action-perception matching experiments in hand actions. By comparing monozygotic and dizygotic twins, researchers show that the activation of the Inferior Parietal Lobule, a MNS region activating during hand action observation and execution, is affected by genetic factors (Araki et al. 2017). In addition, a study shows that a genetic polymorphism affects individual variability in the capacity of visuomotor associative learning (Taschereau-Dumouchel et al. 2016).

The Culture not biology account could explain these results by saying that that genetic variability is not specific to action-perception matching but relates to domain-general intelligence. On this view, the genetic variants affecting the activation of the MNS during the perception of others' behavior, would also equally affect individual associative learning or memory ability in various contexts. In contrast, the Culture per biology account predicts that the MNS retains some forms of specificity, and that operations performed by action-perception matching networks are dissociable from other networks.

In line with the latter hypothesis, consider early phenomena of facial mimicry. Psychological studies show that the frequency of maternal facial gestures, predict patterns of facial mimicry in neonates and in infants (Carina et al. 2018). However, genetic factors are also likely to play a role. Global genetic variations are associated with patterns of neural responses to faces: during observation of facial expression, a stronger activation in classical mirror areas is predicted by global pattern of genetic variance (Dickie et al. 2014). An fMRI study of children and adolescents with deficits in face processing as result of 22q11.2 deletion syndrome, show decreased neural activation in cortical mirror areas (Azuma et al. 2015). Further, the level of norepinephrine in the brain strongly correlates with attention to facial expression, but not with the regulation of emotional cues (Yang et al. 2016), suggesting that a variety of biological factors can exert effects on the brain and behavioral correlates of facial execution and perception matching.

As we have seen, in cases like that of hand behavior, individual learning might have provided the context for the evolution of certain action-perception mechanisms in a social perspective. This is less plausible for other instances of

action-perception, such as that of face coordination. It is true, as the Culture not biology account claims (Heyes 2016), that in contemporary cultural contexts, individuals can learn associating their own facial movements by observing their facial expressions in the mirrors. However, it is unlikely that a genetic pressure for mirror self-recognition has been present during hominin phylogeny. It is instead more likely that the genetic variability associated with facial mimicry and with the action-perception matching mechanism underlining it, has been targeted by natural selection during human phylogeny because of the increased socio-cultural pressure of facial mimicry associated with gestural communication and language development (Tramacere et al. 2017; Tramacere & Ferrari 2016).

Much evidence speaks in favor of this view. Firstly, humans have evolved mimetic muscles that are mainly involved in facial display and speaking, and poorly involved in eating functions (Burrows 2008; Burrows et al. 2016; Schmidt & Cohn 2001). Second, compared to other primate species, human mimetic muscles are highly cordialized and controlled by action-perception matching mechanisms (Ginatempo et al. 2020; Pilurzi et al. 2020), making it plausible that natural selection has operated on the genetic bases of facial mimicry to allow hominins learning facial displays and communication in socio-cultural contexts. Importantly, there is no need to think that natural selection operating on genetic variants had produce determined and fix learning mechanisms, which are not affected by associative learning (Authors' forthcoming article).

Further support for the Culture per biology hypothesis comes from the studies in the clinical field. The activation of the MNS in a social context is associated with mechanisms of neural inhibition, suppressing automatic imitative responses during action observation. The mechanism of neural inhibition during others' action observation seems to be a consequence of the activation of non-mirror areas, such as the prefrontal cortex, the temporo-parietal junction, and the front opercular cortex modulating neural activity across the MNS (Cross et al. 2013). In some cases, the inhibition mechanism is impaired, resulting in neurological disorders known as echophenomena (Ganos et al. 2012). These comprise both echopraxia, that is the automatic repetition of actions; and echolalia, namely the automatic reproduction of sounds and speech (Stengel 1947). Interestingly, although echopraxia and echolalia are often the consequence of deficits in motor activation during action perception, many subjects presenting motor impairments, such as tics or unwilling repetitive movements, are not affected by echophenomena (Fen et al. 2001). This suggests that the neural mechanisms associated with action observation are not a mere generalization of those governing mechanisms of general intelligence, and that specifically to this case, deficits in motor inhibition during actions observation do not necessarily follow deficits in motor inhibition during action execution.

Ecophenomena are not the only cases where variability in the properties of activation of the MNS during action observation do not directly correlate with variations in motor skills. Lesions to the inferior parietal lobule have long been known to cause apraxia, an impairment in the ability to recognize or imitate actions in the absence of elementary sensorimotor deficits (Goldenberg & Karnath 2006). In subjects with Down Syndrome, only during action observation, but not during execution, the MNS shows decreased activation, as compared to control subjects (Virji-Babul et al. 2010). Intriguingly, in these subjects a strength in imitative functions is often observed (Vanvuchelen 2016). Further, the degree of hand dexterity of different individuals modulates MNS regions only during action

execution, but not during action observation (Plata Bello et al. 2014), offering additional support for the hypothesis that the MNS do not varies simply as a function of previous motor experience with the same action.

These results suggest that the activation of the MNS is not a mere by-product of domain-general process of associative learning. Further, they show that strategies based on neural mirroring are relatively independent from other learning strategies, even though integrated in functional networks beyond MNs. Neural mirroring and non-mirroring learning strategies are not only distinguishable at the theoretical level, but they are also dissociable at the neural level. This hypothesis is supported by a recent study (Carrillo et al. 2019) suggesting that in the rat, selected neurons in Anterior Cingulate Cortex, a limbic region of the brain, respond preferentially to the experience of distress in self and others, but less to a conditional stimulus associated with distress in a first-person perspective.

To conclude, we stress that these evidence shows that global pattern of genetic variants produce effect on the characteristics of the circuits where MNs are present and work, as a whole, at a network scale. Genetic variants affecting the connectivity between mirror and non-mirror areas, mechanisms of social attention, and of cortical inhibition, synergistically interact with learning during the development of the MNS, and both genes and learning are likely to produce constraint to the emergence of mirror structures and functions. Further, because evolutionary models are compatible with the view that natural selection processes on genes and general learning mechanisms of development are not mutually exclusive, the Culture per biology account of cultural learning is not only biologically plausible, but also deserves more attention in future research.

7. The Cultural and Biological Evolution of the Human MNS

In this paper, we discuss an evolutionary hypothesis: if a neurocognitive function increases individual fitness, then it is likely that natural selection would shape it. This does not imply any genetic determinism: general processes of learning can play a predominant role in the development of this neurocognitive function, and its modulation and tuning to the socio-cultural context. At the same time, natural selection would shape the learning mechanisms at its basis, and the modality of its interaction with other neural and non-neural physiological processes.

Accordingly, we have seen how several lines of evidence suggest that both natural selection and learning could have played a role in the evolution of the MNS, and its functional recruitment in the social contexts. Various studies show the presence of interindividual variability in processes specifically affecting social cognition, part of which being genetically inheritable (Dickie et al. 2014; Araki et al. 2017). This makes difficult to rule out the effect of natural selection on the evolution of the MNS, and consequently to exclusively embrace the Culture not biology account of cultural learning to explain the evolution of human cultural cognition.

While the Culture not biology account of cultural learning has the merit of providing insights into the ontogeny of MNs, the Culture per biology account does allow formulating a series of interesting hypotheses and predictions. First, a variety of factors (from socio-cultural experiences to genetic variants) differentially predicts the variability of different social functions involving the MNS, and explain their heritability across generations and context. Second, it could be necessary to consider various Mirror Neuron Systems (MNSs): the activation of

different types of MNs in different areas can underlie the perception of different types of actions and emotions; code the execution-perception matching centered on the use of different biological effectors (such as manual and oro-facial movements); and being involved through the interactions with other neural mechanisms in various social functions (Tramacere and Moore 2018; Tramacere, Pievani, and Ferrari 2017). Third, the functional recruitment of the MNS, together with its interactions with other networks and modulatory factors, would be constraint both by biology and learning, and help to explain the development and evolution of social functions, such as cooperation, mentalizing and imitation.

As a result, the MNS could be considered both as a neurobiological cause of socio-cultural learning, whose characteristics will be genetically influenced and environmentally regulated, and as a result of it (Del Giudice et al. 2009; Ferrari et al. 2013). This means that genes and learning are not opposed causes of the neurodevelopmental processes, nor they are mutually exclusive. On the contrary, biological factors such as genes, and socio-cultural experiences reciprocally regulate each other during the development of the MNSs and associated functional outcomes through associative learning.

We suggest that future research should explore connections between biological inheritance and cultural learning in the emergence of relatively interconnected neurocognitive functions. Numerous questions relevant for understanding cultural evolution can be addressed by investigating the biological bases of human cultural cognition. Assuming, in line with the evolutionary models discussed here, that the MNS become more relevant in species living in more complex environments, how mirroring processes evolve in modern humans? How do the various MNSs interact with higher level cognitive abilities used in social cognition, such as mentalizing and imitation? How do genetic variation and environmental factors like culture interact in the development of these higher-level cognitive functions?

We encourage here the development of theoretical frameworks providing links between cross-cultural behavioral research and the fields of genetics and neurosciences, which can be able to harness the vast amount of data that are becoming available to us through the development of novel investigative techniques. Paramount to this framework will be the understanding of the interaction between the various causes and mechanisms involved in the evolution of social cognition and culture.

References

Akçay, E., Cleve, J.V., Feldman, M.W., & Roughgarden, J. 2009, "A Theory for the Evolution of Other-Regard Integrating Proximate and Ultimate Perspectives", *Proceedings of the National Academy of Sciences*, 106, 45, 19061-66.

Araki, T., Onishi, M., Yanagisawa, T., Hirata, M., Watanabe, Y., Ogata, S., Hayakawa, K., Honda, C., Watanabe, M., Iwatani, Y., & Yorifuji, S. 2017, "Frequency-Specific Genetic Influence on Inferior Parietal Lobule Activation Commonly Observed during Action Observation and Execution", *Scientific Reports*, 7, 1, 17660.

Arbib, M.A. 2017, "Toward the Language-Ready Brain: Biological Evolution and Primate Comparisons", *Psychonomic Bulletin & Review*, 24, 1, 142-50.

Arnstein, D., Cui, F., Keysers, C., Maurits, N.M., & Gazzola, V. 2011, "μ-Suppression during Action Observation and Execution Correlates with BOLD in Dorsal Premotor, Inferior Parietal, and SI Cortices", *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 31, 40, 14243-49.

Azuma, R., Deeley, Q., Campbell, L.E., Daly, E.M., Giampietro, V., Brammer, M.J., Murphy, K.C., & Murphy, D.G. 2015, "An fMRI Study of Facial Emotion Processing in Children and Adolescents with 22q11.2 Deletion Syndrome", *Journal of Neurodevelopmental Disorders*, 7, (1), 1.

Barchiesi, G. & Cattaneo, L. 2013, "Early and Late Motor Responses to Action Observation", *Social Cognitive and Affective Neuroscience*, 8, 6, 711-19, DOI: 10.1093/scan/nss049

Barrett, H.C. 2015, *The Shape of Thought: How Mental Adaptations Evolve*, Oxford: Oxford University Press.

Basavaraju, R., Mehta, U.M., & Thirthalli, J. 2020, "Elevated Mirror Neuron System Activity Is Associated with Impaired Theory of Mind in Mania", *Asian Journal of Psychiatry*, 47, 101862.

Boesch, C. 2007, "What Makes Us Human (Homo Sapiens)? The Challenge of Cognitive Cross-Species Comparison", *Journal of Comparative Psychology*, 121, 3, 227-40.

Bonini, L. 2016, "The Extended Mirror Neuron Network: Anatomy, Origin, and Functions", *The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology and Psychiatry*, number, pages.

Borenstein, E. & Ruppin, E. 2005, "The Evolution of Imitation and Mirror Neurons in Adaptive Agents, *Cognitive Systems Research*, 6, 3, 229-42.

Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., & Freund, H.J. 2001, "Action Observation Activates Premotor and Parietal Areas in a Somatotopic Manner: An fMRI Study", *The European Journal of Neuroscience*, 13, 2, 400-404.

Burrows, A.M. 2008, "The Facial Expression Musculature in Primates and Its Evolutionary Significance", *BioEssays: News and Reviews in Molecular, Cellular and Developmental Biology*, 30, 3, 212-25.

Burrows, A.M., Li, L., Waller, B.M., & Micheletta, J. 2016, "Social Variables Exert Selective Pressures in the Evolution and Form of Primate Mimetic Musculature", *Journal of Anatomy*, 228, 4, 595-607.

Carrillo, M., Han, Y., Migliorati, F., Liu, M., Gazzola, V., & Keysers, C. 2019, "Emotional Mirror Neurons in the Rat's Anterior Cingulate Cortex", *Current Biology: CB*, 29, 8, 1301-1312.e6.

Caspers, S., Zilles, K., Laird, A.R., & Eickhoff, S.B. 2010, "ALE Meta-analysis of Action Observation and Imitation in the Human Brain", *NeuroImage*, 50, 3, 1148-67.

Catmur, C. 2015, "Understanding Intentions from Actions: Direct Perception, Inference, and the Roles of Mirror and Mentalizing Systems", *Consciousness and Cognition*, 36, 426-33.

Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., & Heyes, C. 2008, "Through the Looking Glass: Counter-mirror Activation Following Incompatible Sensorimotor Learning", *The European Journal of Neuroscience*, 28, 6, 1208-15.

Catmur, C., Mars, R.B., Rushworth, M.F., & Heyes, C. 2011, "Making Mirrors: Premotor Cortex Stimulation Enhances Mirror and Counter-mirror Motor Facilitation", *Journal of Cognitive Neuroscience*, 23, 9, 2352-62.

Cole, E.J. & Barraclough, N.E. 2018, "Timing of Mirror System Activation when Inferring the Intentions of Others", *Brain Research*, 1700, 109-117.

Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. 2014, "Mirror Neurons: From Origin to Function", *The Behavioral and Brain Sciences*, 37, 2, 177-92.

Cross, K.A., & Iacoboni, M. 2014, "To Imitate or Not: Avoiding Imitation involves Preparatory Inhibition of Motor Resonance", *NeuroImage*, 91, 228-36.

Cross, K.A., Torrisi, S., Reynolds Losin, E.A., & Iacoboni, M. 2013, "Controlling Automatic Imitative Tendencies: Interactions between Mirror Neuron and Cognitive Control Systems", *NeuroImage*, 83, 493-504.

DeCasien, A.R., Barton, R.A., & Higham, J.P. 2022, "Understanding the Human brain: Insights from Comparative Biology", *Trends in Cognitive Sciences*, 26, 5, 432-45.

Del Giudice, M., Manera, V., & Keysers, C. 2009, "Programmed to Learn? The Ontogeny of Mirror Neurons", *Developmental Science*, 12, 2, 350-63.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. 1992, "Understanding Motor Events: A Neurophysiological Study", *Experimental Brain Research*, 91, 1, 176-80.

Dickie, E.W., Tahmasebi, A., French, L., Kovacevic, N., Banaschewski, T., Barker, G.J., Bokde, A., Büchel, C., Conrod, P., Flor, H., Garavan, H., Gallinat, J., Gowland, P., Heinz, A., Ittermann, B., Lawrence, C., Mann, K., Martinot, J.-L., Nees, F., … IMAGEN consortium 2014, "Global Genetic Variations Predict Brain Response to Faces", *PLoS Genetics*, 10, 8, e1004523.

Fadiga, L., Craighero, L., & Olivier, E. 2005, "Human Motor Cortex Excitability during the Perception of Others' Action", *Current Opinion in Neurobiology*, 15, 2, 213-18.

Fen, C.H., Barbosa, E.R., & Miguel, E.C. 2001, "[Gilles de la Tourette Syndrome: A Clinical Study on 58 Cases]". *Arquivos De Neuro-Psiquiatria*, 59, 3-B, 729-32.

Ferrari, P.F., Tramacere, A., Simpson, E.A., & Iriki, A. 2013, "Mirror Neurons through the Lens of Epigenetics", *Trends in Cognitive Sciences*, 17, 9, 450-57.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. 1996, "Action Recognition in the Premotor Cortex", *Brain: A Journal of Neurology*, 119, Pt 2, 593-609.

Ganos, C., Ogrzal, T., Schnitzler, A., & Münchau, A. 2012, "The Pathophysiology of Echopraxia/Echolalia: Relevance to Gilles De La Tourette Syndrome", *Movement Disorders*, 27, 10, 1222-29.

Gentilucci, M. & Corballis, M.C. 2006, "From Manual Gesture to Speech: A Gradual Transition", *Neuroscience and Biobehavioral Reviews*, 30, 7, 949-60.

Ginatempo, F., Manzo, N., Ibanez-Pereda, J., Rocchi, L., Rothwell, J.C., & Deriu, F. 2020, "Happy Faces Selectively Increase the Excitability of Cortical Neurons Innervating Frowning Muscles of the Mouth", *Experimental Brain Research*, 238, 4, 1043-49.

Giret, N., Edeline, J.-M., & Del Negro, C. 2017, "Neural Mechanisms of Vocal Imitation: The Role of Sleep Replay in Shaping Mirror Neurons", *Neuroscience and Biobehavioral Reviews*, 77, 58-73.

Goldenberg, G. & Karnath, H.-O. 2006, "The Neural Basis of Imitation Is Body Part Specific", *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 26, 23, 6282-87.

Hage, S.R. 2018, "Auditory and Audio-Vocal Responses of Single Neurons in the Monkey Ventral Premotor Cortex", *Hearing Research*, 366, 82-89.

Hage, S.R. & Nieder, A. 2015, "Audio-vocal Interaction in Single Neurons of the Monkey Ventrolateral Prefrontal Cortex", *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 35, 18, 7030-40.

Hanuschkin, A., Ganguli, S., & Hahnloser, R.H.R. 2013, "A Hebbian Learning Rule Gives Rise to Mirror Neurons and Links Them to Control Theoretic Inverse Models", *Frontiers in Neural Circuits*, 7, 106.

Heyes, C. 2010, "Where Do Mirror Neurons Come From?", *Neuroscience and Biobehavioral Reviews*, 34, 4, 575-83.

Heyes, C. 2014, "Tinbergen on Mirror Neurons"; *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 369, 1644, 20130180.

Heyes, C. 2016, "Imitation: Not in Our Genes", *Current Biology: CB*, 26, 10, R412-14.

Heyes, C. 2018, *Cognitive Gadgets: The Cultural Evolution of Thinking*, Cambridge, MA: Harvard University Press.

Hickok, G. 2010, "The Role of Mirror Neurons in Speech and Language Processing", *Brain and Language*, 112, 1, 1-2.

Hickok, G. 2014, *The Myth of Mirror Neurons: The Real Neuroscience of Communication and Cognition*, New York: W.W. Norton & Company.

Hogeveen, J., Chartrand, T.L., & Obhi, S.S. 2015, "Social Mimicry Enhances Mu-Suppression During Action Observation", *Cerebral Cortex*, 25, 8, 2076-82.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., & Rizzolatti, G. 1999, "Cortical Mechanisms of Human Imitation", *Science*, 286, 5449, 2526-28.

Jablonka, E., Ginsburg, S., & Dor, D. 2019, "Cognitive Gadgets and Genetic Accommodation", *Behavioral and Brain Sciences*, 42e, 178.

Kraskov, A., Dancause, N., Quallo, M.M., Shepherd, S., & Lemon, R.N. 2009, "Corticospinal Neurons in Macaque Ventral Premotor Cortex with Mirror Properties: A Potential Mechanism for Action Suppression?", *Neuron*, 64, 6, 922-30.

Likowski, K.U., Mühlberger, A., Gerdes, A.B.M., Wieser, M.J., Pauli, P., & Weyers, P. 2012, "Facial Mimicry and the Mirror Neuron System: Simultaneous Acquisition of Facial Electromyography and Functional Magnetic Resonance Imaging", *Frontiers in Human Neuroscience*, 6, 214, DOI: 10.3389/fnhum.2012.00214.

Mafessoni, F. & Lachmann, M. 2019, "The Complexity of Understanding Others as the Evolutionary Origin of Empathy and Emotional Contagion", *Scientific Reports*, 9, 1, 5794.

Michael, J., Sandberg, K., Skewes, J., Wolf, T., Blicher, J., Overgaard, M., & Frith, C.D. 2014, "Continuous Theta-Burst Stimulation Demonstrates a Causal Role of Premotor Homunculus in Action Understanding", *Psychological Science*, 25, 4, 963-72.

Molenberghs, P., Cunnington, R., & Mattingley, J.B. 2012, "Brain Regions with Mirror Properties: A Meta-Analysis of 125 Human fMRI Studies", *Neuroscience and Biobehavioral Reviews*, 36, 1, 341-49.

Nakahashi, W. & Ohtsuki, H. 2015, "When Is Emotional Contagion Adaptive?", *Journal of Theoretical Biology*, 380, 480-88.

Parker, S.T. & Gibson, K.R. 1994, *"Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives*, Cambridge: Cambridge University Press.

Pilurzi, G., Ginatempo, F., Mercante, B., Cattaneo, L., Pavesi, G., Rothwell, J.C., & Deriu, F. 2020, "Role of Cutaneous and Proprioceptive Inputs in Sensorimotor

Integration and Plasticity occurring in the Facial Primary Motor Cortex", *The Journal of Physiology*, 598, 4, 839-51.

Plata Bello, J., Modroño, C., Marcano, F., & González-Mora, J.L. 2014, "The Mirror Neuron System and Motor Dexterity: What Happens?", *Neuroscience*, 275, 285-95.

Pope, S.M., Taglialatela, J.P., Skiba, S.A., & Hopkins, W.D. 2018, "Changes in Frontoparietotemporal Connectivity Following Do-As-I-Do Imitation Training in Chimpanzees (Pan Troglodytes)", *Journal of Cognitive Neuroscience*, 30, 3, 421-31.

Preston, S.D. & de Waal, F.B.M. 2002, "Empathy: Its Ultimate and Proximate Bases", *The Behavioral and Brain Sciences*, 25, 1, 1-20; Discussion 20-71.

Rizzolatti, G. & Arbib, M.A. 1998, "Language Within Our Grasp", *Trends in Neurosciences*, 21, 5, 188-94.

Roberts, T.F., & Mooney, R. 2013, "Motor Circuits Help Encode Auditory Memories of Vocal Models Used to Guide Vocal Learning", *Hearing Research*, 303, 48-57.

Schilbach, L., Eickhoff, S.B., Mojzisch, A., & Vogeley, K. 2008, "What's in a Smile? Neural Correlates of Facial Embodiment During Social Interaction", *Social Neuroscience*, 3, 1, 37-50.

Schmidt, K.L. & Cohn, J.F. 2001, "Human Facial Expressions as Adaptations: Evolutionary Questions in Facial Expression Research", *American Journal of Physical Anthropology*, Suppl. 33, 3-24.

Sperduti, M., Guionnet, S., Fossati, P., & Nadel, J. 2014, "Mirror Neuron System and Mentalizing System Connect during Online Social Interaction", *Cognitive Processing*, 15, 3, 307-16.

Stengel, E. 1947, A Clinical and Psychological Study of Echo-Reactions", *The Journal of Mental Science*, 93, 392, 598-612.

Stout, D. & Hecht, E.E. 2017, "Evolutionary Neuroscience of Cumulative Culture", *Proceedings of the National Academy of Sciences of the United States of America*, 114, 30, 7861-68.

Taschereau-Dumouchel, V., Hétu, S., Michon, P.-E., Vachon-Presseau, E., Massicotte, E., De Beaumont, L., Fecteau, S., Poirier, J., Mercier, C., Chagnon, Y. C., & Jackson, P.L. 2016, "BDNF Val66Met Polymorphism Influences Visuomotor Associative Learning and the Sensitivity to Action Observation", *Scientific Reports*, 6, 34907.

Tennie, C., Call, J., & Tomasello, M. 2009, "Push or Pull: Imitation vs. Emulation in Great Apes and Human Children", *Ethology*, 112, 12, 1159-69.

Ticini, L.F., Schütz-Bosbach, S., & Waszak, F. 2017, "Mirror and (Absence of) Counter-Mirror Responses to Action Sounds Measured with TMS", *Social Cognitive and Affective Neuroscience*, 12, 11, 1748-57.

Tolias, A.S., Keliris, G.A., Smirnakis, S.M., & Logothetis, N.K. 2005, "Neurons in Macaque Area V4 Acquire Directional Tuning after Adaptation to Motion Stimuli", *Nature Neuroscience*, 8, 5, 591.

Tramacere, A. & Ferrari, P.F. 2016, "Faces in the Mirror, From the Neuroscience of Mimicry to the Emergence of Mentalizing", *Journal of Anthropological Sciences = Rivista di Antropologia: JASS*, 94, 113-26.

Tramacere, A. & Moore, R. 2008, "Reconsidering the Role of Manual Imitation in Language Evolution", 37, 319-28.

Tramacere, A., Pievani, T., & Ferrari, P.F. 2017, "Mirror Neurons in the Tree of Life: Mosaic Evolution, Plasticity and Exaptation of Sensorimotor Matching Responses", *Biological Reviews of the Cambridge Philosophical Society*, 92, 3, 1819-41.

Tramacere, A., Wada, K., Okanoya, K., Iriki, A., & Ferrari, P.F. 2019, "Auditory-Motor Matching in Vocal Recognition and Imitative Learning", *Neuroscience*, 409, 223-34.

Ubaldi, S., Barchiesi, G., & Cattaneo, L. 2015, "Bottom-Up and Top-Down Visuomotor Responses to Action Observation", *Cerebral Cortex*, 25, 4, 1032-41.

Van Overwalle, F. & Baetens, K. 2009, "Understanding Others' Actions and Goals by Mirror and Mentalizing Systems: A Meta-Analysis", *NeuroImage*, 48, 3, 564-84.

van Schaik Carel P. & Burkart Judith M. 2011, "Social Learning and Evolution: The Cultural Intelligence Hypothesis", *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 1567, 1008-16.

Vanvuchelen, M. 2016, "A Qualitative Analysis of Imitation Performances of Preschoolers with Down Syndrome", *American Journal on Intellectual and Developmental Disabilities*, 121, 3, 266-75.

Vigneswaran, G., Philipp, R., Lemon, R.N., & Kraskov, A. 2013, "M1 Corticospinal Mirror Neurons and Their Role in Movement Suppression During Action Observation", *Current Biology: CB*, 23, 3, 236-43.

Virji-Babul, N., Moiseev, A., Cheung, T., Weeks, D.J., Cheyne, D., & Ribary, U. 2010, "Neural Mechanisms Underlying Action Observation in Adults with Down syndrome", *American Journal on Intellectual and Developmental Disabilities*, 115, 2, 113-27.

Vogeley, K. 2017, "Two Social Brains: Neural Mechanisms of Intersubjectivity", *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 372, 1727, 20160245.

Whiten, A. 2013, "Monkeys, Apes, Imitation and Mirror Neurons", *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior*, 49, 10, 2941-43.

Whiten, A. & van de Waal, E. 2017, "Social Learning, Culture and the 'Socio-cultural Brain' of Human and Non-Human Primates", *Neuroscience and Biobehavioral Reviews*, 82, 58-75.

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., & Rizzolatti, G. 2003, "Both of Us Disgusted in My Insula: The Common Neural Basis of Seeing and Feeling Disgust", *Neuron*, 40, 3, 655-64.

Woensdregt, M., Cummins, C., & Smith, K. 2021, "A Computational Model of the Cultural Co-evolution of Language and Mindreading", *Synthese*, 199, 1, 1347-85.

Yang, X., Ru, W., Wang, B., Gao, X., Yang, L., Li, S., Xi, S., & Gong, P. 2016, "Investigating the Genetic Basis of Attention to Facial Expressions: The Role of the Norepinephrine Transporter Gene", *Psychiatric Genetics*, 26, 6, 266-71.

Yokoyama, C., Autio, J.A., Ikeda, T., Sallet, J., Mars, R.B., Van Essen, D.C., Glasser, M.F., Sadato, N., & Hayashi, T. 2021, "Comparative Connectomics of the Primate Social Brain", *NeuroImage*, 245, 118693.