

Evolution of mirror systems: a simple mechanism for complex cognitive functions

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Mirror neurons (MNs) were first discovered in monkeys and subsequently in humans and birds. While MNs are deemed to play a number of high-level cognitive functions, here we propose that they serve a unitary form of sensorimotor recognition of others' behavior. We caution that this basic function should not be confounded with the higher order functions that stem from the wider cortical systems in which MNs are embedded. Depending on the species, MNs function at different levels of motor event recognition, from motor goals to fine grained movements, thus contributing to social learning and imitative phenomena. Recent studies show that MNs coding has a prospective nature, suggesting that MNs also play a role in anticipating and predicting the behavior of others during social interactions. The presence of mirroring mechanisms in subcortical structures related to visceromotor reactions and the large diffusion of imitative phenomena among animals suggest that MN systems may be more ancient and widespread than previously thought.

Keywords: mirror neurons; monkey; social cognition; electrophysiology

Introduction

Mirror neurons (MNs), originally identified in the macaque premotor cortex, are a peculiar class of cells that fire both when the monkey performs a motor act (such as grasping, breaking, or tearing) and when it observes a human^{1,2} or another monkey³ performing a similar act. The activation of one's own motor repertoire, while observing others acting, immediately suggested that individuals can exploit their own motor knowledge for recognizing different types of observed actions.^{4,5} Since their discovery, however, MNs have been related to a broad set of potential cognitive functions, creating the impression of MNs as "handy-neurons" and leading to skepticism of their actual explanatory power.⁶

Here, we will review evidence showing that the basic and general function of MNs, described up to now in birds, monkeys, and humans, is a distinct form of recognition of others' behavior based on the activation of one's own motor representations. Furthermore, we will propose that their general and

unitary function (action recognition) is essential to, but should not be confounded with, the higher order cognitive functions of the wider cortical systems in which MNs have been described.

We believe that this approach provides a framework for the identification of a broader evolutionary basis of MNs function, regardless of the level of complexity of the particular species in which they are found. Furthermore, it also helps us to understand the functional role of MNs in distinct domains of social cognition (such as perception, prediction, or learning) in relation to the ecological relevance of each domain for different species.

Action recognition at different levels of complexity

What do we mean by recognition?

The answer to this apparently easy question can help to solve many troubles related to the interpretation of neurophysiological findings on MNs. Literally, *recognition* stands for "know again, recall to mind,"

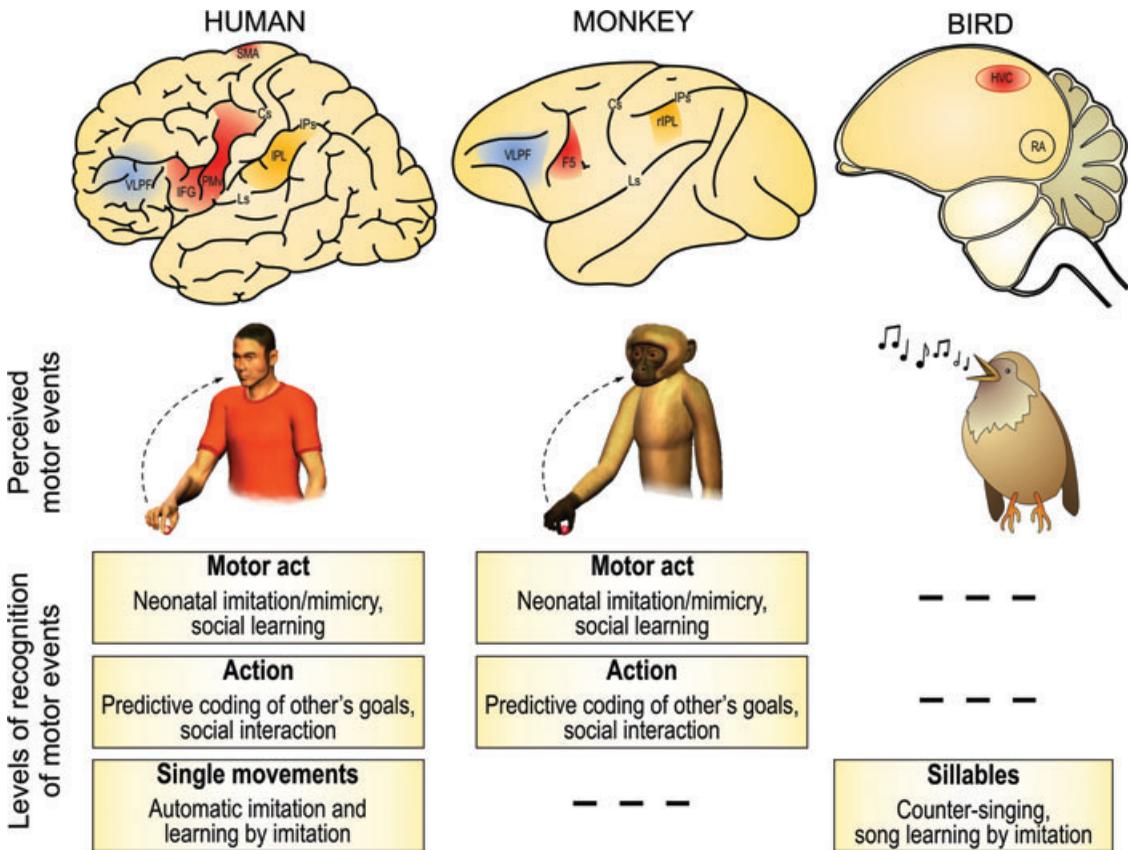


Figure 1. Schematic view of brain regions, coding properties, and functional roles of MNs in the brain of humans, monkeys, and birds. Cortical regions in red identify the crucial nodes of the MN system in the human and monkey cerebral cortex and in the HVC nucleus of the bird brain. The regions in yellow constitute the parietal node of the MN system in the human and monkey brains. Blue cortical regions represent a possible extension of the mirror system through an "indirect" prefrontal pathway.⁴³ VLPF, ventrolateral prefrontal cortex; IFG, inferior frontal gyrus; PMv, ventral premotor cortex; SMA, supplementary motor area; IPL, inferior parietal lobule; Cs, central sulcus; Ls, lateral sulcus; IPs, intraparietal sulcus; rIPL, rostral inferior parietal lobule; RA, robust nucleus of the arcopallium. F5 and HVC are letter-based names.

that is, identifying something or someone from previous encounters or knowledge. Therefore, recognizing others' actions implies the ability to form a link between their sensory description and the individual motor representations. This sensorimotor matching is exactly what MNs appear to do, at different levels of complexity, from motor acts to actions and up to fine-grained movements (see Fig. 1).

Mirroring the goal of observed motor acts

A single motor act, such as "grasping," is formed by various simple movements organized together in an appropriate temporal sequence (i.e., wrist rotation, finger extension, and flexion) in order to attain an immediate motor goal (i.e., taking possession of an object). This is a key organizing prin-

ciple of the cortical motor system.⁷ In fact, single neurons in the monkey ventral premotor cortex fire during the execution of a specific act (i.e., grasping); however, in some cases, they respond regardless of the specific effector used (right/left hand or the mouth)⁸ and even when the act is performed with tools requiring different movement patterns to grasp a target.⁹ The only motor aspect that appears to be common to all these conditions is the goal of the motor act. It has been suggested that the representation of motor acts in terms of their goal at the single neuron level serves to simplify the organization of voluntary movement,^{8,10-14} specifically by reducing the number of independent degrees of freedom to be controlled during performance.

Similarly, when observing others, monkey MNs can simplify the recognition of another's act by matching its sensory description with the corresponding motor representation in the observer's repertoire of motor goals. A consistent body of evidence shows that this matching occurs in several regions of the cortical motor system, namely premotor,^{2,15} primary motor,¹⁶ and parietal¹⁷ cortices. Monkey MNs selectively respond when observing the interaction between the hand² or mouth¹⁸ and a target, but not during the simple presentation of the target object or when viewing mimicked actions.² Furthermore, when observing grasping acts ending behind a screen that occludes the sight of hand–object interaction, MNs can still fire strongly, suggesting that minimal sensory information is sufficient to trigger the internal representation of the goal of the observed act.¹⁹ Interestingly, when hearing the characteristic sound of actions such as a peanut breaking or paper ripping, some premotor MNs with audio–visual properties can respond vigorously, despite the absence of visual information,²⁰ suggesting a consistent independence of MN activity from the modality of the afferent information triggering it.

A recent neurophysiological study involving single neuron recording in the human brain provided the first direct evidence of the existence of MNs in humans.²¹ However, the bulk of the data about human MNs are derived from imaging experiments that have described a cortical system of areas with “mirror” properties homologous to that of the monkey and referred to as “MN system.” More specifically, the core of the human MN system includes the inferior frontal gyrus and the adjacent ventral premotor cortex,^{22,23} the primary motor cortex,²⁴ and the posterior parietal cortex.²³ Neuroimaging²⁵ and neurophysiological^{26–28} studies have shown that, like monkey MNs, the activation of areas within the human MN system occurs not only while performing or viewing hand or mouth actions, but also when listening to the sound produced by an action done with the same effector, suggesting that goal coding is also a key feature of the human MN system. Further support for this view comes from neuropsychological studies on apraxic patients, which show that subjects with limb or bucco–facial apraxia are specifically impaired in the recognition of hand and mouth action-related sounds, respectively.²⁹

Recent studies aimed at exploring the cortical mechanism through which the brains of humans and monkeys represent tool use provide further support for the evolutionary relevance of a system coupling visual and motor representations of acts in terms of their goal. These fMRI experiments³⁰ have shown that a parietofrontal network, remarkably similar in both species, is activated during observation of grasping acts made with tools, as well as during observation and execution of hand grasping acts, in line with previous single neurons studies in monkeys.³¹ However, a specific sector of human inferior parietal lobule appears to be a region unique to hominid evolution as it is specifically activated in humans, but not monkeys, during observation of tool use. Interestingly, this is true even if monkeys were previously trained to proficiently use tools before fMRI experiments.³⁰ Thus, encoding motor acts in terms of their goal may endow the cortical motor system with a primitive, implicit representation of a causal means–end relationship. Although shared in part by humans and monkeys, this system can only be fully exploited for social learning phenomena within the complex machinery of the human brain.

Predictive mirroring of others' actions and social interaction

From the literature reviewed so far, the MN system appears to passively encode others' behavior regardless of the potential interaction that might occur between the observer and the observed agent. This is because the paradigms usually employed to study MNs minimize the opportunities for social interactions. However, recent data challenge this view, demonstrating that MN activity has a prospective nature, which may indicate the importance of the MN system in anticipating and predicting others' behavior.

A series of recent studies reported that in the monkey inferior parietal and ventral premotor cortices, grasping neurons can activate differently when the coded act is embedded into actions aimed at different goals, such as “grasp to eat” or “grasp to place.”^{17,32} Some of these neurons exhibited mirror-like properties by activating when a monkey observed an experimenter grasping. Interestingly, when the monkey performed the action, the neurons discharged differently compared with the observation of grasping depending upon the final

goal of the experimenter's action. Thus, although they fire during grasping motor acts, their discharge provides a predictive coding of the final action goal.

Such a predictive form of action recognition has also been demonstrated in humans in fMRI studies. For example, increased activation has been reported in MN areas when subjects were required to infer the agent's motor goal during the observation of grasping acts in different contexts.³³ Furthermore, transcranial magnetic stimulation (TMS) experiments have revealed that during action observation, the matching motor plan is loaded as a whole at the beginning of the observed movement and, once started, tends to proceed until its completion.³⁴ This finding strongly suggests that the neuronal substrates encoding successive motor chunks forming an action are anatomo-functionally linked together based on the final action goal. Indirect evidence supporting the existence of such a predictive mechanism in humans has also been provided by electromyographic (EMG) experiments in children.³⁵ When a child performed a grasp-to-eat action, the activity of muscles responsible for mouth opening began to rise at the very beginning of the arm reach-to-grasp phase, while no activation was reported when the child grasped an object to place it into a container located near the mouth. Interestingly, a similar result was obtained when children observed an experimenter doing the same actions: when the experimenter grasped food for bringing it to the mouth, there was early activation of the observer's mouth muscles during grasp-to-eat execution; however, during observation of grasp-to-place action, this activation was lacking. These findings suggest that both humans and monkeys are endowed with neural mechanisms capable of predictive recognition of the final goal underlying others' actions.

The predictive mirroring of others' behavior may be particularly important within natural social contexts, since actions of others often imply interactions with others. Further evidence suggesting a role of MNs in action recognition for social interaction is provided by a recent study³⁶ demonstrating that monkey MNs recorded from ventral premotor area F5 can discharge differently according to the location in space of the observed motor acts relative to the monkey. In particular, half of the recorded MNs increased their firing when the observed act was performed in the monkey's peripersonal space, while other MNs preferred the extrapersonal space. Inter-

estingly, a subset of these neurons encoded space in operational terms; indeed, they changed their selectivity for peri- or extrapersonal space according to the possibility of the monkey of interacting with the object. These findings suggest that in addition to encoding observed actions for recognition, space-selective MNs might indicate the choice of a forthcoming behavioral response during social interaction. These situations are extremely frequent in primates, for example, in the case of competitive behaviors, and produce changes in the self-other motion selectivity of cortical neurons in the monkey parietal cortex.³⁷ Although we lack direct evidence of similar effects in humans' brain during action observation, there is evidence from EEG data in human subjects demonstrating that the higher the degree of social interaction implied by the viewed stimuli, the stronger the μ -rhythm suppression.³⁸ This finding suggests that the human MN system can also recognize action for social interaction.

Another important line of evidence, provided by the discovery of parietal neurons mirroring the attention of others, suggests a crucial role of mirroring mechanisms for guiding social interaction. In fact, both humans and monkeys are capable of gaze-following,³⁹⁻⁴¹ that is, they can orient their gaze and attention in the direction other individuals are looking. Shepherd and coworkers⁴² found that single neurons in the lateral intraparietal area (LIP) of macaques, which activate when the monkey looked in a specific direction defining the neuron receptive field, also fired when an observed monkey looked in the preferred direction of the neuron. Interestingly, the timing of these modulations matched the time course of gaze-following behavior. Furthermore, imaging studies support the idea that similar mechanisms might exist in the human brain.⁴³

Taken together, these findings suggest that the core function of MNs is to match the external sensory description of an action observed or heard by an individual and its corresponding internal motor representation. The "automatic recognition" performed by MNs enables the emergence of properties that are well beyond the recognition function, but depend on the specific circuit of brain structures activated.⁴⁴ For example, recent evidence that F5 MN activity can directly affect the descending pathways of the corticospinal tract⁴⁵ indicates that the activation of MNs during action observation simultaneously constitute both the neuronal substrate for

the recognition of the observed action and, fundamental to the imitative process, the mechanism for its motor reenactment.

Precise mirroring of observed movements and learning by imitation

Recognizing motor events in terms of their goal appears to be the main feature of both human and monkey MN systems. On one hand, this broad level of description of the observed movements enables the essential information for action recognition and social interaction to be captured. On the other hand, this matching is not precise enough to enable another extremely important social function—learning by imitation. This ability critically requires an extremely precise form of recognition of others movement in order to copy it with high fidelity.

A fascinating example of highly precise mirroring has recently been provided by the discovery of audio-motor MNs in the sparrow forebrain. These neurons exhibit a singular motor response when the bird sings a specific song sequence, but they also respond with a temporally identical pattern of discharge to the auditory presentation of the same song sequence in other birds.⁴⁶ Moreover, the response boundaries in these neurons in response to changes in note duration accurately predict the categorical perceptual boundary that is typical of that sparrow population.⁴⁷ Thus, the audio-vocal mirror mechanism matches the sensory and motor description of single syllables of a song sequence in a highly precise way, providing the neural basis for the precise recognition of species-specific communicative vocal signals. Here, the matching appears to occur at the level of very specific, discrete “motor chunks” and their sensory consequences, very likely playing an important role in how species-specific songs are learned through imitative processes.^{48,49}

In humans, there is consistent evidence that cortical motor areas are activated during observations of simple movements (i.e., single joint displacements) with good spatial and temporal fidelity.^{50–53} This capacity could be the basis of the uniquely human ability to copy the exact pattern of totally new observed movements during imitation learning,^{54,55} and appears to rely on a large circuit encompassing the classical regions of the putative human MN system.^{44,56,57} In particular, distinct sectors of the prefrontal cortex would mediate the selection and combination of elementary motor representations

for the observed movements provided by the MN system. The presence of a similar neural mechanism for precise mirroring of discrete movements *in taxa* as distant as human and birds suggests that such a mechanism could have been evolved to support imitative phenomena in species with sophisticated communicative capacities.⁵⁸

Where do mirror systems come from?

Ontogeny

John Locke wrote that “no man’s knowledge here can go beyond his experience.”⁵⁹ This idea appears to be contradicted by several empirical findings in developmental psychology and neuroscience^{60,61} that suggest that specific sensorimotor skills and cognitive competences are somehow predetermined very early in infancy. In spite of this, it has also been shown that sensorimotor experience is crucial for shaping brain circuits by affecting the way the brain can process sensory information and control movement.^{62,63} It is, therefore, important to clarify whether our brains mirror others’ behaviors from birth or whether they need to learn in order to accomplish this.

Up to now, there has been no way for directly addressing this issue. However, an increasing amount of data suggest the existence of extremely early, if not even innate, automatic recognition mechanisms in both humans and monkeys. Indeed, behavioral data indicate that newborn macaques,⁶⁴ chimpanzees,⁶⁵ and humans⁶⁶ can imitate facial gestures. It is clear that infants do not have visual access to their own face. Thus, the “correspondence problem”⁶⁷ between the perceptual features of others’ facial gestures and the representations of the corresponding motor pattern in the observer’s brain is hard to solve from a purely associative learning perspective.⁶ In contrast, there is also evidence that infant macaques reared from birth without seeing faces can still recognize and discriminate faces two years later,⁶⁸ demonstrating an experience-independent ability to process faces. These behavioral phenomena clearly demonstrate the existence of an early functioning recognition mechanism, even though it has yet to be directly investigated whether this mechanism is based on MNs already properly functioning at birth.

The existence of some innate forms of a sensorimotor matching mechanism, possibly based on a MN system, does not imply in any way that learning

processes do not occur. On the contrary, sensorimotor experience has a crucial role in shaping the trajectory of MN system development and in refining the tuning of specific neuronal response properties. A recent proposal maintained that the visuomotor integration occurring in MNs for different effectors (hand and mouth) has different developmental trajectories and may be differentially sensitive to experience.⁶⁹ In the case of mouth MNs, the integration of visual and motor information necessary for facial mirroring should already be present very early in life (at least in its basic components),^{70,71} although the social environment at birth immediately starts to play a key role in shaping face mirroring. In fact, the primary sources of feedback infants receive about their own face gestures come from a caregiver. In both humans^{71,72} and monkeys,⁷³ caregivers often imitate infants' facial gestures, playing an important role in the development of the infant's social competence and, very likely, influencing the development of MNs responsive to face and mouth gestures.¹⁸ In contrast, the ontogenetic origin of hand MNs² very likely relies on different developmental routes. It has been proposed^{74–76} that the processes of visuomotor coupling can be strengthened through "Hebbian learning." For example, a certain population of premotor neurons can fire when the infant performs a particular arm/hand action that generates a simultaneous somatosensory, visual, and acoustic feedback related one's own moving hand. Because this feedback is synchronized to the motor discharge, it would increase the probability of having a sensorimotor matching at the single neuron (MN) level.

Recent ultrasonographic data^{77,78} suggest that this sensorimotor tuning may initiate prenatally, when fetuses start to refine their motor skills by moving in the womb. Once the neuronal connections have been pruned and well established for the visual guidance of the hand through sensorimotor experience, primarily after birth, these same circuits can activate when the infant observes an action performed by another individual. Likely, at this later stage, MNs become part of a larger functional circuit specifically committed for interpreting others' actions.

Phylogeny

Mirror systems represent a parsimonious mechanism to couple external sensory information with correspondent internal motor representations. This

matching process occurring at the single neuron level fits well with the common definition of *recognition*, that is, "recall to mind." Viewing or hearing actions, gestures, or vocalizations of others, despite the highly complex and variable physical features of the observed motion or the heard sound, immediately "recall to mind" a univocal motor idea: the motor representation corresponding to the experienced action. A direct route from sensory representations to the internal motor knowledge would make it possible to filter out most of the useless details and easily access to the content of the perceived input: motor goals, action goals, or discrete movements.

We have no direct evidence about the evolution of MN systems. However, observed behavior mirroring not only occurs in cortical areas involved in the control of specific effectors (i.e., arm and mouth), but also has been shown to occur in phylogenetically ancient structures, including the basal ganglia⁷⁹ and subcortical regions related to visceromotor reactions such as the insular⁸⁰ and cingulate⁸¹ cortices. This clearly suggests that several mirroring mechanisms could be more ancient than those originally discovered in primate neocortical areas. For example, emotional responses have recently been evoked in awake monkeys by electrical stimulation of the insula, supporting its causal role in determining affective states.⁸² In other mammals such as mice, vicarious acquisition of fear through observation of conspecifics suffering from aversive stimuli is impaired by the inactivation of the anterior cingulate cortex, which is crucial for affective pain processing.⁸³ Finally, the recent discovery of audio-vocal MNs in birds⁴⁶ supports the idea of an ancient phylogenetic origin of the mirror mechanism as a dedicated system for social learning and communication. Audio-vocal neurons have been also shown to enable categorical perception of others' songs,⁴⁷ as it has been previously suggested for monkey MNs and recognition of others' motor actions.⁴

From these examples, it is evident that the functional refinements of mirror mechanisms depend on the socio-ecology of the species and are more relevant for vocal communication in birds, vicarious learning in mice, and hand/mouth gestures in primates. However, all MN systems identified have a shared common feature: they rely on the motor and/or visceromotor repertoire of the individual. This suggests that the original functional role of neurons that will acquire mirroring properties,

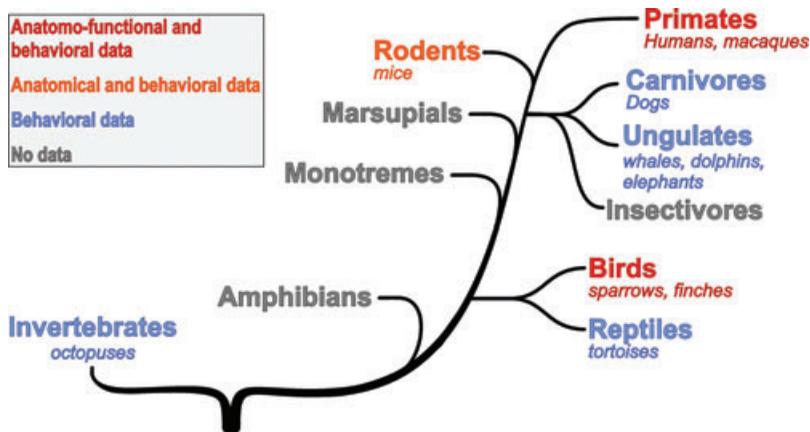


Figure 2. Phylogenetic tree of mirroring mechanisms. Red groups include species where direct evidence of single MNs is available. Orange groups include cases of indirect convergent evidence at both the anatomical and the behavioral level (no recording of single neuron activity). Blue groups indicate species where the presence of MNs might be hypothesized on the basis of behavioral evidence, but is not yet supported by neuroscientific data.

during ontogeny as well as during phylogeny, might be monitoring one's own motor or visceromotor functions. Extending recent proposals,^{69,84,85} we hypothesize that in the course of evolution, this system for tracking own motor and visceromotor behavior was "exapted"⁵⁸ and exploited within a social domain to interpret others' actions and/or sounds for social interaction and communicative purposes.

Conclusions

In their basic properties, MNs constitute a relatively simple action–perception mechanism that could have been exploited several times in the course of animal evolution: first as a monitoring system for tracking one's own behavior, then by functioning as an extended recognition system matching one's own and other motor representations, and finally for contributing to speech perception and production in humans.^{86,87} Despite the higher cognitive functions it could serve in some species, the basic mirroring mechanism is very likely much simpler and widespread in the animal kingdom than previously imagined (Fig. 2).

Behavioral and ethological studies have shown that a number of animal species have rich behavioral⁸⁸ and/or vocal⁸⁹ interactions with conspecifics, ranging from body synchronization and mimicry of similar motor patterns to learning action sequences by copying them with high fidelity. Besides primates,⁹⁰ elephants,⁹¹ dogs,⁹² rodents,⁹³ cetaceans,⁹⁴ and birds,⁹⁵ an astonishing example is provided by

the cephalopoda *Octopus vulgaris*, which can benefit from the observation of a trained demonstrator performing a motor task to learn to solve the same task more rapidly.^{96,97} Recent studies indicate that even a nonsocial reptile, the red-footed tortoise, shows some forms of behavioral mirroring.^{98,99}

Until now, direct evidence for MNs has only been available in monkeys, humans, and birds due to technical/methodological difficulties or ethical problems that single neuron recordings involve in many species. Clearly, these limits prevent the reconstruction of a phylogenetic tree of MN systems. However, the behavioral data reviewed here suggest that MNs might have been retained from ancient brain structures, appear to have been well preserved during evolution, and accomplish similar recognition functions, although in different domains and in several species not necessarily closely related to each other.

This would be another one of the many instances⁵⁷ demonstrating how evolution has shaped not only anatomical, genetic, and developmental traits, but also the underlying neural mechanisms of complex cognitive capacities.

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Conflict of interest

The authors declare no conflicts of interest.

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