

The evolutionary link between mirror neurons and imitation: An evolutionary adaptive agents model

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Abstract: This commentary validates the fundamental evolutionary interconnection between the emergence of imitation and the mirror system. We present a novel computational framework for studying the evolutionary origins of imitative behavior and examining the emerging underlying mechanisms. Evolutionary adaptive agents that evolved in this framework demonstrate the emergence of neural “mirror” mechanisms analogous to those found in biological systems.

Uncovering the evolutionary origins of neural mechanisms is bound to be a difficult task; fossil records or even genomic data can provide very little help. Hence, the author of the target article should be commended for laying out a comprehensive and thorough theory for the evolution of imitation and language. In particular, in considering the first stages in the evolution of language, Arbib argues that the mirror system initially evolved to provide a visual feedback on one’s own action, bestowing also the ability to understand the actions of others (stage S2), and that further evolution was required for this system to support the copying of actions and eventually imitation (stages S3 and S4). However, the functional link between the mirror system and the capacity to imitate, although compelling, has not yet been demonstrated clearly. We wish to demonstrate that the existence of a mirror system, capable of matching the actions of self to observed actions of others, is fundamentally linked to imitative behavior and that, in fact, the evolution of imitation promotes the emergence of neural mirroring.

Neurally driven evolutionary adaptive agents (Ruppin 2002) form an appealing and intuitive approach for studying and obtaining insights into the evolutionary origins of the mirror system. These agents, controlled by an artificial neural-network “brain,” inhabit an artificial environment and are evaluated according to their success in performing a certain task. The agents’ neurocontrollers evolve via genetic algorithms that encapsulate some of the essential characteristics of natural evolution (e.g., inheritance, variation, and selection).

We have recently presented such a novel computational model for studying the emergence of imitative behavior and the mirror system (Borenstein & Ruppin 2004; 2005). In contradistinction to previous engineering-based approaches that explicitly incorporate biologically inspired models of imitation (Billard 2000; Demiris & Hayes 2002; Demiris & Johnson 2003; Marom et al. 2002; Oztop & Arbib 2002), we employ an evolutionary framework and examine the mechanism that evolved to support imitation. Because it is an emerging mechanism (rather than an engineered one), we believe it is likely to share the same fundamental principles driving natural systems.

In our model, a population of agents evolves to perform specific actions successfully according to certain environmental cues. Each agent’s controller is an adaptive neural network, wherein synaptic weights can vary over time according to various Hebbian learning rules. The genome of these agents thus encodes not only the initial synaptic weights but also the specific learning rule and learning rate that govern the dynamics of each synapse (Floreato & Urzelai 2000). Agents are placed in a changing environment that can take one of several “world states” and should learn to perform the appropriate action in each world state. However, the mapping between the possible world states and appropriate actions is randomly selected anew in the beginning of the agent’s life, preventing a successful behavior from becoming genetically determined. Agents can infer the appropriate state-action mapping

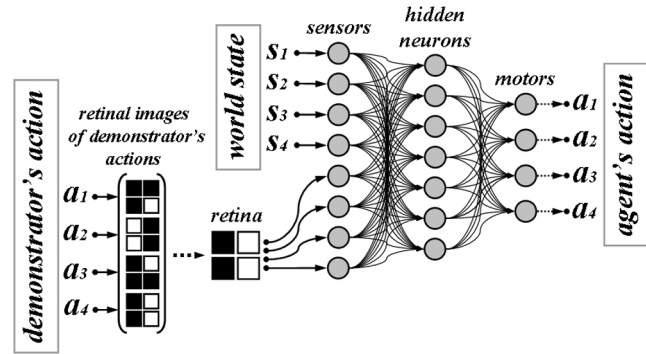


Figure 1 (Borenstein & Ruppin). The agent’s sensorimotor system and neurocontroller. The sensory input is binary and includes the current world state and a retinal “image” of the demonstrator’s action (when visible). The retinal image for each possible demonstrator’s action and a retinal input example are illustrated. The motor output determines which actions are executed by the agent. The network synapses are adaptive, and their connection strength may change during life according to the specified learning rules.

only from an occasional retinal-sensory input of a demonstrator, successfully performing the appropriate action in each world state (Fig. 1). These settings promote the emergence of an imitation-based learning strategy, although no such strategy is explicitly introduced into the model.

Applying this model, we successfully developed evolutionary adaptive agents capable of learning by imitation. After only a few demonstrations, agents successfully master the behavioral task, regularly executing the proper action in each world state. Moreover, examining the dynamics of the neural mechanisms that have emerged, we found that many of these agents embody a neural mirroring device analogous to that found in biological systems. That is, certain neurons in the network’s hidden layer are each associated with a certain action and discharge only when this action is either executed by the agent or observed (Fig. 2). Further analysis of these networks reveals complex dynamics, incorporating both pre-wired perceptual-motor coupling and learned state-action associations, to accomplish the required task.

This framework provides a fully accessible, yet biologically plausible, distilled model for imitation and can serve as a vehicle to study the mechanisms that underlie imitation in biological systems. In particular, this simple model demonstrates the crucial role of the mirror system in imitative behavior; in our model, mirror neurons’ emergence is derived solely from the necessity to imitate observed actions. These findings validate the strong link between the capacity to imitate and the ability to match observed and executed actions and thus support Arbib’s claim for the functional links between the mirror system and imitation. However, whereas Arbib hypothesizes that the evolution of the mirror system preceded the evolution of imitation, this model additionally suggests an alternative possible evolutionary route, grounding the emergence of mirror neurons in the evolution of imitative behavior. Evidently, at least in this simple evolutionary framework, neural mirroring can coevolve in parallel with the evolution of imitation. We believe that evolutionary adaptive agents models, such as the one described above, form a promising test bed for studying the evolution of various neural mechanisms that underlie complex cognitive behaviors. Further research of artificially evolving systems can shed new light on some of the key issues concerning the evolution of perception, imitation, and language.

ACKNOWLEDGMENT

Elhanan Borenstein is supported by the Yeshaya Horowitz Association through the Center for Complexity Science.

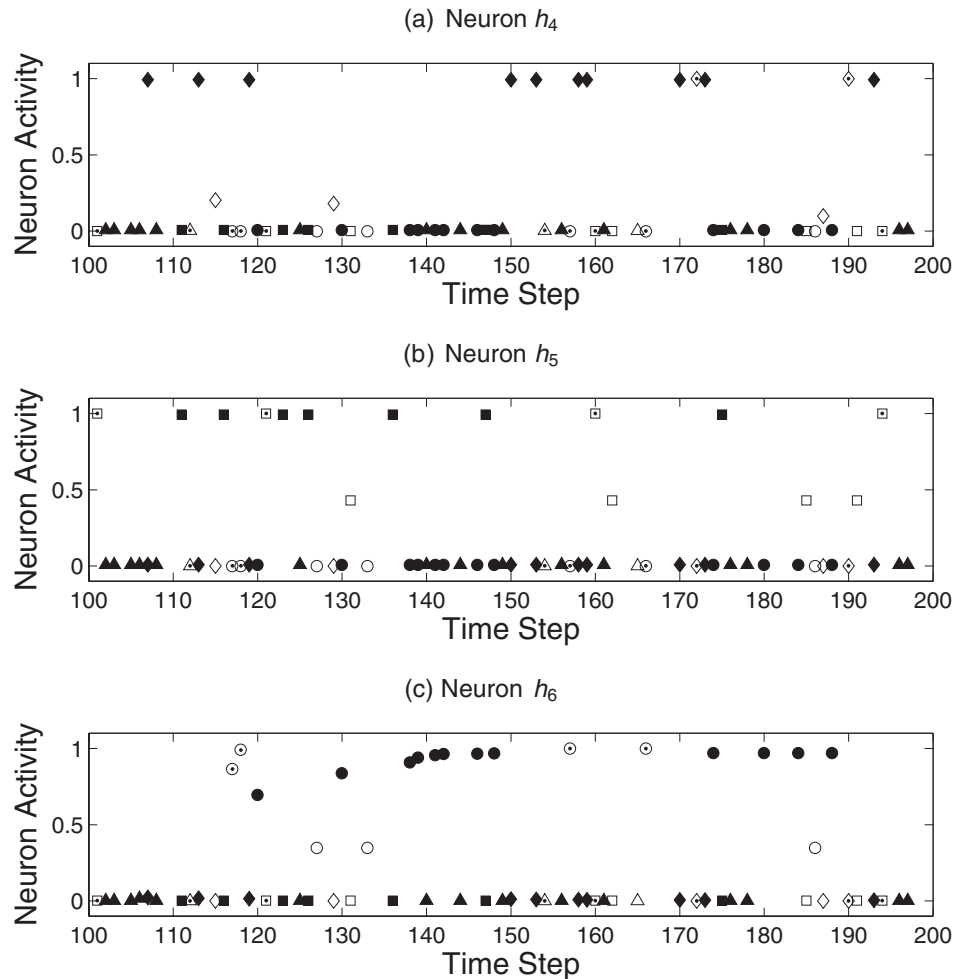


Figure 2 (Borenstein & Ruppin). The activation level of three hidden neurons in a specific successful agent during time steps 100 to 200. Circles, squares, diamonds, and triangles represent the four possible actions in the repertoire. An empty shape indicates that the action was only observed but not executed, a filled shape indicates that the action was executed by the agent (stimulated by a visible world state) but not observed, and a dotted shape indicates time steps in which the action was both observed and executed. Evidently, each of these neurons is associated with one specific action and discharges whenever this action is observed or executed.

Sharpening Occam’s razor: Is there need for a hand-signing stage prior to vocal communication?

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Abstract: We commend Arbib for his original proposal that a mirror neuron system may have participated in language origins. However, in our view he proposes a complex evolutionary scenario that could be more parsimonious. We see no necessity to propose a hand-based signing stage as ancestral to vocal communication. The prefrontal system involved in human speech may have its precursors in the monkey’s inferior frontal cortical domain, which is responsive to vocalizations and is related to laryngeal control.

In the target article, Arbib extends his earlier hypothesis about the role of mirror neurons for grasping in the motor control of language (Rizzolatti & Arbib 1998), to a more detailed and fine-grained scenario for language evolution. We agree with and celebrate the main proposals that a mirror neuron system has had a fundamental role in the evolution of human communication and that imitation was important in prelinguistic evolution. We also agree that there has probably been an important vocal-gestural in-

teraction in the evolution of communication. In these and other aspects, our viewpoints complement each other (Aboitiz & García 1997). We proposed that language networks originated as a specialization from ancestral working memory networks involved in vocal communication, and Figure 6 of the target article is a good attempt to synthesize both hypotheses. However, we are not so sure yet about the claim that gestural language was a precursor for vocal communication, for several reasons:

First, phylogenetic evidence indicates that in nonhuman primates, vocal communication transmits external meaning (i.e., about events in the world) and is more diverse than gestural communication (Acardi 2003; Leavens 2003; Seyfarth & Cheney 2003a). Second, there is evidence suggesting that the control of vocalizations in the monkey could be partly carried out by cortical areas close to F5 and does not depend exclusively on the anterior cingulate cortex. If this is so, the neural precursor for language would not need to be sought in a hand-based coordination system. For example, in the monkey there is an important overlap between area F5 and the cortical larynx representation (Jürgens 2003). Electrical stimulation of this area can elicit vocal fold movements (Hast et al. 1974), and cortical lesions in the supplementary motor area can significantly reduce the total number of vocalizations emitted by monkeys (Gemba et al. 1997; Kirzinger & Jürgens 1982). Furthermore, Romanski and Goldman-Rakic (2002) recently described, in Brodmann areas 12 and 45 of the monkey, neurons that respond strongly to vocalizations.