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ORIGINAL ARTICLE

From grasping to complex imitation: mirror systems on the path to language

Michael A. Arbib · James Bonaiuto

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Abstract We focus on the evolution of action capabilities which set the stage for language, rather than analyzing how further brain evolution built on these capabilities to yield a language-ready brain. Our framework is given by the Mirror System Hypothesis, which charts a progression from a monkey-like mirror neuron system (MNS) to a chimpanzee-like mirror system that supports simple imitation and thence to a human-like mirror system that supports complex imitation and language. We present the MNS2 model, a new model of action recognition learning by mirror neurons of the macaque brain and augmented competitive queuing, a model of opportunistic scheduling of action sequences as background for analysis of modeling strategies for "simple imitation" as seen in the great apes and "complex/goal-directed imitation" as seen in humans. Implications for the study of language are briefly noted.

Keywords Mirror system hypothesis · Brain evolution · Language evolution · Primate evolution · Neural models · Imitation · Mirror neurons · Sequential behavior

1 Background: reviewing the mirror system hypothesis

We will work within an existing framework (the Mirror System Hypothesis MSH) which advances the claim that the evolution of the language-ready brain rested upon

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M. A. Arbib
Computer Science, University of Southern California, Los Angeles, CA 90089-2520, USA

M. A. Arbib · J. Bonaiuto
Neuroscience, University of Southern California, Los Angeles, CA 90089-2520, USA
e-mail: bonaiuto@usc.edu

M. A. Arbib (✉) · J. Bonaiuto
USC Brain Project, University of Southern California, Los Angeles, CA 90089-2520, USA
e-mail: arbib@usc.edu

the evolution in hominids of a capacity for complex imitation, focusing particularly upon the changes in the brain that preceded, and made possible, a brain which supports communication using protosign.

The evolutionary framework that we adopt here comes from comparative neurobiology—we compare the mirror neurons for grasping of the macaque monkey brain to the mirror systems of the human brain, and use this comparison to ground the MSH on the evolution of the language-ready brain. First, the monkey. Both premotor area F5 and parietal area PF of the macaque brain contain *mirror neurons* each of which fires vigorously both when the monkey executes a certain limited set of actions and when the monkey observes some other perform a similar action. By contrast, *canonical neurons* in F5 fire vigorously when the monkey executes certain actions but not when it observes the actions of others. Turning to the human, we must rely on brain imaging rather than single-neuron recording. Imaging data show that the human brain contains *mirror systems* in both frontal and parietal lobes, namely regions that show high activation both when a human performs a manual action and when the human observes a manual action, but not when the human simply observes an object. It is widely assumed that such mirror regions contain mirror neurons, based on similarities between the human and macaque brain.

Strikingly, the frontal mirror system for grasping in the human is associated with Broca's area, hitherto thought of as an area for speech production but now better understood for its involvement in the production of language as a multi-modal performance engaging face, voice and hands. The *MSH* (Rizzolatti and Arbib 1998; Arbib 2005, 2006) asserts that the *parity requirement* for language in humans—that what counts for the speaker must count approximately the same for the hearer—is met because Broca's area (often associated with speech production) evolved atop the mirror system for grasping with its capacity to generate and recognize a set of actions.

This is a hypothesis on the evolution of the language-ready brain, rather than of the structure of language itself. The crucial point is that humans have capacities denied to monkeys. Mirror regions in a human can be activated when the subject imitates an action, or even just imagines it, but there is a consensus that monkeys cannot imitate save in the most rudimentary sense. By contrast, chimpanzees exhibit "simple imitation", the ability to approximate an action after observing and attempting its repetition many times; while humans alone among the primates have the capacity for "complex imitation", being able to recognize another's performance immediately as a combination of more-or-less familiar actions and to use this recognition to approximate the action, with increasing practice yielding increasing skill. This ability provides a crucial substrate for the child learning language, but it also provides—through its perceptual component—brain mechanisms that could be adapted for the ability to recognize the words of a novel sentence and how they fit together in a hierarchical structure to convey meaning.

Arbib (2005) modified and developed MSH by hypothesizing seven stages in the evolution of language. The first three stages are pre-hominid:

- **S1:** Grasping.
- **S2:** A mirror system for grasping, shared with the common ancestor of human and monkey.

- **S3:** A system for simple imitation of grasping shared with the common ancestor of human and chimpanzee.

The next three stages distinguish the hominid line from that of the great apes:

- **S4:** A complex imitation system for grasping.
- **S5:** *Protosign*, a manual-based communication system that involves the breakthrough from employing manual actions for praxis to using them for pantomime (not just of manual actions), and then going beyond pantomime to add conventionalized gestures that can disambiguate pantomimes.
- **S6:** *Protospeech*, resulting from linking the mechanisms for mediating the semantics of protosign to a vocal apparatus of increasing flexibility.

Arbib argues that protosign and protospeech evolved together in an expanding spiral and that brain mechanisms supporting Stages S1 through S6 suffice to support Stage S7:

- **S7:** *Language*: the change from action-object frames to verb-argument structures to syntax and semantics.

The commentaries published in Arbib (2005) provide arguments and counter-arguments for these various claims.

The present article does not revisit the evolutionary argument, but instead addresses the challenge of developing models of the brain mechanisms which support this evolutionary succession. We focus here on models for the earlier, rather than the later, stages in this progression, introducing a new model of action recognition learning by macaque mirror neurons which addresses data on auditory input, a model for opportunistic planning of sequential behavior, and studies of how to embed a macaque-like mirror system in a larger ape-like or human-like circuit to support “simple imitation” and then “complex imitation”. Other articles (e.g., those collected in Arbib 2006) carry the story forward to protolanguage and language. The closing discussion then returns to the relevance of these mechanisms for language and its evolution.

2 Grasping

The motor control system for skilled manual action (Stage 1 of MSH) lays the basis for the later evolution of protosign by providing the possibility for an open repertoire of manual actions and postures which was later harnessed for communicative pantomimes, signs, and gestures. Note that we do not mean that dexterity evolved “in order to” make language possible; rather dexterity evolved to support an adaptively valuable range of actions in primates. However, the MSH does assert that the historically contingent evolution of the human language-ready brain exploited this prior repertoire, rather than building directly on ancestral brain mechanisms controlling vocalizations akin to the alarm calls, exhibited by present-day monkeys. Here, though, we focus on the development of manual dexterity in present-day infants, whether human or monkey.

The Infant Learning to Grasp Model (ILGM; Oztop et al. 2004) simulates reinforcement learning of motor parameter values for grasping through trial-and-error learning. In current work we are extending this model by developing the Infant Learning Grasping and Affordances (ILGA) model. A central theme in the framework of action-oriented perception is the idea of *affordances* for action (Gibson 1966). An affordance is a directly perceivable opportunity for action, and it is believed that various areas in the primate parietal cortex represent affordances and link them with actions in the premotor cortex (Sakata et al. 1998; Fagg and Arbib 1998; Murata et al. 2000). In ILGA, both object affordances and the motor parameter values needed to exploit those affordances in grasping are learned simultaneously. In ILGM and the basic version of ILGA, an attempted grasp receives positive reinforcement if it leads to the stable grasp of an object. ILGA simulations are currently ongoing; while the details and simulation results for ILGM are contained in Oztop et al. (2004). The crucial point of these models is their high adaptability. We do not require that basic grasps like the precision pinch and the power grasp be specified genetically. Rather, we show by computer simulation that flexible hand geometry and appropriately structured neural networks which can change on the basis of reinforcement learning can together yield a repertoire of such actions through interaction with the world around the infant. Elsewhere, we have shown how such flexibility may explain aspects of language acquisition in the 2-year-old child, obviating the need for an innate Universal Grammar to underwrite the basic structures of the child's syntax (see Arbib and Hill 1988). Bringing these two strands of research together is a current goal.

3 A mirror system for grasping

Stage 2 of the MSH focuses on the basic mirror system for manual action that we share with monkeys. The extension of this "mirror capacity" from praxis to communication (as our ancestral brains evolved to support pantomime and, in turn, protosign) provides an essential component of the evolution of the language-ready brain (Stage S5 of the MSH). The present section focuses on our recent modeling efforts which extended our earlier model of the monkey mirror system to address more recent data on mirror neurons (Oztop and Arbib 2002).

The MNS model of Oztop and Arbib (2002), is based on the view that, when the monkey grasps an object, canonical neurons provide a premotor encoding of the type of grasp employed. The grasp will conform to one of the *affordances* of the object (i.e., the shape of one of the graspable parts of the object). MNS then provides a learning mechanism which trains potential mirror neurons to associate visual input encoding the trajectory of a hand relative to an observed object with the canonical neuron encoding of that grasp. Since the visual input encodes hand movement relative to the object (or more specifically, to one of the affordances of the object), rather than retinotopically, the trained system is then able to recognize the actions of others—which will be in the absence of canonical neuron activity—by activating mirror neurons associated with the observed object-centered trajectory of the other's behavior.

The learning mechanism used in the MNS model was a feed-forward backpropagation network of units with one hidden layer which required an unnatural recoding of its input. Bonaiuto et al. (2007) developed a model, MNS2, which could process the time series of hand–object relationships without such recoding, using an adaptive recurrent network (Fig. 1) to learn to classify grasps based on the temporal sequence of hand–object relations. This was a Jordan-type recurrent network with sigmoidal activation functions meant to approximate the firing rate of actual neurons as proportional to weighted synaptic input. The learning algorithm used was backpropagation through time (Werbos 1990).

Umiltá et al. (2001) have shown that mirror neurons in the macaque monkey can recognize a grasp if the monkey has seen the target object which was then hidden, but cannot recognize the action lacking current or recent input on the affordances and location of the object. MNS2 incorporates working memory and dynamic remapping components (Fig. 2) which allow the model to recognize grasps even when the final stage of object contact is hidden and must be inferred. Before being hidden, the object position and its affordance information are stored in working memory. Once the hand is no longer visible, the working memory of wrist position is updated using the still-visible forearm position. If the model observes an object which is then hidden by a screen, and then observes a grasp that disappears behind that screen, the wrist trajectory will be extrapolated and the grasp will be classified accordingly.

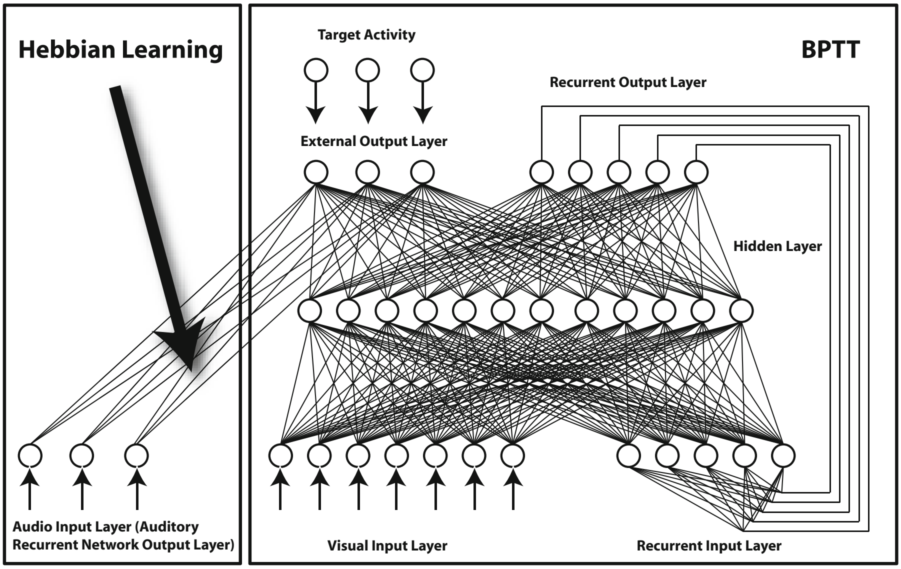

Fig. 1 The network structure of the MNS2 model. The visual and auditory input layers correspond to input from lower-level visual and auditory centers. The hidden layer represents the inferior parietal area PF/PFG. Through training, the external output layer acquires an activation profile similar to F5 mirror neurons, given training target activity from F5 canonical neurons

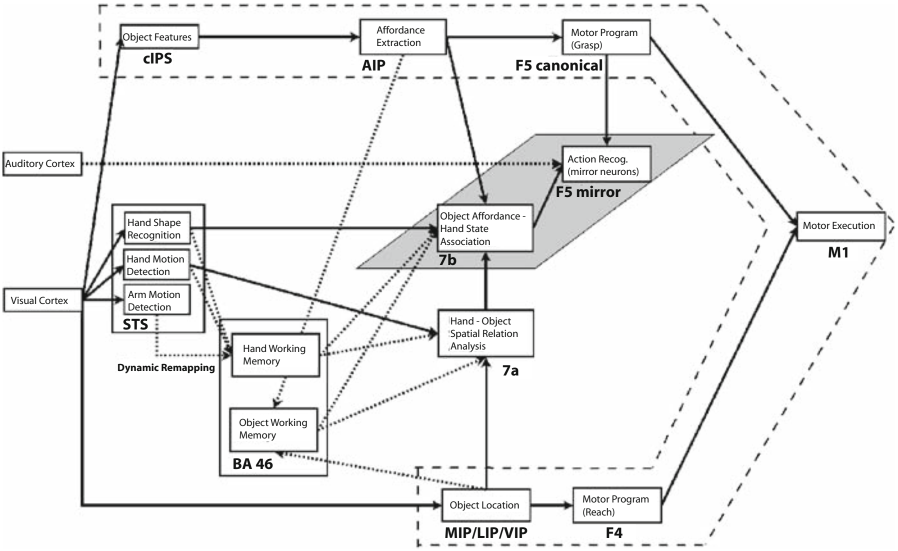

Fig. 2 System diagram for the MNS2 model (Bonaiuto et al. 2007), updating the MNS model (Oztop and Arbib 2002). The dashed outline shows the system for generating the reach to and grasp of an observed object. Here, the visual system extracts the affordances of an object (i.e., the way in which the object can be grasped) rather than recognizing the category of the object. The remaining circuitry defines the mirror system and the subsystems which feed it. The encoding of the grasp motor program (F5 canonical) provides the training signal for a recurrent network which models the areas 7b and F5 mirror, shown here in the gray parallelogram, by the activity of its hidden and external output layers, respectively. The dotted arrows denote the connections unique to the mirror neuron system (MNS2) model. Auditory information about actions reaches the F5 mirror neurons via the auditory cortex. Visual data on hand-object spatial relations is input into the Object Affordance-Hand State Association schema and into working memory. When this information is not available externally, the dynamically remapped working memory trace serves in its place

However, the more important contribution of MNS2 within the context of MSH is that it addresses data on “audiovisual” mirror neurons which associate sounds with manual actions. Köhler et al. (2002—see Fig. 3 right) found that some of the mirror neurons in area F5 of the macaque premotor cortex responsive to the sight of actions associated with characteristic noises (such as peanut breaking) are just as responsive for the sounds of these actions.

Bonaiuto et al. (2007) associate each sound with a distinct pattern of activity which is applied to audio input units which are fully connected to the output layer of the recurrent neural network, corresponding to a direct connection from auditory cortex to F5. These connection weights are modified using Hebbian learning. In this way, any sound that is consistently perceived during multiple occurrences of an executed action becomes associated with that action and incorporated into its representation. This type of audio information is inherently actor-invariant and this allows the monkey to recognize that another individual is performing that action when the associated sound is heard.

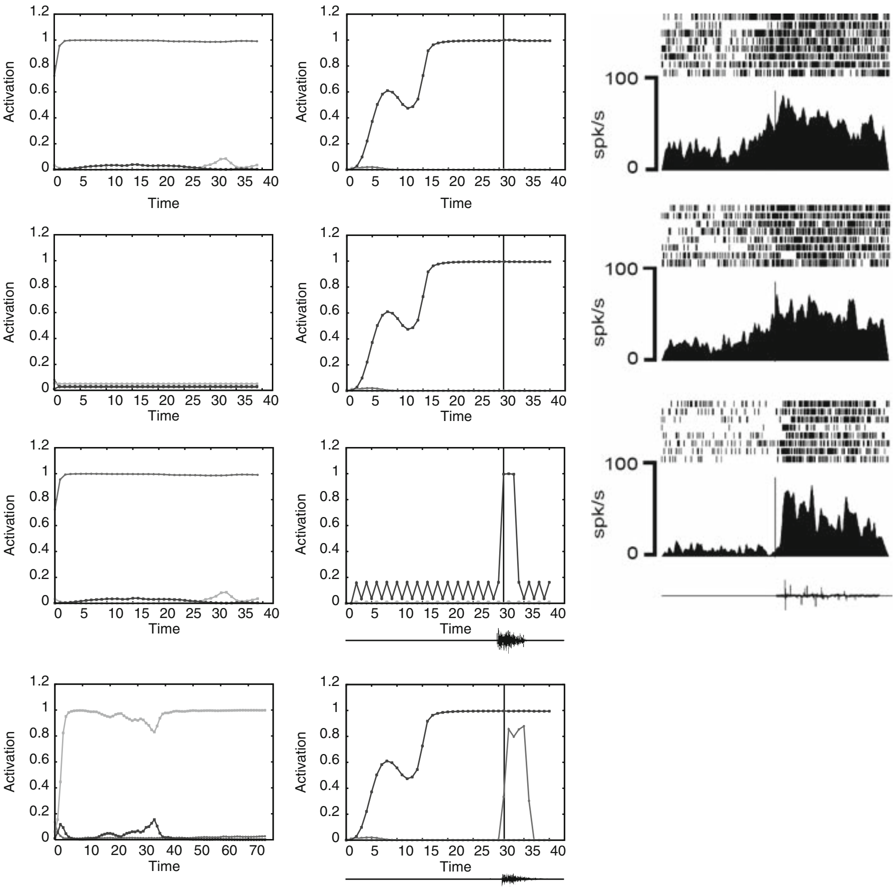

Fig. 3 Left: activation of the model's external output layer when presented with a precision grasp sequence containing (*from top to bottom*) visual and congruent audio, visual only, audio only, and incongruent visual and audio information. The *black vertical lines* indicate the time step at which the hand made contact with the object. The unit encoding the precision grasp shows the greatest level of activation in all conditions, while the unit corresponding to power grasps shows a smaller level of transient activity in the incongruent condition. At the *bottom* is an oscillogram of the sound associated with the precision grasp. *Right*: activation from Köhler et al. (2002) of an audiovisual mirror neuron responding to (*from top to bottom*) the visual and audio components, visual component alone, and audio component alone of a peanut-breaking action (Reproduced with permission from Köhler et al. 2002. Copyright 2002 AAAS)

4 Flexible action selection

4.1 Dual routes and the need for an action buffer

It is often suggested that mirror neurons are the substrate for imitation, matching observed actions onto motor programs producing similar or equivalent actions. However, we noted earlier that only humans have "complex imitation", the ability to imitate sequences of behaviors and approximate novel actions as variants of known actions after one or just a few viewings of this novel behavior. What, then, changed, to make the human mirror system part of a system that supports such imitation? As backdrop for our own work, we draw some important lessons from apraxia.

DeRenzi (1989) reports that some apraxics exhibit a *semantic deficit*—having difficulty both in classifying gestures and in performing familiar gestures on command—yet may be able to copy the pattern of movement of such a gesture without "getting the meaning" of the action of which it is part. We call this residual ability *low-level imitation* to distinguish it from imitation based on recognition and "replay" of a goal-directed action. With Rothi et al. (1991), we thus propose a dual route imitation learning model to serve as a platform for studying apraxia (Fig. 4). The *direct route* for imitation of meaningless and intransitive gestures converts a visual representation of limb motion into a set of intermediate limb postures or motions for subsequent execution (low-level imitation). The *indirect route* for imitation of known gestures recognizes and then reconstructs known actions whether or not they are object-directed. (Note: For some apraxics, performance of an action upon an object may be far better when the object is present than when pantomime of the action must be performed in the absence of the object—the presence of affordances here plays an essential role.)

For Rothi et al. (1991), the language system at left simply serves as a model for their conceptual model of the praxis system at right, with the semantics of objects playing a bridging role. For work on MSH, the challenge is to understand how the system on the left evolved "atop" the system on the right. For example, Itti and Arbib (2005) discuss how to extend the semantics from objects to "scenes" structured by actions, but this topic is beyond the scope of the present paper. Here, we address a strange omission in Rothi et al.'s figure that we highlight in Fig. 4: although they include a phonological buffer for putting words together, they omit an "action buffer" for putting actions together.

Correcting this omission will be a major part of what follows, since a crucial aspect of the extending MSH is to explore the extent to which precursors of the syntax of languages can be seen in the "syntax" of praxic action (Roy and Arbib 2005). We thus turn to a new theory of the "action buffer", showing how a strict ordering of a sequence of actions (CQ, competitive queuing) may be complemented by an opportunistic scheduling of actions (ACQ, augmented competitive queuing). We will then argue that even cats, and thus presumably our common ancestors with the cats, had ACQ, including a rudimentary mirror system, and that this gave them a measure of flexibility required to respond quickly to environmental changes. While not directly concerning imitation, we feel that this work is crucial in linking isolated systems for action and action recognition such as those discussed in Stages S1 and S2 of the MSH into integrated systems for imitation such as those proposed in Stages S3 and S4. After discussing ACQ we will return to imitation, offering a hierarchical version of augmented competitive queuing (hACQ) and charting ways in which it may be used to model the form of simple imitation exhibited by apes which is known as imitation by behavior parsing (Byrne 2003). The rest of the paper will then briefly suggest research challenges in probing the brain mechanisms which support complex/goal-directed imitation, and briefly discuss the relevance of this to the evolution of the human language-ready brain.

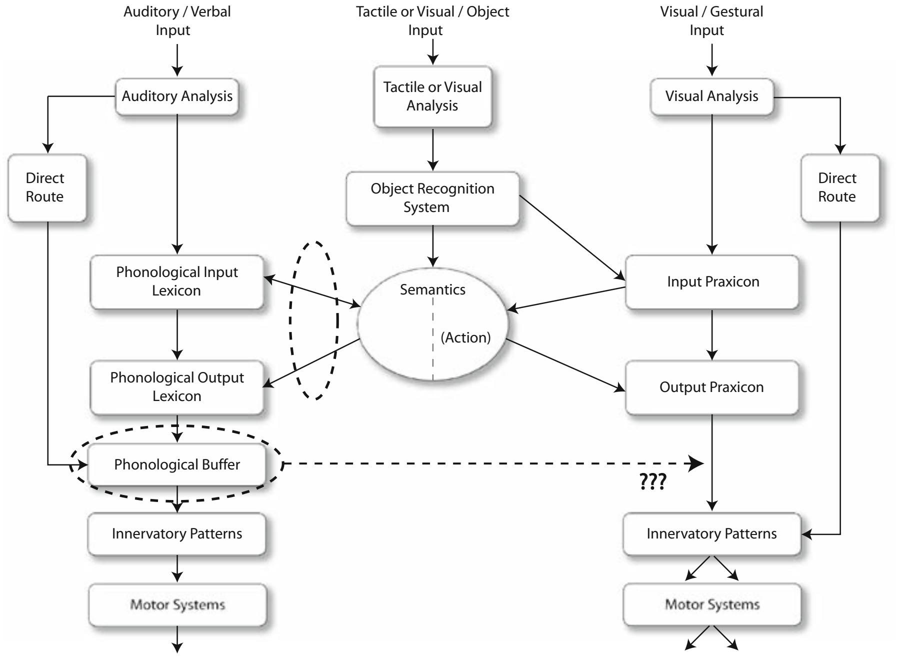

Fig. 4 A dual route imitation learning model balancing language and praxis. We stress that the *right-hand side* should be augmented by an "action buffer", and emphasize the bidirectional link between lexicon and semantics (Adapted from Rothi et al. 1991)

4.2 Augmented competitive queuing

Competitive queuing (CQ, Bullock and Rhodes 2003; Houghton and Hartley 1995) converts a spatial representation of a sequence into a temporal pattern of execution. The first layer of the CQ network (Fig. 5) contains a single unit for each stored sequence. The next two layers each have units corresponding to all the unit actions from which the sequences are composed. Activation of a unit in the first, sequence storage layer, in turn activates a parallel representation in the parallel planning layer, in such a way that the earlier an action occurs in the sequence, the higher the weight of the projection to its unit from the sequence storage layer unit, and thus the higher its activity in the planning layer. Each unit in the parallel planning layer projects to a corresponding unit in the third layer—the competitive choice layer. This layer implements a winner-take-all (WTA) process in which the most active element is selected for execution by temporarily inhibiting the other, less active elements (lateral inhibition). The winning unit thereafter inhibits its corresponding unit in the parallel planning layer (inhibition of return), removing it from the competition to determine subsequent actions. In this manner the spatial sequence representation in the parallel planning layer is converted into a temporal sequence of firing units in the competitive choice layer. The model as described does not handle those sequences where an action may be repeated several times, such as

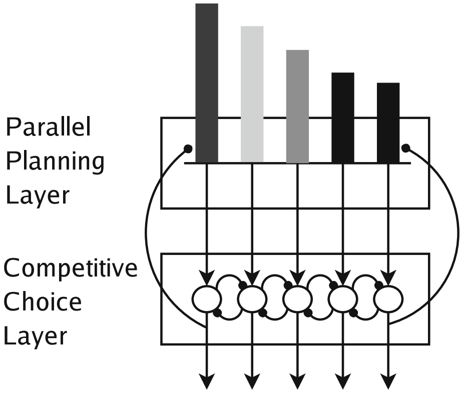

Fig. 5 Competitive queuing: the sequence storage layer represents entire sequences. A planning layer represents sequence elements in parallel with varying activation levels. A competitive choice layer selects the most activated element for execution (using a winner-take-all mechanism) and the corresponding element in the planning layer is subsequently inhibited (inhibition of return)

ACAGAACW. To address this, Houghton and Hartley (1995) introduced a context-varying signal to modulate the parallel planning layer. This parallels the function of the prefrontal cortex in modulating the basal ganglia in the model of sequence learning in Dominey et al. (1995).

We motivate our discussion of ACQ with a surprising example—a cat reaching for food that is in a glass tube. We will see that this example shows the power of flexible scheduling of action. Alstermark et al. (1981) experimentally lesioned the spinal cord of cats in order to determine the role of propriospinal neurons in forelimb movements. These experiments also happened to illustrate interesting aspects of the cat's motor planning and learning capabilities. The experimental setup in this study consisted of a piece of food placed in a horizontal tube facing the cat (Fig. 6). In order to eat the food, the cat was required to reach its forelimb into the tube, grasp the food with its paw, and bring the food to its mouth. Not reported in the paper, is the account (B. Alstermark, personal communication 1990) that after the lesion, the cat would reach inside the tube, and repeatedly attempt to grasp the food and fail. However, these repeated failed grasp attempts would eventually succeed in displacing the food from the tube by a raking movement, and the cat would then bend its head down, grasp the food from the ground with its jaws and eat it. After only two or three trials, the cat began to rake the food out of the tube, a more efficient process than random displacement by failed grasps.

It is assumed that before the lesion the cat already had a motor program for getting the food out of the tube and eating it. Rather than learning an entirely new skill, or refining and tuning an already-learned skill, it seems that modification is occurring on some sort of decision variable that controls which motor schema to execute at a particular time. The fact that after lesioning it took only a few trials for the cat to modify this motor program suggests that this is a form of learning that takes place on a faster time scale than classical models of motor learning.

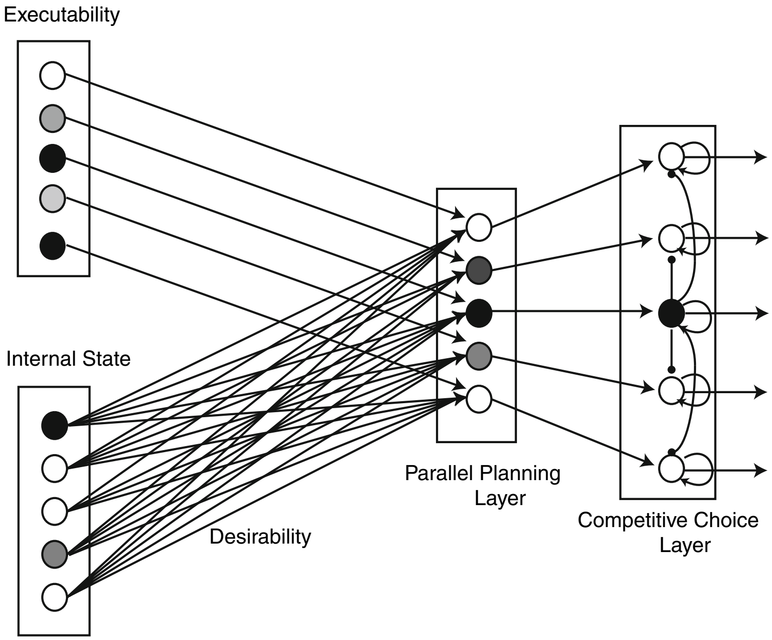

Fig. 6 The basic network for augmented competitive queuing (ACQ). The activation of motor schemas in the parallel planning layer is derived by composing desirability values from the internal state and executability values from affordance extraction

On the basis of these and other considerations, we have developed (the details are in a paper submitted for publication) a form of “augmented competitive queuing” (ACQ). A key difference from “classical” CQ is that the activation levels of motor program elements are dynamically computed in each “time step” rather than being completely specified before sequence execution and there is no inhibition of return. ACQ is based on three principles:

Rather than being controlled by computer-style flow diagrams, behavior emerges dynamically from *coordinated control programs* via the cooperation and competition of interacting perceptual and motor schemas.

Motor schema activation is determined by a *priority signal*, computed in the Parallel Planning layer, which increases with both executability and desirability. *Executability* is determined by available affordances (Gibson 1966) in the environment and the estimated probability of an action’s success. *Desirability* represents the estimated value of an action in leading to reward, depends on current context and motivation, and is dynamically updated via reinforcement learning.

An observation/execution matching (mirror) system may contribute to the rapid reorganization of motor programs in the face of disruption when a known schema can be recognized as “filling the gap” for disrupted schemas.

This last point deserves special emphasis. It is usual to think of the mirror system as encoding one’s own intended actions and the observed actions of others. Here, we offer a radically new role for mirror neurons: the recognition of one’s own unintended actions. This will become clear in the further discussion of Alstermark's cat below.

In the present model, the network shown in Fig. 6 is implemented as arrays of leaky integrator neurons. The desirability of each motor element as a function of experience is learned via temporal difference (TD) learning (Sutton and Barto 1998), a form of reinforcement learning that several authors have associated with the basal ganglia (e.g., Suri and Schultz 1998). The idea is this: "Basic" reinforcement learning is a way of changing the weights in a system to increase the chance that an action that elicits positive reinforcement will be repeated, and decrease the chance that an action that elicits negative reinforcement will be repeated. The catch is that reinforcement may be intermittent—for example, the animal has to execute many actions before it gets to eat the food. However, over time, one can learn what actions are more likely, in certain circumstances to lead to positive rather than negative reinforcement, TD learning formalizes this, and provides a way to train an "adaptive critic" to estimate the "expected future reinforcement" so that this estimate—rather than the actual, intermittent reinforcement—can be used in adjusting the weights relative to the current action.

The "mirror system for apparent actions", the new role for mirror neurons posited in (3), comes into play because the actions to be reinforced within the current context are determined by *internal* and *external* recognition of self-generated actions. Internal action recognition is provided by an efference copy of the motor command just executed. External action recognition is determined by visual, auditory, tactile, and proprioceptive input. Typically, these signals coincide, but when they do not, multiple motor schemas can be reinforced. Although mirror systems for action recognition have only been found in the macaque (Rizzolatti et al. 1996) and in humans (Iacoboni et al. 2005), we posit that the cat (among other species) has a primitive mirror system for recognition of at least some of its own actions. In the example of Alstermark's cat, we argue that the attempts to grasp the food that result in its displacement from the tube activate the mirror neurons for the action of raking the food from the tube, even though the raking action was not intended. We further argue that success will reinforce not only the action that was actually executed but also any action the mirror system recognizes during the course of that execution. The power of our model is that it provides a simple mechanism that yields a result that might otherwise seem to depend on high-level cognitive processes—supporting the flexible reorganization of coordinated control programs to achieve important goals despite changing circumstances.

An important feature of the TD algorithm is that future rewards are discounted by a factor that increases with time: Given the choice of \$1 today and \$2 tomorrow, we might be happy to wait till tomorrow, but if the choice is between \$1 today and \$2 in two year's time, most would choose today's dollar. The effect of using TD learning is thus that desirability values for actions that may lead to a positively reinforcing goal are assigned to actions in increasing order to the extent that the actions tend to occur closer to achievement of a rewarding goal. Note that the desirability is dependent on the internal "drive state"—what is desirable when one is hungry is different from what is desirable when one is thirsty. In other words, the development of motor program sequences through reinforcement relies on the reinforcement signal being appropriate to the current drives or goals (Arbib and Lieblich 1977; Guazzelli et al. 1998). ACQ ensures that the executable motor element with the highest priority is executed at each time step. This method can take advantage of serendipitous events and omit actions from a sequence whose goals are already accomplished. If some external event sufficiently increases the executability of a motor element that is normally executed late in a motor program, it will be selected over early elements because TD learning assigns higher value functions to states late in a sequence since these have greater expectation of (discounted) future reinforcement.

In order to test the ability of the model to rapidly reorganize learned motor programs, we modeled the performance of a simplified model of Alstermark's cat before and after a lesion to the grasp-with-paw motor schema. Before the lesion, the grasp-with-paw schema would successfully grasp the food. The lesion was represented by having the grasp-with-paw schema instead change the distance between the food and the mouth by a small, random amount, with a mean displacement towards the cat. This corresponds to the animal bringing its paw into contact with the food, displacing it, and retracting its paw, but failing to maintain a stable grasp.

The flow chart on the left of Fig. 7 corresponds to the normal behavior of the cat. Note, however, that the cat is *not* executing the program in computer-like serial execute-and-test fashion. Rather, the actions at the right have greater desirability to the extent that they appear higher in the diagram. The tests at the left correspond to executability conditions. With these settings, the parallel network in Fig. 6 yields the behavior that is also represented in Fig. 7 (left).

Initially, the Bat at Food with Paw motor schema has little desirability in the context of the task, but once the grasp is disabled it rapidly gains desirability because the mirror system's recognition of an apparent action has brought it into play. After lesioning and retraining, the batting action is executed instead of the reach and grasp action. This occurs because after lesioning the grasp with paw motor schema, the execution of the grasp motor schema causes the food to be randomly displaced towards the animal 60% of the time. This causes the perception of that failed grasp to look like a successful bat 60% of the time (whereas grasp execution does not) and actually causes TD learning to occur on the Bat at Food with Paw motor schema as well as the grasp with paw motor schema (due to the efferent copy). The mismatch of externally and internally recognized actions during the perception of the failed grasp causes the executability of the intended action—grasp with paw—to be decreased.

The flow chart on the right of Fig. 7 corresponds to the behavior of the cat after its rapid adjustment to the lesion of its ability to grasp effectively. It is interesting to note that this motor program includes an element (bat with paw) that is repeated not a static number of times, but until the next action in the program (grasp with mouth) is executable. Note that this follows immediately from the ACQ scheme of Fig. 6 as a result of the TD learning of new desirability values in the light of changing circumstances. By contrast, designing a neurally plausible method of restructuring programs of the kind shown in Fig. 7 seems far less plausible.

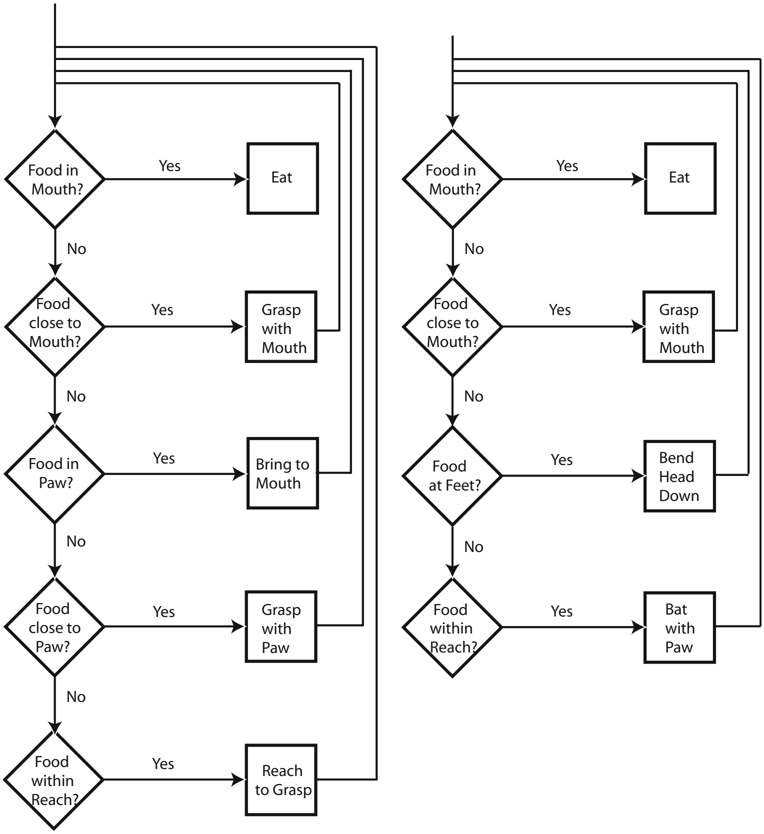

Fig. 7 *Left*: the original motor program developed through temporal difference learning for eating a piece of food in a horizontal tube. *Right*: the same motor program modified after the "Grasp Food with Paw" motor schema is lesioned

5 Imitation evolving

Our goal in this section is to examine a progression of modeling ideas which address the evolutionary progression from the limited (some say non-existent) imitation abilities of monkeys to the "simple imitation" of the great apes and the "complex imitation" of humans. Complex imitation involves many processes that are building blocks of the capability for language such as the ability to parse a continuous stream of perceived actions into meaningful hierarchies of chunks, make inferences as to the intentions of the actor who produced those actions, and use these mechanisms to modulate the production of one's own actions. A substantial portion of the nonhuman imitation literature involves a debate over what is and is not "true imitation" and what species do and do not imitate. Our aim is not so much to argue over the terminology—debating over whether or not a particular behavior involves imitation—so much as to try to understand what different brain mechanisms may underlie behavioral differences between monkeys, apes, and humans. We argue that this understanding will help us better understand the evolution of brain mechanisms for action which paved the way for the evolution of the human language-ready brain.

5.1 “Imitation” in monkeys?

Voelkl and Huber (2000) describe what they call “true” imitation in marmosets. They found that marmosets who observed a demonstrator opening a jar with the hand were more likely to then use their own hand when opening the jar, and those that observed the jar being opened with the mouth were more likely to then use their mouth. While the claim is that the marmosets are “imitating” the use of the hand versus the mouth to open a jar, we view this as an instance of effector priming rather than imitation. Instances of what might be labeled “imitation” in monkeys may also be attributed to social facilitation or stimulus enhancement. In social facilitation, the presence of another individual increases one’s propensity for any type of action (Clayton 1978). Effector priming is intermediate between social facilitation and imitation in that the propensity for using the same limb—as distinct from the use of a specific action involving that limb—is increased through observation. Stimulus and local enhancement are both visual attention-biasing methods that direct activity to the location of observed activity (Zentall 2001). Stimulus enhancement biases attention for objects which have similar features to the target of the observed action. Local enhancement simply biases attention for the location of the observed action. When combined, stimulus and local enhancement and effector priming or social facilitation increase the probability that behavior appears imitative by biasing the target and means of action. While these forms of social learning are pre-imitative, they may well have set the stage for imitation by providing the social conditions necessary for imitation to be an adaptive behavior.

5.2 Simple imitation

We turn next to what we have called “simple imitation” as exhibited by the great apes, the ability to approximate an action after observing and attempting its repetition many times. For example, Myowa-Yamakoshi and Matsuzawa (1999) provide an example of a chimpanzee learning to imitate a goal-directed behavior over a dozen or more trials—and then reproducing the end-state relation of two objects rather than the movements involved in achieving that end-state. However, it must be stressed that simple imitation is not so simple, and that with sufficiently long periods of observation (extending perhaps over several months or more), simple imitation may extend to quite complicated behaviors. Byrne (2003) describes the food processing techniques of gorillas (e.g., in gathering nettles and preparing them for “sting-free” eating) as bimanually coordinated hierarchical actions and represents them in goal-directed flow diagrams reminiscent of Fig. 7. As we have seen, ACQ provides an alternative to conventional flow diagram representations of actions by using competition between schemas based on dynamic ranking by priority. The flow diagrams describing gorilla feeding behavior involve both competition between schemas and their cooperation in bimanual coordination. This leads us to ask the question—can we do for Byrne's gorillas what we did for Alstermark's cat? In this paper we present a sketch of an answer for development elsewhere. We suggest that one key to this task will be the recognition that complex behaviors introduce goals and subgoals. Desirability may depend on the current subgoal rather than some overarching goal, in the same way that secondary reinforcers may displace primary reinforcers in guiding animal behavior.

To address this, we are currently developing a novel approach to dynamic planning intermediate between the two extremes of recalling a fixed sequence planned entirely in advance (CQ) and purely reactive generation of successive actions (ACQ). In hierarchical ACQ (hACQ), parts of a plan can be prespecified by the selection of subgoals, but the organization is updatable given unexpected events. The key idea is that at any time, hACQ may assign priority to a single action, to a fixed sequence (spawning a new CQ process), or to a semi-encapsulated goal-oriented subprogram for execution (spawning a new hACQ process). The problem is to keep track of processes while various nested subprocesses are being executed. We thus introduce a working memory for subgoals which maintains a trace of goals and subgoals as the hierarchical motor program is traversed, while the context module maintains a distributed representation of the current subgoal that modulates the activity of the parallel planning layer. This architecture allows a recursive loop from parallel planning layer to competitive choice layer to subgoal working memory to the context module back to the parallel planning layer. Neurons in the parallel planning layer might come to represent sequences of subactions by a process of chunking actions that are repeatedly executed temporally adjacent to each other. This scheme requires some sort of reset signal to the subgoal working memory signifying that a subgoal has been successfully completed or otherwise abandoned and to remove it from the working memory representation.

In most discussions, single mirror neurons are referred to as encoding particular actions. We suggest that they in fact form a distributed (population) code of the features of an observed action. This opens the possibility for generalization to novel actions. In order to learn the hierarchical structure of complex actions through observation, feedback from the mirror system into hACQ could be used to determine which motor schemas to reinforce. Repeated observation could adapt imitation of novel actions via connections between the mirror system and the motor schemas activated by hACQ.

The process of *imitation by behavior parsing* in great apes described by Byrne (2003) involves the statistical extraction of the hierarchical organization of a complex action through repeated observation. The higher-level organization of an action is learned from observation, while the details of each element of the action are shaped through individual trial-and-error. These ideas have a correlate in ACQ where repeated, exploratory action is required to learn desirability and in hACQ where elements that are repeatedly executed temporally adjacent to each other can become chunked into a higher-level action representation. In our model, actions recognized on the basis of both internal (efference copies) and external (visual, tactile, etc.) information are used to determine the targets of TD reinforcement learning. Normally these internally and externally recognized actions coincide. However our explicit study of ACQ has shown that when they differ, motor program reorganization can occur. In the case of imitation, assuming the focus of visual attention is on the demonstrator, the externally recognized action will correspond to that of the demonstrator while the internally recognized action will be the one actually executed. When these do not coincide, repeated observation coupled with individual trial-and-error learning will be required in order to extract the structure from the observed movement and shape a hierarchical motor program corresponding to it.

Recall now the ILGA model from Sect. 2 which models the combined learning of novel grasps and the corresponding affordances. We are currently investigating ways to combine hACQ with ILGA to learn motor program organization and novel actions simultaneously through imitation and individual trial-and-error learning. With an extension of the reinforcement signal from stability of grasp to rewarding actions that yield observable goals other than exploiting affordances for grasping, ILGA will be able to learn novel motor actions by repeated observation and trial-and-error. The population encoding of a novel action in the mirror system can provide a basis for ILGA to recognize approximations of novel actions as a basis for eventual mastery of the novel action in its entirety. Again, we stress that this is work in progress. Our aim here is to show some of the computational challenges to be met in progressing through stages S1 through S4 of the MSH. In particular, we have shown how the mechanisms already in place for stages S1 and S2 may be combined into a system for simple imitation in S3 and have made clear the need for recognizing and generating hierarchical actions even for ape-like imitation by behavior parsing. With this we turn to the human capacity for complex imitation.

5.3 Complex/goal-directed imitation

Behavior parsing implicitly extracts and represents actions in terms of goals and subgoals, but requires a long period of repeated exposure for its success. Humans can, frequently, extract the hierarchical subgoal structure of a novel action in a single trial and, as a result, imitate it to some approximation. Our characterization of *complex imitation* in this paper extends our earlier view (Arbib 2002) of complex imitation as imitation of sequences of variants of known actions by integrating it with the notion (Wohlschläger et al. 2003) of *goal-directed imitation* as based on a hierarchy of extracted goals and subgoals. Wohlschläger et al. (2003) attribute differences in imitative abilities across species to differences in working memory capacity. However, this is not evident from the current data (Call and Tomasello 1995; Call et al. 2005; Horner and Whiten 2005; Nagell et al. 1993; Tomasello et al. 1993; Whiten et al. 1996), and differences in imitative ability could very well be due to differences in the mechanism(s) of hierarchical movement aspect decomposition.

Indeed, the fact that humans can imitate intransitive movements (see the direct route for imitation of meaningless actions in Fig. 4) does not seem to be due to an increased working memory capacity, but rather the ability to decompose aspects of intransitive movements such as relative limb postures and via points. The direct route can interact with the indirect route to recognize novel actions as variants (via the direct route) of known actions (via the indirect route). Through a process of successive approximation, complex movements can be reproduced with increasing accuracy by increased attention being paid to its subparts. This increased attention may result in a finer-scaled decomposition of the observed movement, resulting in execution of a more congruent movement.

Together the indirect and direct routes for imitation would interact through the activation of premotor populations in ILGA (as in Sect. 5.2) that encode motor parameters for action. Rather than simply rewarding ILGA for randomly producing movements similar to novel observed actions, the mirror system population encoding of the novel action could be used to prime premotor neural populations in ILGA to represent the appropriate motor parameter values (representing the activity of the direct route). The indirect route could excite ILGA neural populations in response to known observed actions (corresponding to a mirror to canonical neuron projection). The indirect route would bias ILGA toward executing recognized actions, while the activity of the direct route would modulate ILGA motor parameter representations to incorporate variants on these actions. A challenge for future modeling is to understand how these elements (known transitive action and intransitive “corrections”) may be combined to encode a new action that can then be evoked as a unitary action within future behaviors.

The fact that humans can (approximately) imitate complex actions in a single trial suggests that some symbolic representation of the observed action is used to guide subsequent action rather than the somewhat slow process of reinforcement learning posited in ACQ for externally recognized actions. Instead of slowly updating the connection weights that represent action desirability, a rapid modulation of motor schema priority by a symbolic working memory could be used. If a higher-level action (rather than a lower-level action primitive) is recognized in an observed complex action, a label associated with that action might be added to an evolving symbolic representation of the overall action in working memory. This representation would include the actions recognized, their hierarchical and temporal relations, as well as their relationship to the environment (what is the target of the action, etc.). During execution, a parallel hACQ mechanism may parse the hierarchical symbolic representation of the action in working memory, and the selected action symbol from this process would bias the main hACQ mechanism toward selection of its associated action. While the details of the action may need to be refined through individual experience or successive approximation, the coarse-grained working memory representation can be used to roughly approximate the observed organization of action. In support of this symbolization theory of complex imitation, Bandura et al. (1966) found interference effects when children were asked to imitate a complex sequence of actions while concurrently involved in a competing symbolization task and facilitation when subjects verbalized the observed actions. At Stage S4 of the evolutionary progression there was no verbalization, but Bandura et al.’s data are consistent with the view that the emergence of complex imitation provided mechanisms of vital importance to the later emergence of (proto) language.

6 Discussion

The *MSH* asserts that the *parity requirement* for language is met because Broca’s area evolved atop the mirror system for grasping with its capacity to generate and recognize a set of actions. We have presented a progression of models that attempt to track the course of the evolution of motor control structures from grasping to complex imitation. After reviewing the MNS2 model for how the mirror system for grasping may recognize actions already in the primate's repertoire, we moved on to the organization of sequential actions. We showed how ACQ combined a mirror system for apparent actions with a system utilizing executability, desirability and reinforcement learning of executed and apparent actions. As a result, ACQ can generate flexible, goal-directed behaviors that can be rapidly reorganized in the face of disruption. The extension to this framework, hACQ, is being developed to allow hierarchical action representations and enable dynamic planning to go beyond the separate advantages of preplanned sequences and total reactivity. Intriguingly, the success of hACQ in supporting complex imitation appears to involve a quasi-symbolic representation of goals in relation to actions. We hypothesize that an elaboration of hACQ evolved atop the more primitive hACQ through duplication and differentiation of connectivity to dynamically parse hierarchical symbolic structures in order to bias the unfolding of hierarchically structured action—and that this in turn established necessary processes for the emergence of language as a hierarchical system of perception and production.

Another interest of the direct, as distinct from the indirect, route, is its importance for Stage S5 posited for MSH, the evolution of *Protosign*, a manual-based communication system. Interestingly, where the motor programs for nonhuman primate vocalizations seem resistant to learning—the call repertoire seems essentially innate—it appears that the great apes (as distinct from monkeys) are capable of acquiring novel manual gestures, in part by ontogenetic ritualization (coming to use a reduced form of a praxic action as a communicative gesture—just as a beckoning gesture may be the reduced form of the act of pulling someone closer; Tomasello and Call 1997) but perhaps by social learning as well. Indeed, a particular group of great apes may exhibit on the order of 20 gestures with perhaps half idiosyncratic to that group. This is dramatically different from the ability of the human child to acquire tens of thousands of words (whether spoken or, in the case of deaf children, signed). What evolutionary changes in the brain may have supported this expanded capability? The virtue of ontogenetic ritualization is that it builds upon the praxic action from which it is formed. But this capacity may be a transitional form in the evolution of the direct route—which could have evolved in response to two different pressures, one to better imitate the subtleties of praxic actions, and the other to support the ability to learn gestures directly rather than via their praxic counterpart. The ability to directly learn gestures allows one to acquire observed gestures which have been ritualized between two other individuals and use them to affect the behavior of those individuals without going through the lengthy process of ritualization with those individuals oneself. This more evolved form of gesture acquisition involves a type of learning that can build on the observation of details of intransitive gestures rather than being guided through success in achieving a goal through action upon the affordances of objects (as modeled by ILGA). Here reinforcement based on communicative success may guide the learning of which aspects of visual similarity of the executed movement to the observed movement ensure its suitability as a version of the imitated gesture.

Finally, we recall (Sect. 2) that some macaque mirror neurons can respond to auditory as well as visual cues to mediate recognition of an action. These may be especially relevant to the use of protosign (Stage S5 of the MSH in Sect. 1) as scaffolding for protospeech (Stage S6)—helping support the augmentation of gesture by vocal articulation in the evolution of language (see Roy and Arbib 2005, for a review of data on coupling of manual and articulatory gestures in humans). These multi-modal mirror neurons may have allowed arbitrary vocalizations to become associated with communicative gestures, facilitating the emergence of a speech-centered language from a system of manual gestures. If this is indeed the case, the development of audio-visual mirror neurons may have implications for the recognition of communicative actions and ground the multi-modality of language (Fogassi and Ferrari 2004).

Our challenge now is to build upon the progress we have made in modeling systems essential to Stages S1 through S4 of the MSH to seek new insights into the brain mechanisms which support protosign, protospeech and, in their full elaboration, language—and then factor what we have learned into a fuller account of the evolution of the language-ready brain.

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