system of principles, each with certain possibilities of parametric variation" (Chomsky 1981, p. 224). The minimalist program (Chomsky 1995), that replaced the Principles and Parameters account, focuses on “powerful third factor effects” (Chomsky 2012, p. 46), allegedly constraining language acquisition. But neither of these frameworks seems to provide a satisfactory account for language acquisition (Belhme 2014).

For this reason, alternatives have been suggested (e.g., Elman et al. 1996; MacWhinney 2004; Sampson 2002; Tomasello 2003). Relevant here is one proposal (Arbib 2005; 2010) that involves mirror neurons. It assumes that Broca’s area evolved atop an already existing mirror system for grasping with its capacity to generate and recognize a set of actions. Possibly, in language acquisition “mirror neurons for words encode recognition of the articulatory form … but must be linked to other neural networks for the encoding of meaning” (Arbib 2010, p. 15). It is of course implausible that genetically pre-programmed MNs could be implicated in the highly flexible imitation required by language acquisition. Instead, the evidence suggests that there are quasi-mirror neurons ready to become mirror neurons for novel actions demonstrated by others but which, prior to imitation, do not have this capacity.

Regarding the adaptive value of the language related MN-system, it has been suggested that language evolution was a gradual process that provided us step by step with brain mechanisms supporting (i) the ability to recognize performance as a set of familiar movements, (ii) complex action recognition, and (iii) mechanisms for complex imitation (Oztop et al. 2013, p. 52).

There is no a priori reason to question that such improvements in cognitive abilities could have been selected for. For an adequate evaluation of the function of MNs we need to keep in mind that they did not evolve in isolation but as part of an embodied cognitive system. The “[a]ctivity seen in [human] mirror systems involves not only mirror neurons but other cell types as well… and [s]uch activity may reflect widespread influence of prefrontal cortex and ventral pathways as well as the classic STS→IFL→IFG pathway” (Arbib 2010, p. 14). Under a more holistic analysis Cook et al.’s claim that “there is no positive evidence that MNs are a genetic adaptation or exaptation, or that their development has been canalized, for action understanding” (sect. 9, my emphasis) seems too strong, again missing the point that genetics may specify how neurons may learn, not what they learn.

According to the authors, Cook et al., the standard view of MNs is that they represent an adaptation by the organism, and are thus genetically predetermined. By contrast, Cook et al. assert that mirror mechanisms are not predetermined or even probabilistically determined, but instead develop as a function of sensorimotor associative learning. My objection to this position is that associative learning may be necessary, but it is not sufficient for the development of MNs. In the absence of a proper balancing of evidence, I will present three lines of evidence that question the sufficiency of associative learning for explaining the development of mirror mechanisms: (1) Genetic predispositions interact with associative learning; (2) infants show predispositions to imitate human as opposed to nonhuman actions, and (3) there are differences in learning during early and later development.

The first reason to question a strict associative account is because it cannot explain why some behaviors are learned more easily than others. Cook et al. claim that the observation–execution matching properties of mirror mechanisms are not a specific genetic predisposition, but rather a domain-general process of associative learning found in a wide range of vertebrate and invertebrate species. This position implies that all correlated sensory–motor experiences should be learned equally well by the organism, but this claim is not supported by the data. As the authors are aware, following the pioneering research of Garcia (e.g., Garcia et al. 1995), it was shown that rats could not associate visual and auditory cues with food that made them ill, but could learn to associate olfactory cues with such foods (see Gould & Marler [1987] for other examples). These findings are not surprising from an adaptive standpoint (though I suspect escheved by Cook et al.) because rats are biologically prepared to learn some things more readily than others. In the natural world, odor is a more reliable cue than color for rats because they are primarily nocturnal, so odor is better associated with dangerous foods than is color. The conclusion from these sorts of studies is that animals are biased to learn some associations more easily than others even though the contingencies are the same. Thus, it appears that there are genetic predispositions that interact with the success of associative learning.

The second reason to question the associative account derives from evidence showing that infants are biased to imitate human as opposed to nonhuman actions. In the target article, imitation is considered a behavioral index of the presence of mirror mechanisms. If all sensorimotor associative learning is sufficient to explain imitation, then infants should be as likely to imitate mechanical as opposed to human actions. However, the critical evidence is at best mixed. For example, Meltzoff (1995) demonstrated that 18-month-old infants could imitate the actions of an adult pulling apart a barbell but not the actions of the human experimenter, and 9-month-old infants failed to commit the search error on the B test trial because they covertly imitated the search behavior of the experimenter during the A trials. By contrast, Boyer et al. (2011) substituted a pair of mechanical claws for the human experimenter, and 9-month-old infants failed to commit the search error suggesting that they were less likely to covertly imitate the goal-directed behavior of the claws. It thus appears that infants, like the rats described above, are predisposed to learn some sensorimotor associations more readily than others. These findings are thus consistent with the human and nonhuman research literature suggesting that MNs are more likely to become activated to the observation of human actions than to mechanical devices or tools (Liepelt & Brass 2010; Longo & Bertenthal 2009; Woodward 1998). If associative learning was sufficient for the development of mirror mechanisms, the response to human generated actions should not be privileged.

The last challenge concerns whether sensorimotor training studies with adults, considered an important source of support

The insufficiency of associative learning for explaining development: Three challenges to the associative account

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Abstract: Three challenges to the sufficiency of the associative account for explaining the development of mirror mechanisms are discussed: Genetic predispositions interact with associative learning, infants show predispositions to imitate human as opposed to nonhuman actions, and early and later learning involve different mechanisms. Legitimate objections to an extreme nativist account are raised, but the proposed solution is equally problematic.

As a developmental scientist, I greatly appreciate this target article drawing attention to the importance of clarifying the origins of mirror neurons (MNs). This is no easy feat and I believe that this article is testament to the complexity of the problem.
for the associative account, are necessarily relevant to the development of mirror mechanisms. This evidence is questionable because the training studies involve behavioral assessments which are inferred to reflect mirror mechanisms, but there is no direct evidence that the underlying mirror mechanisms are modified nor is there evidence that these observed short-term changes can translate into more permanent long-term effects. Also, at the neural level, there are two types of experiential learning (Greenough et al. 1987). One type is limited to sensitive periods during early development and is characterized by an overproduction of new synapses in anticipation of specific experiences that will contribute to the development of species typical behaviors, such as locomotion and language development (Bertenthal & Campos 1987). By contrast, experience-dependent processes are associated with the formation of new synapses that develop in response to unique experiences of the individual organism throughout development. If Cook et al. are correct that mirror mechanisms are exclusively a function of an inductive process involving sensorimotor learning, their development would correspond to an experience-dependent process. Currently, this claim is not defensible given that it is just as likely that the early behaviors associated with mirror mechanisms, such as imitation, are species-typical behaviors and thus just as likely to be mediated by an experience-expectant process which predisposes infants to develop mirror mechanisms.

In conclusion, the target article raises legitimate reasons to question an extreme nativist position regarding the development of mirror mechanisms, but errs in the opposite direction by claiming a strong empiricist position. If a more probabilistic than pre-determined view of epigenesis is considered (Gottlieb 2007), it is difficult to imagine how a genetic predisposition could not contribute to the development of mirror mechanisms.

**Associative learning is necessary but not sufficient for mirror neuron development**

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**Abstract:** Existing computational models of the mirror system demonstrate the additional circuitry needed for mirror neurons to display the range of properties that they exhibit. Such models emphasize the need for existing connectivity to form visuomotor associations, processing to reduce the space of possible inputs, and demonstrate the role neurons with mirror properties might play in monitoring one’s own actions.

The primary hypothesis set forth by Cook et al. is that mirror neurons (MNs) are the result of generic associative learning processes, rather than the result of evolutionary selection for action understanding. They claim that the standard view of mirror neurons, what they call the “genetic account,” suggests that the predisposition to develop MNs is heritable and was selected for on the basis of their role in action understanding. However, in their characterization of the genetic account, Cook et al. do allow for the role of experience in shaping MNs. Computational models that simulate the development of MNs through experience show that this is possible through associative learning mechanisms, but that the connectivity to form these associations must already be in place and that this connectivity must be somewhat specialized for control of hand actions.

Cook et al. describe the “exaptation hypothesis” as claiming that MNs require a special kind of sensorimotor learning. However, a closer look at several of the computational models developed under this hypothesis, such as the Mirror Neuron System (MNS) model (Oztop & Arbib 2002), reveals that they do in fact use standard learning algorithms completely compatible with the associative learning account. What makes these models work is the structure of their input representations and their connectivity. The pure associative learning account seems to assume that every neuron is either directly or indirectly connected with every other neuron in the brain. Such an architecture would require significantly more trials of action and observation in order to correctly associate visual stimuli with the relevant motor representations.

The simplest version of the genetic account would predict that MNs would be found in different areas of the brain, depending on the unique history of each individual. This is not the case, at least in monkeys, and this seems to be due to a genetic influence on the patterns of connectivity expressed by each brain region. Indeed, as Cook et al. claim, there is a “wealth of the stimulus” — so much that the space of possible hand–object interaction representations in the visual and motor domains makes the associative learning account computationally intractable. What makes the “exaptation hypothesis” models able to handle such a space is the fact that the inputs are constrained to represent the hand–object relationships and trajectory for performing manual actions. This is thought to occur throughout motor development as the infant learns to extract the relevant features from visual stimuli for controlling the hand relative to the object (Oztop et al. 2004). Once the inputs are restricted to those necessary to control transitive actions, “domain-general learning processes” can proceed to associate the visual representation with the motor program at various levels of abstraction.

Although the learning algorithm in the MNS model was compatible with the associative learning account, the network required extensive pre-processing of its input. Mirror neurons respond to observation of dynamic hand actions and therefore must process trajectories in the space of hand–object relationships. Mirror neurons will often respond to observation of a grasp before the hand contacts the object. In order to predict the outcome of a grasp before its completion, the MNS model transformed a temporal sequence of hand–object relations into a spatial pattern of neural activity for input to the network. A subsequent version of the MNS model, MNS2, discarded this preprocessing step by using a recurrent neural network and a modified learning algorithm to handle raw input sequences (Bonaiuto et al. 2007). These models show that although MNs may acquire their properties through associative-style learning processes, extra circuitry is required to perform the computations necessary for processing dynamic visual input from object-directed hand actions.

The MNS2 model additionally proposed that audiovisual MNs develop their auditory properties through simple associative learning. However, in this model, extra mechanisms such as working memory and dynamic remapping were required to handle the case where MNs correctly predict the outcome of a grasp when the final portion was obscured. It is not clear how these functions could be developed through pure associative learning.

Giese and Poggio (2003) present a model of visual tuning in the mirror system that is the most compatible with the associative learning account. This model currently does not include a learning mechanism, but it does address the existence of view-dependent and -independent mirror neurons and does not require reconstruction of the arm and hand shape. However, it still requires extensive processing to transform visual input into a reduced space such that it can be associated with motor signals.

The Augmented Competitive Queuing (ACQ) model embeds a network such as those in the MNS and MNS2 models in a larger network that learns self-actions (Bonaiuto & Arbib 2010). In this model, MN activity signals recognition of successful completion of one’s own actions. Their output is used as an eligibility trace in reinforcement learning algorithms that modify the recognized action’s desirability — how likely an action is to lead to a reward; and executability — how likely an action can be successfully