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Mirror neurons: From origin to function

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Abstract: This article argues that mirror neurons originate in sensorimotor associative learning and therefore a new approach is needed to investigate their functions. Mirror neurons were discovered about 20 years ago in the monkey brain, and there is now evidence that they are also present in the human brain. The intriguing feature of many mirror neurons is that they fire not only when the animal is performing an action, such as grasping an object using a power grip, but also when the animal passively observes a similar action performed by another agent. It is widely believed that mirror neurons are a genetic adaptation for action understanding; that they were designed by evolution to fulfill a specific socio-cognitive function. In contrast, we argue that mirror neurons are forged by domain-general processes of associative learning in the course of individual development, and, although they may have psychological functions, they do not necessarily have a specific evolutionary purpose or adaptive function. The evidence supporting this view shows that (1) mirror neurons do not consistently encode action "goals"; (2) the contingency- and context-sensitive nature of associative learning explains the full range of mirror neuron properties; (3) human infants receive enough sensorimotor experience to support associative learning of mirror neurons ("wealth of the stimulus"); and (4) mirror neurons can be changed in radical ways by sensorimotor training. The associative account implies that reliable information about the function of mirror neurons can be obtained only by research based on developmental history, system-level theory, and careful experimentation.

Keywords: action understanding; associative learning; contextual modulation; contingency; genetic adaptation; imitation; mirror neuron; poverty of the stimulus; sensorimotor experience.

1. Introduction

Mirror neurons (MNs) were discovered serendipitously in 1992 and given their brilliant name four years later (di Pellegrino et al. 1992; Gallese et al. 1996). The striking feature of many MNs is that they fire not only when a monkey is performing an action, such as grasping an object using a power grip, but also when the monkey passively observes a similar action performed by another. Neurons with this capacity to match observed and executed actions, to code both "my action" and "your action," were originally found in area F5 of the ventral premotor cortex (PMC) (di Pellegrino et al. 1992; Gallese et al. 1996) and the inferior parietal lobule (IPL) (Bonini et al. 2010; Fogassi et al. 2005) of the monkey brain. There is now a substantial body of evidence suggesting that MNs are also present in the human brain (Molenberghs et al. 2012).

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MNs have received a great deal of attention from specialists and in the scientific and public media. Hailed as "cells that read minds" (Blakesee 2006), "the neurons that shaped civilization" (Ramachandran 2009), and a "revolution" in understanding social behavior (Iacoboni 2008), MNs have been ascribed a wide variety of functions. The primary candidates relate to action understanding (Gallese & Sinigaglia 2011; Rizzolatti et al. 1996), imitation (Iacoboni et al. 1999), and language processing (Rizzolatti & Arbib 1998). However, signifying the way in which MNs have captured the attention and imagination of neuroscientists, psychologists, and philosophers, they have also been implicated in: embodied simulation (Aziz-Zadeh et al. 2006b), empathy (Avenanti et al. 2005), emotion recognition (Enticott et al. 2008), intention-reading (Iacoboni et al. 2005), language acquisition (Theoret & Pascual-Leone 2002), language evolution (Arbib 2005), manual communication (Rizzolatti et al. 1996), sign language processing (Corina & Knapp 2006), speech perception (Glenberg et al. 2008), speech production (Kuhn & Brass 2008), music processing (Gridley & Hoff 2006), sexual orientation (Ponseti et al. 2006), and aesthetic experience (Cinzia & Gallese 2009). In addition, it has been suggested that MN dysfunction contributes to a number of disorders, including autism (Dapretto et al. 2006; Nishitani et al. 2004; J. H. Williams et al. 2001), schizophrenia (Arbib & Mundhenk 2005), Down's syndrome (Virji-Babul et al. 2008), multiple sclerosis (Rocca et al. 2008), cigarette addiction (Pineda & Oberman 2006), and obesity (Cohen 2008).

Thus, much of the first 20 years of MN research has been devoted to theorizing and speculation about their functions. In contrast, the primary focus of this article is the origin of MNs. Our principal questions are not "What do MNs do?" or "What are they for?", but "What is the process that gives MNs their 'mirrorness'; their fascinating, cardinal capacity to match observed with executed actions?"

The standard view of MNs, which we will call the "genetic account," alloys a claim about the origin of MNs with a claim about their function. It suggests that the mirrorness of MNs is due primarily to heritable genetic factors, and that the genetic predisposition to develop MNs evolved because MNs facilitate action understanding. In the sense of "an adaptation" developed by G. C. Williams, and used in Evolutionary Psychology, the genetic account casts MNs as an adaptation for action understanding. In contrast, we argue in this article that the balance of evidence currently favors an "associative account" of MNs, which separates questions about their origin and function. It suggests that MNs acquire their capacity to match observed with executed actions through domain-general processes of sensorimotor associative learning, and that the role of MNs in action understanding, or any other social cognitive function, is an open empirical question. The associative account is functionally permissive; it allows, but does not assume, that MNs make a positive contribution to social cognition. Thus, there are three critical differences between the genetic and associative accounts: (1) The former combines, and the latter dissociates, questions about origin and function. (2) The genetic account suggests that natural selection has acted directly on MNs, whereas the associative account suggests that natural selection has played a background role; for example, acting on domain-general mechanisms of associative learning. (3) The genetic account assigns a relatively minor, facilitative role to sensory and/or motor experience in the development of MNs, whereas the associative account suggests that sensorimotor experience plays a major, instructive role in their development.

We begin, in section 2, with some basic information about the ways in which MNs have been defined and investigated in both monkeys and humans.[1] In the third section we present the genetic and associative accounts, and introduce four kinds of evidence that have the potential to favor one of these hypotheses over the other. Sections 4–7 discuss each of these types of evidence in turn. In section 8 we survey recent theories that are, or appear to be, alternatives to the genetic and associative accounts, and suggest that the associative account is stronger. Finally, in section 9 we argue that the associative account has major methodological implications for research investigating the functions of MNs. Unlike the genetic account, the associative account doesn't claim to tell us what MNs do or what they are for, but it does tell us how we can find out.

2. Mirror neuron basics

2.1. Locations and definitions

MNs have been found in the monkey brain (*Macaca nemistrina* and *Macaca mulatta*), not only in "classical" areas – ventral PMC and IPL – but also in "non-classical" areas, including primary motor cortex (Dushanova & Donoghue 2010; Tkach et al. 2007) and dorsal PMC (Tkach et al. 2007). There is also evidence of single neurons, or circumscribed populations of neurons, with sensorimotor matching properties in classical areas of the human brain, including posterior regions of the inferior frontal gyrus (IFG; considered the human homologue of the monkey F5) (Kilner et al. 2009) and inferior parietal cortex (Chong et al. 2008), and non-classical areas of the human brain, including dorsal PMC, superior parietal lobule, and cerebellum (Molenberghs et al. 2012), supplementary motor area, and medial temporal lobe (Mukamel et al. 2010).

Some researchers apply the term "mirror neuron" only to neurons found in classical areas (Brown & Brune 2012; Molenberghs et al. 2012), whereas others, like us, use the term to refer to neurons in both classical and non-classical areas (Gallese & Sinigaglia 2011; Keysers & Gazzola 2010). In addition to this variation in anatomical specificity, some researchers reserve the term "mirror neuron" for units that discharge during the observation and execution of precisely (Dinstein et al. 2008b; Keysers 2009) or broadly similar actions (Kilner et al. 2009), whereas others use the term, at least on occasions, to refer to any neuron that is responsive to both the observation and execution of action, regardless of whether the observed and executed actions are even broadly similar to one another (Gallese et al. 1996; Rizzolatti & Craighero 2004). In accord with the majority of researchers in the field, and the meaning of the word "mirror," we take it to be a cardinal feature of MNs that they are responsive to observation and execution of similar actions. However, following common usage, we also refer to "logically related" MNs (see sect. 2.2), which fire during observation and execution of dissimilar actions, as "mirror neurons."

2.2. Monkeys

Early studies of the field properties of monkey MNs – the sensory and motoric conditions in which they fire – revealed three basic types: "Strictly congruent" MNs discharge during observation and execution of the same action, for example, precision grip. "Broadly congruent" MNs are typically active during the execution of one action (e.g., precision grip) and during the observation of one or more similar, but not identical, actions (e.g., power grip alone, or precision grip, power grip, and grasping with the mouth). "Logically related" MNs respond to different actions in observe and execute conditions. For example, they fire during the observation of an experimenter placing food in front of the monkey, and when the monkey grasps the food in order to eat it. MNs do not respond to the presentation of objects alone (di Pellegrino et al. 1992). However, "canonical neurons," which are active during object observation and performance of an action that is commonly performed on that object, are co-located with MNs both in area F5 (Murata et al. 1997) and in the anterior intraparietal sulcus (Murata et al. 2000).

To date, monkey MNs have been found that are responsive to the observation and execution of hand and mouth actions. The hand actions include grasping, placing, manipulating with the fingers, and holding (di Pellegrino et al. 1992; Gallese et al. 1996). The mouth actions include ingestive behaviors such as breaking food items, chewing and sucking, and communicative gestures such as lip-smacking, lip-protrusion, and tongue-protrusion (Ferrari et al. 2003).

2.3. Humans

Only one study purports to offer direct evidence – from single cell recording – of MNs in the human brain (Mukamel et al. 2010). However, there is a considerable body of indirect evidence – from neuroimaging, transcranial magnetic stimulation (TMS), and behavioral studies – suggesting that human brains contain MNs or comparable "mirror mechanisms"; circumscribed cortical areas involved in both action production and observation (Glenberg 2011).

2.3.1. Neuroimaging. Functional magnetic resonance imaging (fMRI) has identified regions of PMC (both classic BA6 and BA44) and inferior parietal areas that are active during both action observation and execution (Aziz-Zadeh et al. 2006a; Buccino et al. 2004; Carr et al. 2003; Grèzes et al. 2003; Iacoboni et al. 1999; Leslie et al. 2004; Tanaka & Inui 2002; Vogt et al. 2007). Overlapping responses to action observation and execution have been found in single-subject analyses of unsmoothed data (Gazzola & Keysers 2009), confirming that the foregoing reports are not artifacts of group averaging. Most recently, repetition suppression protocols have been used to provide evidence of mirror populations encoding visual and motor representations of the same action. These paradigms exploit the logic that repeated stimulus presentation or action execution causes a decrease in neural responses (Grill-Spector et al. 2006). "Cross-modal" repetition suppression effects have been reported, whereby action observation followed by execution of the same action, or vice versa, elicits repetition suppression in inferior parietal regions (Chong et al. 2008; Lingnau et al. 2009) and in PMC (Kilner et al. 2009; Lingnau et al. 2009).

2.3.2. Mirror pattern of MEPs. A human mirror mechanism is further suggested by "mirror" motor evoked potentials (MEPs) elicited during action observation (Fadiga et al. 1995). When TMS is applied to M1 during passive action observation, the amplitude of the MEPs recorded from the muscles required to execute that action is greater than the amplitude of the MEPs recorded when observing a different action. For example, observing index and little finger abduction movements selectively facilitates the amplitude of MEPs recorded from the first dorsal interosseus and abductor digiti minimi muscles, responsible for index and little finger movements, respectively (Catmur et al. 2011). That action observation selectively increases corticospinal excitability to action relevant muscles is suggestive of "mirror" sensorimotor connectivity.

2.3.3. Automatic imitation. Automatic imitation is said to occur when observation of an action involuntarily facilitates performance of a topographically similar action (body parts make the same movements relative, not to external frames of reference, but to one another) and/or interferes with performance of a topographically dissimilar action (Brass et al. 2001; Stürmer et al. 2000). Humans show robust automatic imitation when they observe hand, arm, foot, and mouth movements (Heyes 2011). This is regarded by many researchers as evidence of a human mirror mechanism (Blakemore & Frith 2005; Ferrari et al. 2009a; Iacoboni 2009; Kilner et al. 2003; Longo et al. 2008; van Schie et al. 2008). Supporting this view, several studies have shown that application of disruptive TMS to the IFG – a classical mirror area – interferes with automatic imitation (Catmur et al. 2009; Newman-Norlund et al. 2010).

3. The mirrorness of mirror neurons: Genetic or associative?

This section presents the standard, genetic account of the origin of MNs and the alternative associative account.

3.1. Genes for mirroring?

The genetic account assumes: (1) Among common ancestors of extant monkeys and humans, some individuals had a stronger genetic predisposition to develop MNs, and (2) these individuals were more reproductively successful than those with a weaker genetic predisposition because the development of MNs enhanced their capacity to understand the actions of other agents. Consequently, (3) a genetic predisposition to develop MNs became universal, or nearly universal, in monkeys and humans. (4) Motor experience (the performance of actions) and/or sensory experience (the observation of actions) plays a facilitative (Gottlieb 1976) or permissive (Gilbert 2003) role in the development of MNs, but their matching properties are primarily due to this genetic predisposition.

The term "action understanding" was introduced by Rizzolatti and colleagues to characterize the function of MNs (Rizzolatti & Fadiga 1998; Rizzolatti et al. 1996). As far as we are aware, it had not previously been used in research on animal or human cognition. The term plays a key role in the genetic account; it describes the adaptive function of MNs, the effects that made them a target of positive selection pressure. However, there is still no consensus about exactly what is meant by "action understanding," or how it differs from cognate functions such as "action perception," "action recognition," and "action selection" (Gallese et al. 2011). Attempts to clarify have emphasized that, in comparison with purely visual processing of action, MN activity relates to the "meaning" of an action and yields a "richer understanding," "real understanding," or "understanding from within" (Gallese et al. 2011; Rizzolatti & Sinigaglia 2010). As we discuss further in section 8, these descriptions do not provide an operational definition of action understanding, that is, a definition that would allow behavior based on (this kind of) action understanding to be distinguished empirically from behavior based on other processes.

Until recently, the genetic account was largely implicit in discussions of the "evolution" of MNs (Gallese & Goldman 1998; Rizzolatti & Arbib 1998; Rizzolatti & Craighero 2004; M. J. Rochat et al. 2010). For example, it has been suggested that "the mirror neuron mechanism is a mechanism of great evolutionary importance through which primates understand actions done by their conspecifics" (Rizzolatti & Craighero 2004, p. 172) and that "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" (Bonini & Ferrari 2011, p. 172). A number of discussions have also expressed the view that MNs are present at birth (Ferrari et al. 2009; Gallese et al. 2009; Lepage & Theoret 2007; Rizzolatti & Fadiga 1998), a feature commonly associated with traits for which there is strong genetic predisposition (Mameli & Bateson 2006). For example, Casile and colleagues have suggested that "both face processing and the mirror neuron system, or at least the part involved in facial movements, rely on a brain network that is present already at birth and whose elements are probably genetically predetermined" (Casile et al. 2011, p. 531).

In its starkest form, the genetic hypothesis would suggest that gene-based natural selection has provided each individual – monkey and human – with MNs that code the mapping between a fixed set of observed and executed actions, and that experience plays a minimal role in the development of the observation-execution matching properties of these neurons. However, the genetic hypothesis does not necessarily assume that experience plays a minimal role. For example, in a recent explicit statement of the genetic account, Gallese et al. (2009) suggested that links form during gestation between motor regions and "to-become-visual" regions that will subsequently mediate sensorimotor matching abilities in young infants. They implied that these projections are genetically predisposed to target certain visual areas, and therefore that the matching properties of MNs are produced by information encoded in the genome. However, they also suggested that motor experience plays a part in preparing motor regions to send projections to visual areas, and that visual experience may also facilitate the maturation of fully functioning MNs.

3.2. A product of associative learning

The associative hypothesis assumes that gene-based natural selection has played a significant background role with respect to the development of MNs; for example, in shaping the anatomy of visual and motor cortex for visual guidance of action, and in producing the capacity for associative learning in neural tissue. However, it suggests that the cardinal matching properties of MNs are a product, not of a specific genetic predisposition, but of domain-general processes of associative learning – the same kind of learning that produces Pavlovian and instrumental conditioning phenomena (Catmur et al. 2009; Heyes 2010; Ray & Heyes 2011). Associative learning is found in a wide range of vertebrate and invertebrate species, indicating that it is an evolutionarily ancient and highly conserved adaptation for tracking predictive relationships between events (Heyes 2012b; Schultz & Dickinson 2000).

Figure 1 is a schematic representation of how MNs could acquire their matching properties through sensorimotor associative learning. Before associative learning, sensory neurons in the superior temporal sulcus (STS), responsive to different high-level visual properties of observed action (Oram & Perrett 1994; 1996), are weakly connected, directly or indirectly, to motor neurons in PMC (Rizzolatti et al. 1988) and parietal cortex (Gallese et al. 2002). Some of these connections may be stronger than others, but the links between sensory and motor neurons coding similar actions are not consistently stronger than other, nonmatching links. The kind of learning that produces MNs occurs when there is correlated (i.e., contiguous and contingent) excitation of sensory neurons and motor neurons that code similar actions. For example, when an adult imitates an infant's facial movements, there might be correlated excitation of neurons that are responsive to the observation and execution of lip protrusion. Correlated excitation of the sensory and motor neurons increases the strength of the connection between them, so that subsequent excitation of the sensory neuron propagates to the motor neuron. Thereafter, the motor neuron fires, not only during execution of lip protrusion, but also, via its connection with the sensory neuron, during observation of lip protrusion; what was originally a motor neuron has become a lip protrusion MN. Correlated excitation of sensory and motor neurons encoding the same property of action occurs not only when humans are imitated, but also when we observe our own actions (directly or using an optical mirror); observe others during the kind of synchronous activities involved in sports and dance training; and as a consequence of "acquired equivalence" experience, for example, when the same sound (a word, or a sound produced by an action) is paired sometimes with observation of an action and sometimes with its execution (Catmur et al. 2009; Ray & Heyes 2011).

There are several important things to note about the associative hypothesis:

1. *Strong experience-dependence* – It suggests that correlated sensorimotor experience plays an inductive

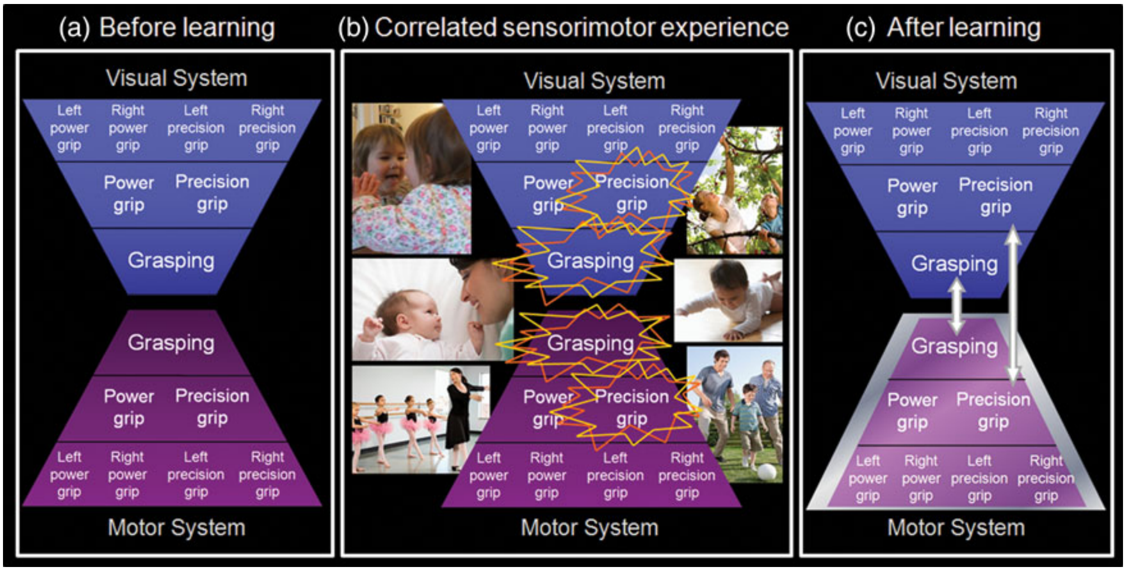

Figure 1. Mirror neurons from associative learning. (a) Before learning, sensory neurons in STS, encoding visual descriptions of observed action, are not systematically connected to motor neurons in premotor and parietal areas involved in the production of similar actions. (b) Through social interaction and self-observation in the course of typical development, agents receive correlated sensorimotor experience; they see and do the same action at about the same time (contiguity), with one event predicting the other (contingency). This experience produces correlated activation of sensory and motor neurons coding similar actions, and, through associative learning, (c) strengthens connections between these neurons. Due to these connections, neurons that were once involved only in the execution of action will also discharge during observation of a similar action; motor neurons become MNs (see sect. 3.2). Because the visual system and motor system are organised hierarchically, some types of sensorimotor experience produce correlated activation of sensory and motor neurons coding relatively low-level features of action (e.g., left or right hand, power or precision grip), and thereby generate strictly congruent, hand- and direction-sensitive MNs. Other types produce correlated activation of neurons coding relatively high-level features (e.g., grasping) and generate broadly congruent MNs (see sect. 5.1).

(Gottlieb 1976) or instructive (Gilbert 2003) role; without this kind of experience, MNs would not develop at all.

2. *Social construction* – It proposes that much of the sensorimotor experience required for MN development comes from being imitated, synchronous action, and exposure to action words (Ray & Heyes 2011), and therefore that MNs are to a very large extent built through social interaction.

3. *Contingency* – Following contemporary learning theory, the associative account specifies that MN development requires, not just that sensory and motor neurons "fire together" in a Hebbian way (contiguity), but that the event provoking firing of one predicts the event provoking firing of the other (contingency; Cook et al. 2010).

4. *Testability* – The associative account makes novel predictions about the development and mature properties of MNs, many of which have already been tested and supported by experiments using a variety of methods (see sect. 7).

Thus, the associative hypothesis implies that the characteristic, matching properties of MNs result from a genetically evolved process, associative learning, but this process was not "designed" by genetic evolution to produce MNs. Rather, it just happens to produce MNs when the developing system receives correlated experience of observing and executing similar actions. When the system receives correlated experience of observing objects and executing actions, the same associative process produces canonical neurons. When the system receives correlated experience of observing one action and executing a different action, the same associative process produces logically related MNs.

3.3. Not nature versus nurture

The contrast between the genetic and associative hypotheses does not represent a dichotomous nature–nurture debate. It has been recognized for decades that the development of all phenotypic characteristics depends on the interaction of nature *and* nurture, genes *and* the environment, evolution *and* learning (Elman et al. 1996; Oyama 1985). Rather, the two accounts differ in the specific roles they assign to genetic evolution and to learning, and in the types of experience they take to be important, in producing the characteristic matching properties of MNs. The genetic hypothesis says that genetic evolution has played a specific and decisive role, and learning – based on sensory and/or motor experience – plays a merely facilitative role, in the development of MNs. In contrast, the associative hypothesis says that genetic evolution has played a non-specific background role, and that the characteristic matching properties of MNs are forged by sensorimotor learning.

Regarding the function of MNs, the genetic account assumes that they play a fundamental role in action understanding, and that this is why a specific genetic predisposition to develop MNs was favored by natural selection. In other words, it proposes that action understanding is the "adaptive function" of MNs, or that MNs are "an adaptation" for action understanding. In this way, the genetic account offers a hypothesis about the function of MNs as an explanation for their origins. In contrast, the associative account separates questions about the origin and function of MNs. It suggests that MNs develop through associative learning, and that further research is needed to find out how they contribute to social cognition (see sect. 9). If this research reveals that MNs make positive contributions to social cognition, these would be "psychological uses" or "psychological functions," but not necessarily "adaptive functions"; they may not have enhanced reproductive fitness, nor resulted in the evolution of mechanisms specifically designed to foster the development of MNs (see sect. 8). Rather, it is possible that MNs are constructed by domain-general processes of associative learning, and are recruited in the course of development to contribute to one or more psychological functions, without either the construction or the recruitment processes having become a specific target of gene-based selection (Elman et al. 1996).

In this respect, MNs may be like beak morphology in Neotropical woodcreepers, which has been selected for foraging and food manipulation (a non-social function, analogous to visuomotor capability) but also has effects on song production (a social function, analogous to action understanding; Derryberry et al. 2012). Another more closely related example comes from honeybees, which are able to use associative learning to discriminate among human faces (Dyer et al. 2005). Given the taxonomic- and domain-generality of associative learning, and the fact that human faces were not part of the environment in which honeybee nervous systems evolved, we can be sure that associative learning is not an adaptation for face discrimination in honeybees. However, when they are put in an environment where faces are important, honeybees can use associative learning about faces to optimize their foraging behavior. Another example, which may be closely related in a different way, is the area of the human occipito-temporal cortex known as the "visual word form area" (VWFA; Petersen et al. 1990). This area plays an important role in reading, but, given the recent emergence of literacy in human history, the VWFA is very unlikely to be a genetic adaptation for reading. Rather, the reading-related properties of the VWFA are forged in the course of development, by literacy training, from a system adapted for generic object recognition.

3.4. Four kinds of evidence

Four evidence-based arguments are crucial in deciding between the genetic and associative accounts. The first provided the inspiration and foundation for the genetic hypothesis. It suggests that the field properties of MNs indicate that they were designed for action understanding. The terms "design" and "purpose" are used here as they were by G. C. Williams in his seminal work on *Adaptation and Natural Selection* (Williams 1966). Williams described adaptations as designed by natural selection to fulfill a particular purpose, and emphasized that the mark of an adaptation is that it has features making it peculiarly apt to achieve a specific end in a highly efficient way. For example, "An examination of the legs and feet of the fox forces the conclusion that they are designed for running and walking, not for the packing or removal of snow" (p. 13). In a similar way, supporters of the genetic hypothesis argue that examination of the field properties of MNs – and, in particular, their "goal" coding – forces the conclusion that MNs are designed for action understanding. In section 3 we examine the field properties of MNs and suggest that this argument is not compelling.

The second argument is complementary to the first; it has a similar form but advocates the associative hypothesis. It suggests that research using conditioning procedures shows associative learning to be the right kind of learning to produce MNs. Specifically, as we discuss in section 5, the ways in which associative learning tracks contingent relationships, and enables contextual modulation of these connections, makes it apt to produce MNs (and non-matching visuomotor neurons) in typical developmental environments.

The second pair of arguments draws on research examining the development of MNs and their modification through sensorimotor experience. Section 6 discusses research with infants and adults that has been used to support a "poverty of the stimulus" argument (Chomsky 1975); to suggest that MNs emerge too early in development or, more generally, after too little sensorimotor experience, to have been forged by associative learning. In contrast, we offer a "wealth of the stimulus" argument.

Finally, section 7 focuses on evidence that, even in adulthood, the properties of MNs can be changed in radical ways by relatively brief periods of sensorimotor experience. We argue, against various objections, that this evidence is sound and therefore supports the associative hypothesis by showing that it has produced novel, testable predictions which have been confirmed by experiment.

4. Designed for action understanding

Supporters of the genetic hypothesis argue that examination of the field properties of MNs shows that they encode "goals," and this characteristic indicates that they were designed by genetic evolution to mediate action understanding (Bonini & Ferrari 2011; Rizzolatti & Craighero 2004; Rizzolatti & Sinigaglia 2010). We therefore begin our survey of the evidence by considering how well the neurophysiological data accord with this view. The term "goal" affords numerous interpretations (Hickok 2009). We will consider two definitions commonly adopted, assuming that MNs encode "goals" if they encode object-directed actions (sect. 4.1) or high-level action intentions (sect. 4.2).

4.1. Goals as object-directed actions

Early descriptions of MN field properties reported that pantomimed actions (e.g., miming a precision grip in the absence of an object) and intransitive actions (e.g., tongue-protrusion) did not elicit MN responses (di Pellegrino et al. 1992; Gallese et al. 1996). In contrast, robust responses were reported when monkeys observed object-directed actions. This pattern raised the possibility that MNs encode "goals" in the sense that they are responsive only to object-directed actions (di Pellegrino et al. 1992; Gallese et al. 1996).

However, a close reading of the single-cell data suggests that only a small subset of MNs appeared to have been "designed for" encoding action goals in these terms. A subset of the MNs described in the early reports continued to respond, albeit less strongly, to pantomimed or intransitive actions (di Pellegrino et al. 1992; Gallese et al. 1996, Figure 5b), and subsequent studies confirmed that sizable proportions, perhaps the majority, of MNs exhibit robust responses to the observation of object-free body movement. Kraskov et al. (2009) reported that 73% of MN responses modulated by observation of object-directed grasping showed similar modulation during observation of pantomimed grasping. Also, substantial proportions of MNs respond to intransitive mouth movements such as lip-smacking, lip-protrusion, and tongue-protrusion (Ferrari et al. 2003).

Single-unit data also show that, even when they are responding to object-directed actions, MNs have field properties suggesting that they were not tuned to do this by genetic evolution. For example, after training in which tools were used to pass food items to monkeys, MNs were discovered that respond to the observation of actions such as grasping with pliers (Ferrari et al. 2005). Similarly, "audiovisual" MNs respond to unnatural sounds associated with actions; for example, the sound of metal striking metal, plastic crumpling, and paper tearing (Keysers et al. 2003; Kohler et al. 2002). Importantly, large numbers of tool-use and audiovisual MNs respond more to the sight of tool-actions and to action sounds than to the sight of gripping or tearing executed with the hands. The fact that these MNs respond maximally to unnatural stimuli – that is, stimuli to which the evolutionary ancestors of contemporary monkeys could not possibly have been exposed – is hard to reconcile with the genetic hypothesis (Cook 2012; see sect. 7).

4.2. Goals as high-level intentions

The term "goal" has also been used to refer to what, at a high level of generality, the actor intends to achieve through their behavior – for example, "grasp in order to eat" (Fogassi et al. 2005) or "taking possession of an object" (M. J. Rochat et al. 2010). Rizzolatti and Sinigaglia (2010, p. 269) state: "only those [neurons] that can encode the goal of the motor behavior of another individual with the greatest degree of generality can be considered to be crucial for action understanding." The suggestion that MNs encode high-level action intentions is made plausible by reports that MN responses to grasping can be modulated by the final outcome of the motor sequence (Bonini et al. 2010; Fogassi et al. 2005). It is also consistent with reports that some broadly congruent MNs respond to the observation of multiple actions; for example, any "grasping" action executed with the hand or mouth (Gallese et al. 1996).

However, the single-cell data again suggest that relatively few MNs have the field properties one would expect of a system designed by genetic evolution to represent high-level action intentions. For example, Gallese et al. (1996) reported that during action observation 37.5% of MNs responded differently depending on whether the action was executed with the left or right hand, and 64% showed direction sensitivity, preferring either left-to-right or right-to-left grasping actions. Similarly, many MNs (53%) respond selectively to the observation of actions executed within ("peripersonal" MNs) or beyond ("extrapersonal" MNs), not the actor's, but the observing monkey's reach (Caggiano et al. 2009). The majority (74%) of MNs also exhibit view-dependent responses; some MNs are tuned to egocentric (first-person) presentation, while others respond maximally to allocentric (third-person) perspectives (Caggiano et al. 2011). Each of these classes of

MN is sensitive to features of action that fall well below the "greatest degree of generality" of intentions such as "grasping in order to eat" or "taking possession of an object."

The field properties of logically related MNs are perhaps the hardest to reconcile with the idea that MNs were designed by genetic evolution to mediate action understanding by activating in the observer the same "goal" that is guiding the actor's behavior. Logically related MNs fire when a monkey observes an action with one goal (e.g., placing food items on a table, with the intention of giving food to the monkey) and when the monkey executes an action with a different goal (e.g., grasping the food with a precision-grip and bringing it to the mouth, with the intention of eating). Thus, these MNs respond to different object-directed actions, with different intentions, in observe and execute conditions.

5. The right kind of learning

The previous section argued that many MNs have field properties incompatible with the hypothesis that they were designed by genetic evolution to mediate action understanding via goal coding. In complementary fashion, this section argues that research on the roles of contingency and contextual modulation in associative learning enables the associative hypothesis to provide a unified account of all the MN field properties reported to date.

5.1. *Predictive relationships*

It has long been recognized that associative learning depends, not only on contiguity – events occurring close together in time – but also on contingency – the degree to which one event reliably predicts the other. Where the predictive relationship between two events is weak – that is, where one event is equally likely to occur in the presence and absence of the other event – contiguous pairings produce little or no learning (Elsner & Hommel 2004; Rescorla 1968; Schultz & Dickinson 2000). The associative account therefore predicts that MNs will acquire sensorimotor matching properties only when an individual experiences contingencies between sensory events and performed actions (Cooper et al. 2013b). This feature of associative learning ensures that the matching properties of MNs reflect, not just chance co-occurrences, but sensorimotor relationships that occur reliably in the individual's environment. Evidence that the human mirror mechanism is modified by contingent but not by non-contingent sensorimotor experience has been reported by Cook et al. (2010).

Contingency sensitivity explains the mix of strictly congruent MNs, sensitive to the low-level features of observed actions (type of grip, effector used, direction of movement, viewpoint, proximity to the observer), and broadly congruent MNs, responsive to multiple related actions irrespective of the manner of their execution. Both visual and motor systems are known to be organized hierarchically (Felleman & Van Essen 1991; Giese & Poggio 2003; Jeannerod 1994; Perrett et al. 1989), comprising different populations encoding relatively low-level representations (e.g., descriptions of particular "precision" or "power" grips) and more abstract representations (e.g., descriptions of "grasping"). Therefore, contingencies can be experienced between both low- and high-level sensory and motor representations. When a monkey observes itself performing a precision grip, the excitation of sensory and motor populations encoding a specific grip are correlated. However, during group feeding, a monkey might observe and perform a range of grasping actions, thereby causing correlated excitation of higher-level visual and motoric descriptions of grasping. Contingency sensitivity therefore explains the existence of both strictly congruent MNs, tuned to a particular sensory representation (e.g., a right-to-left precision grip executed with the right hand viewed egocentrically), and broadly congruent MNs, responsive to the observation of a number of related actions.

Contingency sensitivity also explains the existence of logically related, audiovisual, and tool-use MNs. According to the associative hypothesis, MNs acquire sensorimotor properties whenever individuals experience a contingency between "seeing" and "doing." There is no requirement that contingencies are between action performance and the observation of the same action, or indeed of natural action-related stimuli, such as the sight of animate motion or sounds that could have been heard by ancestors of contemporary monkeys. Both monkeys and humans frequently experience non-matching sensorimotor contingencies, where the observation of one action predicts the execution of another; for example, you release and I grasp (Newman-Norlund et al. 2007; Tiedens & Fragale 2003). The associative account therefore explains in a very straightforward way why logically related MNs respond to different actions in observe and execute conditions. Equally, the associative account explains in a simple way why "tool-use" MNs (Ferrari et al. 2005) develop when action performance is reliably predicted by the sight of actions performed with tools (e.g., food items being gripped with pliers), and why "audiovisual" MNs (Keysers et al. 2003; Kohler et al. 2002) develop when action performance predicts characteristic action sounds (e.g., paper tearing or plastic crumpling; Cook 2012).

5.2. *Contextual modulation*

Studies of conditioning indicate that learned responses are often subject to contextual control; if a stimulus is associated with two responses, each in a different context, then the context determines which response is cued by the stimulus (Bouton 1993; 1994; Peck & Bouton 1990). For example, Peck and Bouton (1990) initially placed rats in a conditioning chamber with a distinctive scent (e.g., coconut) where they learned to expect electric shock following a tone. The rats were then transferred to a second chamber with a different scent (e.g., aniseed) where the same tone predicted the delivery of food. The rats quickly learned the new contingency and conditioned foraging responses replaced conditioned freezing. However, learning in the second phase was context dependent. When the rats were returned to the first chamber, or transferred to a third chamber with a novel scent, the tone once again elicited freezing. By drawing on the components of associative learning theory that explain this kind of effect, the associative account of MNs can explain contextual modulation of MN firing (Cook et al. 2012a).

Many, possibly all, of the findings cited as evidence that monkey MNs code action goals can also be interpreted within an associative framework as evidence that MNs are subject to contextual control. For example, some MNs show stronger visual responses to object-directed grasping than to pantomimed grasping in object-absent contexts (Gallese et al. 1996), and in some cases, the modulating influence of the object-context can be seen even when the target object is occluded prior to contact with the hand (Umiltà et al. 2001). Similarly, MN responses during the observation of grasping may be modulated by the type of object being grasped (Caggiano et al. 2012), with some MNs responding more strongly in the presence of high-value (food, or non-food objects predictive of reward), and some in the presence of low-value (non-food objects not associated with reward) stimuli. In the clearest example, the same motor act, grasping with a precision grip, elicits different MN responses dependent on whether the action is observed in the presence ("grasp to place") or absence ("grasp to eat") of a plastic cup (Bonini et al. 2010; Fogassi et al. 2005). Rather than the plastic cup providing a cue to the actor's intention, it may act as a contextual cue modulating the operation of two associations. In the same way that the sound of the tone elicited different behaviors when presented in the coconut and aniseed contexts (Peck & Bouton 1990), observing a precision grip may excite different MNs in the cup-present and cup-absent contexts.

Thus, many of the field properties cited as evidence of goal (intention) coding by MNs can also be explained by contextual modulation within an associative framework. Under the "goal" interpretation, these field properties constitute direct evidence that MNs mediate action understanding. Under the associative interpretation, they are very interesting but not decisive. The flexibility apparent in the field properties of MNs gives them the potential to make a useful contribution to social behavior. However, further research, examining the behavior of whole organisms, not only of neurons, is needed to find out how this potential is realized (see sect. 9).

6. Wealth and poverty of the stimulus

Research involving infants (sect. 6.1) and adults (sect. 6.2) has been used to support a poverty argument suggesting that MNs emerge too early in development or, more generally, after too little sensorimotor experience, to have been forged by associative learning.

6.1. Mirroring in infancy

It has been argued that: (1) imitation is mediated by MNs (or a mirror mechanism); (2) both human and monkey infants are able to imitate observed actions when they have had minimal opportunity for visuomotor learning; and (3) therefore, the associative account of the origin of MNs must be wrong (Gallese et al. 2011). The structure of this argument is valid, but the evidence supporting the second assumption (e.g., Heimann et al. 1989; Meltzoff & Moore 1977; Nagy et al. 2005) has been challenged in two respects. Building on previous analyses (e.g., Anisfeld 1996), a recent review found evidence that human neonates copy only one action – tongue-protrusion – and that this copying does not show the specificity characteristic of imitation or of MNs (Ray & Heyes 2011). Figure 2 illustrates the first of these points. For each of the action types tested in young infants, it shows the number of published studies reporting positive evidence of imitation and the number reporting negative evidence. This is a highly conservative measure of how often young infants have failed imitation tests, because it is much harder to publish negative than positive results (Fanelli 2012). Nonetheless, Figure 2 shows that the number of positive reports substantially exceeds the number of negative reports only for tongue-protrusion. Evidence that even the tongue-protrusion effect lacks the specificity characteristic of imitation and MNs – that it is an exploratory response, rather than an effect in which action observation is met with performance only of a similar action – comes from research showing that tongue-protrusion can be elicited by a range of arousing stimuli, including flashing lights and lively music (Jones 1996; 2006), and that it is greater when infants observe a mechanical "tongue" or disembodied mouth (Soussignan et al. 2011).[2] More broadly, evidence that the development of imitation is crucially dependent on learning is provided by a study of 2-year-old twins showing that individual differences in imitation were a result predominantly of environmental rather than genetic factors (McEwen et al. 2007), and by a recent study of infants indicating that individual differences in associative learning ability at 1-month predicted imitative performance eight months later (Reeb-Sutherland et al. 2012).

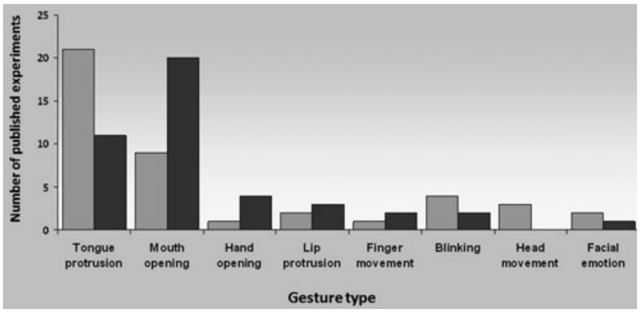

Figure 2. Summary of experiments seeking evidence of gesture imitation in human infants (adapted from Ray & Heyes 2011). "Gesture type" refers to the target or modelled movement. Positive frequencies (lighter bars) indicate the number of published experiments reporting positive cross-target comparisons (i.e., infants performed the target action more often after observing the target action than after observing an alternative action). Negative frequencies (darker bars) indicate the number of experiments reporting failure to find a significant difference in cross-target comparison.

Turning from human to monkey infants, Ferrari et al. (2006) reported immediate imitation of tongue-protrusion and lip-smacking in 3-days-old monkeys. However, the effects were not present on days 1, 7, and 14 postpartum, and it is not clear whether they were replicated in a subsequent study using a similar procedure (Paukner et al. 2011). The later study did report imitation of lip-smacking in monkeys less than one week old, but this effect seems to have been due to a low frequency of lip-smacking in the control condition, when infants were observing a static neutral face, rather than to an elevated frequency of lip-smacking when the infants were observing lip-smacking. Therefore, in common with the data from human infants, studies of imitation in newborn monkeys do not currently support a poverty argument.

A similar poverty argument suggests that the associative account must be wrong because (1) suppression of alpha band (~6–13 Hz) oscillations over central scalp locations during action observation (and execution) reflects the operation of MNs or a mirror mechanism, and (2) electroencephalographic (EEG) studies indicate that both human and monkey infants show alpha suppression when they have had minimal opportunity for sensorimotor learning (Gallese et al. 2011; Nyström et al. 2011). In this case, both of the assumptions are questionable. First, the functional significance of alpha band oscillatory activity is poorly understood even in human adults, and is yet more difficult to interpret in human and monkey infants where, for example, less information is available about the source (Marshall & Meltzoff 2011). Second, human adult studies have traced the likely source of central alpha suppression during action execution to the somatosensory cortex (Hari & Salmelin 1997), suggesting that it may not index motor processing at all.[3] Third, even if alpha suppression does index motor processing, it does not show that the motor activation matches or mirrors the actions observed (Marshall & Meltzoff 2011; Pfurtscheller et al. 2000). For example, alpha suppression during observation of lip-smacking, which has been reported in neonatal monkeys (Ferrari et al. 2012), may reflect a generalized readiness to act, or arousal-related motor activation of tongue-protrusion, rather than motor activation of lip-smacking, and thereby the occurrence of MN or mirror mechanism activity. Furthermore, studies of human infants, which provide superior source information, have not shown that central alpha suppression occurs when infants have had insufficient correlated sensorimotor experience to build a mirror mechanism through associative learning. Indeed, studies of human infants suggest an age-related trend consistent with the associative hypothesis (see Marshall et al. [2011] for a review).

Sound evidence of MN activity in newborns – which, we suggest, has not been provided by research to date on imitation and alpha suppression – would be inconsistent with the associative model. However, it is important to note that the associative account is predicated on a "wealth of the stimulus" argument and therefore anticipates MN activity in young infants (Ray & Heyes 2011). This wealth argument points out that human developmental environments typically contain multiple sources of the kind of correlated sensorimotor experience necessary to build MNs; each of these sources is rich; and the mechanisms of associative learning can make swift and efficient use of these sources. The range of sources available to young human infants includes self-observation, being imitated by adults, being rewarded by adults for imitation, and the kind of experience in which, for example, lip movements make the same smacking or popping sound when observed and executed. Evidence of the richness of these sources comes from studies showing that infants spend a high proportion of their waking hours observing their own hands in motion (P. Rochat 1998; White et al. 1964); in face-to-face interaction with a caregiver, they are imitated on average once every minute (Jones 2009; Pawlby 1977; Uzgiris et al. 1989); and "noisy actions," which provide an early source of acquired equivalence experience, are among the first that infants imitate (Jones 2009). A common misconception about associative learning is that it always occurs slowly. Directly relevant evidence that this is not the case comes from studies showing that, when the contingency is high, infants can learn action-effect associations in just a few trials (Paulus et al. 2012; Verschoor et al. 2010).

6.2. *Motor training in adulthood*

It has been claimed that the associative account "cannot explain why motor experience obtained without visual feedback can affect perception of human biological motion related to that experience" (Gallese et al. 2011, p. 383). This claim assumes that the perception of human biological motion is mediated by MNs or a mirror mechanism, and appeals to a subtle poverty argument; it suggests that the fundamental properties of MNs – the way in which they map observed with executed actions – can be changed by motor experience alone, that is, in the absence of correlated sensorimotor experience.

Two types of evidence, from studies that were not designed to investigate MNs, have been cited in support of this subtle poverty argument (Gallese et al. 2011). First, when observing point-light displays of whole body movements such as walking, from a third party perspective, people are better able to recognize themselves than to recognize their friends (Beardsworth & Buckner 1981; Loula et al. 2005). Second, practice in executing actions can improve visual discrimination of those actions, even when actors are prevented from observing their movements during execution (Casile & Giese 2006; Hecht et al. 2001). These motor training effects, and the self-recognition advantage, are interesting and important phenomena in their own right. If they were mediated by a mirror mechanism – that is, a mechanism in which there is a direct, unmediated connection between visual and motor representations of action – they would also support a poverty argument. However, a recent study provides evidence that these effects depend on an indirect mechanism representing temporal cues. It shows, using avatar facial motion stimuli, that the self-recognition advantage is maintained despite gross distortion of the kind of spatial cues that characterize biological motion, but is abolished by even relatively minor disturbance of domain-general temporal cues (Cook et al. 2012b). In the absence of appropriate visual experience, actors appear to be able to use their considerable knowledge of the rhythmic characteristics of their own actions to recognize and better represent allocentric movement displays. Thus, motor training effects and the self-recognition advantage are of independent interest, but they do not support a poverty argument because current evidence suggests that they do not depend on a mirror mechanism.

7. Sensorimotor learning changes mirror neurons

7.1. *Testing the predictions of the associative account*

The associative account has been explicitly tested in experiments examining the effects of laboratory-based sensorimotor training on mirror mechanisms in human adults. Building on the results of more naturalistic studies (Calvo-Merino et al. 2005; 2006; Cross et al. 2006; Ferrari et al. 2005; Haslinger et al. 2005; Jackson et al. 2006; Keysers et al. 2003; Kohler et al. 2002; Margulis et al. 2009; Vogt et al. 2007), these experiments have isolated the effects of sensorimotor experience from those of purely visual and purely motor experience. Using all of the measures of mirror mechanism activity commonly applied to humans (sect. 2.3), they have shown that relatively brief periods of sensorimotor experience can enhance (Press et al. 2007; Wiggett et al. 2012), abolish (Cook et al. 2010; 2012a; Gillmeister et al. 2008; Heyes et al. 2005; Wiggett et al. 2011), reverse (Catmur et al. 2007; 2008; 2011), and induce (Landmann et al. 2011; Petroni et al. 2010; Press et al. 2012a) mirror mechanism activity. Each of these findings confirms a novel prediction of the associative account: it reveals flexibility of exactly the kind one would expect if MNs/mechanisms are forged by sensorimotor associative learning. In contrast, this kind of flexibility does not provide any support for the genetic hypothesis. Indeed, if MNs were a genetic adaptation, some evolutionary frameworks would predict that the development of MNs would be protected or "buffered" against environmental perturbations that could interfere with their adaptive function (Cosmides & Tooby 1994; Pinker 1997). In the case of a genetic adaptation for action understanding, this would include perturbations with the potential to divert MNs from coding properties of action, rather than of inanimate stimuli, and from coding similar, rather than dissimilar, observed and executed actions.

Evidence that MNs/mechanisms are not resistant to coding inanimate stimuli comes from studies showing that arbitrary sound, color, and shape stimuli can induce mirror MEP (D'Ausilio et al. 2006; Petroni et al. 2010), fMRI (Cross et al. 2009; Landmann et al. 2011; Press et al. 2012a) and behavioral effects (Press et al. 2007) following sensorimotor training (Press 2011). For example, Press and colleagues gave participants approximately 50 minutes of sensorimotor training in which they repeatedly opened their hand when seeing a robotic pincer open, and closed their hand when seeing the robotic pincer close (Press et al. 2007). Prior to this training, the pincer movement elicited less automatic imitation (see sect. 2.3) than human hand movement, but 24 hours after training, the automatic imitation effect was as strong for the pincer movement as for the human hand.

Evidence that MNs/mechanisms are not resistant to coding dissimilar actions comes from studies showing that non-matching (or "counter-mirror") sensorimotor training abolishes automatic imitation (Cook et al. 2010; 2012a; Gillmeister et al. 2008; Heyes et al. 2005; Wiggett et al. 2011), and reverses both fMRI (Catmur et al. 2008) and MEP mirror responses (Catmur et al. 2007). For example, Catmur and colleagues gave participants approximately 90 minutes of non-matching sensorimotor training in which they repeatedly made an index finger movement while observing a little finger movement, and vice versa (Catmur et al. 2007). Before this training the participants showed mirror MEP responses, for example, observation of index finger movement elicited more activity in an index finger muscle than observation of little finger movement, and vice versa for the little finger muscle. After training, this pattern was reversed, for example, observation of index finger movement elicited more activity in the little finger muscle than observation of little finger movement.

7.2. *Objections to sensorimotor training evidence*

Objections to this evidence suggest, in various ways, that it does not show that sensorimotor experience can change MNs/mechanisms. For example, it has been suggested that the evidence comes only from studies of object-free actions and yet MNs code only object-directed actions (Rizzolatti & Sinigaglia 2010). However, a study of pianists has shown that experience modulates mirror responses to object-directed actions (Haslinger et al. 2005) and, as discussed in sect. 4.1, monkey studies of communicative gestures (Ferrari et al. 2003) and pantomimed reaching movements (Kraskov et al. 2009) have identified MNs that code object-free actions.

A related concern is that, because they use indirect measures (fMRI, MEPs, and automatic imitation), rather than single-cell recording, sensorimotor learning experiments may not be measuring MN responses. Section 2.3 reviewed the evidence for human MNs from a range of experimental techniques. These include conjunction of neural responses during action observation and performance (Gazzola & Keysers 2009; Iacoboni et al. 1999; Vogt et al. 2007), suppression of neural responses to cross-modally (perceptual-motor or motor-perceptual) repeated actions (Kilner et al. 2009; Press et al. 2012b), muscle-specific MEPs (Catmur et al. 2011; Fadiga et al. 1995), and automatic imitation (Brass et al. 2001; Stürmer et al. 2000). In isolation, each of these measures is imperfect (Caggiano et al. 2013), but together they provide strong converging evidence for human MNs. Sensorimotor learning effects have been demonstrated for all these measures of mirror responses: fMRI conjunction (Catmur et al. 2008; Landmann et al. 2011); repetition suppression (Press et al. 2012a); MEPs (Catmur et al. 2007; 2011; D'Ausilio et al. 2006; Petroni et al. 2010); and automatic imitation (Cook et al. 2010; 2012a; Gillmeister et al. 2008; Heyes et al. 2005; Press et al. 2007; Wiggett et al. 2011). Thus, converging evidence using multiple techniques strongly suggests that sensorimotor learning experiments are measuring – and changing – MN responses. Furthermore, although experiments specifically testing sensorimotor learning (in which sensory, motor, and sensorimotor experience are compared and/or controlled) have not been performed using single-unit recording, this conclusion is supported by single-unit data showing that experience with tools creates MN responses to observed tool use (Ferrari et al. 2005; M. J. Rochat et al. 2010; see sect. 4).

Considerations regarding anatomical specificity raise another possible objection to the sensorimotor training evidence: Sensorimotor experience may only affect neurons in non-classical mirror areas (e.g., dorsal PMC). However, while recordings of monkey MNs have mostly been confined to ventral PMC and IPL, measurements in humans using single-unit recording and fMRI conjunction suggest that MNs are more widespread (e.g., Arnstein et al. 2011; Gazzola & Keysers 2009; Landmann et al. 2011; Mukamel et al. 2010; Vogt et al. 2007). Furthermore, paired-pulse TMS indicates that functional connections from dorsal (as well as ventral) PMC to primary motor cortex enhance muscle-specific MEP responses to action observation (Catmur et al. 2011). Thus, several sources of evidence suggest that MNs are not restricted to classical mirror areas. Therefore, even if sensorimotor experience were altering neuronal responses only outside ventral PMC and inferior parietal cortex, it could still be affecting MNs. However, there is also evidence that sensorimotor learning affects classical mirror areas. Many studies have demonstrated effects of sensorimotor experience on classical mirror areas (Cross et al. 2009; Haslinger et al. 2005; Landmann et al. 2011; Margulis et al. 2009; Vogt et al. 2007); counter-mirror sensorimotor learning reverses ventral PMC and inferior parietal cortex responses to observed actions (Catmur et al. 2008); and such learning is supported by ventral PMC-M1 connections (Catmur et al. 2011). Furthermore, localizing the effects of sensorimotor learning to specific neural populations using repetition suppression suggested that sensorimotor experience affects MNs in classical mirror areas (Press et al. 2012a). Therefore, it appears that MNs are not restricted to classical mirror areas and that sensorimotor experience has effects both on classical mirror areas and elsewhere.

A final possibility is that counter-mirror training changes relatively late neural responses to action observation, leaving earlier responses, mediated by MNs, intact (Barchiesi & Cattaneo 2013). Such a finding might indicate that counter-mirror responses result from a more indirect route (e.g., via prefrontal areas for rule retrieval) than mirror responses. Barchiesi and Cattaneo (2013) tested this hypothesis using a task that is likely to have provoked coding of domain-general spatial cues, rather than action-specific topographic cues, and therefore to have failed to index mirror responses at any time-point. A more recent study, using a more specific test of mirror responses, found effects of counter-mirror training on MEPs from 200 msec, the earliest time-point at which mirror responses have been observed in monkeys and humans (Cavallo et al. 2013; see also Catmur et al. 2011).[4] Thus, effects of counter-mirror training occur at the time when complex information about the observed action has just reached PMC, making it improbable that mirror and counter-mirror effects occur at different times. It is likely that a prefrontal route is involved *during* the training session, when participants retrieve a rule in order to implement task instructions (e.g., "if index, do little"). However, the finding that *after* counter-mirror training, effects of training are present in MEPs from 200 msec suggests that such rule-based responding merely initiates associative learning: after learning, action observation activates counter-mirror responses as quickly as the original mirror responses.

In summary: Although there are currently no studies systematically testing the effects of sensorimotor learning on MN responses in monkeys, a substantial body of evidence from studies of training and expertise in humans has confirmed the predictions of the associative account, showing that mirror responses can be changed in radical ways by sensorimotor learning. Furthermore, these studies have provided no evidence that MNs/mechanisms are buffered or protected against sensorimotor experience of a kind that makes them code inanimate stimuli and dissimilar actions.

8. Other models: Canalization and exaptation

This article focuses on the genetic and associative accounts of the origins of MNs because these were the first models to be proposed, and the associative hypothesis is the most fully developed alternative to the standard, genetic view. For example, unlike other alternatives, it has been used to generate and test novel empirical predictions. However, two other alternatives, which have been motivated in part by the data generated in these tests (see sect. 7) should be considered. One raises the possibility that the development of MNs is "canalized," and the other that it represents an "exaptation" for action understanding. These are interesting possibilities but, we argue, they are not supported by the evidence reviewed in sections 4–7.

8.1. Canalization

It has been suggested that MNs are acquired through "Hebbian learning" (Keysers & Perrett 2004) and that their development is supported or "canalized" by genetically predisposed features of the perceptual-motor system, including the tendency of infants to look at their own hands in motion (Del Giudice et al. 2009). On one reading, this canalization hypothesis is identical in substance to the associative hypothesis; it is helpful in providing a more detailed neuronal model of how sensorimotor experience makes MNs out of motor neurons, and, in contrast with the associative hypothesis, it emphasizes self-observation over social interaction as a source of relevant sensorimotor experience in development, but otherwise the canalization hypothesis is identical to the associative account. On this reading, the term "Hebbian learning" is understood to be a synonym for "associative learning," and the canalization hypothesis suggests that if the infants' tendency to look at their own hands in motion is an adaptation (Clifton et al. 1994; Meer et al. 1996) – if this attentional bias evolved "for" anything – it was to promote the development of precise visuomotor control, rather than MNs and action understanding.

On another reading, which we think is less likely to represent the authors' intentions, "Hebbian learning" differs from "associative learning" in depending on contiguity alone, rather than both contiguity and contingency (see sect. 3.2), and the infant preference for manual self-observation evolved specifically to promote the development of MNs and action understanding. If this reading is correct, the canalization hypothesis is a hybrid of the associative and genetic accounts; it claims that MNs develop through (Hebbian) sensorimotor learning *and* constitute a genetic adaptation for action understanding. However, this hybrid model would not be supported by current evidence for three reasons. First, there is no evidence that the tendency of infants to look at their own hands evolved to promote the development of MNs or action understanding rather than visuomotor control (Del Giudice et al. 2009). Second, experimental data and modeling work have indicated that the sensorimotor learning which changes MNs depends on contingency as well as on contiguity (Cook et al. 2010; Cooper et al. 2013b). Third, if MNs are forged by contingency-based sensorimotor learning, there is no problem for evolution (or scientists) to solve through canalization for MN development. If it was based on contiguity alone, there is a risk that sensorimotor learning would produce lots of "junk associations" – visuomotor neurons mapping observed and executed actions that happen to have co-occurred by chance. However, contingency-based (i.e., associative) learning could produce the observed distribution of strictly congruent, broadly congruent, and non-matching MNs all by itself, without MN-specific canalization (see sect. 5.1).

8.2. Exaptation

Another interesting hybrid of the genetic and associative hypotheses has been developed by Arbib and colleagues (e.g., Arbib 2005; Oztop et al. 2006). They propose that MNs are produced, not by domain-general mechanisms of Hebbian or associative sensorimotor learning, but by a special kind of sensorimotor learning which receives input from self-observation of hand motion. This special kind of learning is an "exaptation" for action understanding: It evolved from more domain-general mechanisms, such as those producing canonical neurons, specifically to promote action understanding through the production of MNs. This exaptation hypothesis does not specify, in psychological or neurological terms, exactly what is distinctive about the kind of sensorimotor learning that produces MNs. However, it suggests that "some extra structure is required, both to constrain the variables relevant for the system, and to track trajectories of those relevant variables," and that the function of this extra structure is to ensure coding of goals or "hand-object relationships" (Oztop et al. 2006, p. 269). Bonini and Ferrari (2011) recently advanced a similar exaptation hypothesis, also motivated by the need to explain why MNs consistently encode goals. However, as we have argued in section 4, the evidence from single-unit recording in monkeys suggests that MNs do not consistently encode goals. Therefore, the primary motivation for invoking exaptation is not compelling. Furthermore, there is no evidence that the sensorimotor learning involved in MN development is modified or constrained relative to the associative learning that occurs in standard conditioning experiments. On the contrary, there is experimental evidence that it is sensitive to contingency, subject to contextual modulation, and open to the encoding of both animate and inanimate stimuli in exactly the same way as standard associative learning (see sects. 5 and 7).

A recent article (Casile et al. 2011) adds another element to the hybrid model advanced by Arbib and colleagues. It suggests that a special, exapted form of sensorimotor learning underwrites the development of hand-related MNs, but the development of facial MNs is minimally dependent on experience. This suggestion is designed to accommodate evidence from studies of imitation and EEG suppression in newborns, which some authors have interpreted as showing that facial MNs are present at or shortly after birth. As we reported in section 6, this evidence has been challenged on a number of counts. Independent motivation and support for the idea that hand and face MNs have different origins would be provided by evidence that face MNs are less susceptible than hand MNs to modification by sensorimotor experience. However, as far as we are aware, this novel prediction of the hand/face hybrid model has not been tested, and a recent study of improvement in facial imitation suggests that face MNs are as susceptible to modification by sensorimotor experience as hand MNs (Cook et al. 2013). Thus, until it is used to generate and test novel predictions, the hand/face hybrid model stands as an intriguing but essentially ad hoc hypothesis.

Hybrid modelling is a promising direction for future research. However, to preserve predictive power, it is essential to check not only that hybrid models are consistent with existing data, but also that they have independent support. We have argued that both of these conditions are met by the associative account, and that neither is currently fulfilled by canalization and exaptation models.

9. A new approach to the function of mirror neurons

We have argued that, at present, there is no positive evidence that MNs are a genetic adaptation or exaptation, or that their development has been canalized, for action understanding. However, the associative hypothesis is functionally permissive; it does not deny that MNs make a positive – possibly even an adaptive – contribution to social cognition. Rather, the associative hypothesis implies that a new approach is required to find out what MNs contribute to social behavior.

9.1. From reflection to theory-based experimentation

In the 20 years since MNs were discovered, theories relating to their function have been inspired by a method which (if you like a pun) could be called "reflection." This method focuses on the field properties of the MNs found in a sample of laboratory monkeys with unreported developmental histories. It asks, usually without reference to preexisting computational or psychological theory, what neurons with these field properties would be "good for"; that is, what they might enable the animal to do. For example, early reports that MNs discharged when monkeys saw and produced object-directed actions inspired the theory that MNs mediate "action understanding" via "motor resonance," when neither of these was an established category of psychological functioning. Even now, opposition to the idea that MNs mediate action understanding tends to be answered by stressing their field properties (Gallese et al. 2011). The associative account suggests that the reflection method needs to be changed and extended in three principal ways.

9.1.1. Developmental history. If MNs were a genetic adaptation, it is likely that their properties would be relatively invariant across developmental environments. Therefore, it would be possible to make valid inferences about species-typical properties of MNs based on a relatively small and developmentally atypical sample of individuals. If MNs are instead a product of associative learning, this kind of inference is not valid. Whether or not an individual has MNs, which actions are encoded by their MNs, and at what level of abstraction, will all depend on the types of sensorimotor experience received by the individual in the course of their development. Therefore, the associative account implies that it is crucial for studies of laboratory monkeys to report, and ideally to control, the animals' developmental history; that is, the kinds of sensorimotor experience to which they have been exposed. It also suggests that, if we want to know the species-typical properties of monkey MNs, it will be necessary to test monkeys that have received all and only the types of sensorimotor experience typically available to them under free-living conditions. A corollary of this is that we cannot assume that the mirror mechanisms found in the members of one human culture are representative of the whole human species. With its emphasis on the role of social practices – such as the imitation of infants by adults, sports and dance training, and mirror self-observation – in driving the development of MNs, the associative account provides specific, theory-driven motivation for cross-cultural studies of mirroring.

9.1.2. System-level theory. If MNs were a genetic adaptation, one could argue that new categories of psychological functioning – such as "action understanding" and "motor resonance" – are necessary to characterize what they do. It could be argued that, since they were "specially created" by evolution, MNs are likely to have a highly distinctive, largely independent, and previously unrecognized psychological function. In contrast, by showing that established psychological theory – associative learning theory – can cast light on the origin of MNs, the associative account underlines the value of embedding research on MN function within system-level psychological and computational theories of how the brain produces behavior (Giese & Poggio 2003; Kilner 2011; Kilner et al. 2007a). This implies that hypotheses about MN function should specify a part in a process – a process that goes all the way from peripheral sensory input to overt motor output – that MNs are thought to fulfill. The name assigned to this part is not important in itself. What is important is that the hypothetical function of MNs is distinguished clearly from other components of the same overall process. For example, in this kind of system-level, theory-guided approach, "action understanding" would be distinguished from components that are likely to be more purely perceptual (which might be called "action perception" or "action recognition"), more purely motoric (e.g., "action execution"), or to constitute a higher level of "understanding" (e.g., "mentalizing"). This approach would also make it clear whether the hypothetical function is thought to be optional or obligatory; whether it can be, or must be, done by MNs. The kind of system-level theoretical approach required in research on the functions of MNs is exemplified by studies of their role in speech perception (Lotto et al. 2009; Scott et al. 2009).

A system-level theoretical approach would also overcome a problem that has haunted discussions of the "action understanding" hypothesis since MNs were discovered: Is this hypothesis claiming that MN activity causes or constitutes "action understanding"? The former is an empirically testable hypothesis suggesting that there is a distinctive behavioral competence (the nature of which has not yet been specified, see sect. 3.1), called "action understanding," to which the activity of MNs contributes. The latter implies that the firing of MNs during action observation is, in itself, a form of "action understanding"; it does not need to have further consequences in order to qualify as "action understanding." This claim is not subject to empirical evaluation; it is true, or otherwise, by virtue of the meanings of words.

9.1.3. Experimentation. Empirical (rather than constitutive) claims about the function of MNs need to be tested by experiments looking for, at minimum, covariation between MN activity and behavioral competence, and, ideally, testing for effects on behavioral competence of interventions that change MN activity. A brief survey of recent research of this kind – using fMRI, TMS, and the effects of focal brain lesions in human participants – is provided in the next section. At present, this research faces two major challenges. First, because the hypothetical functions of MNs typically are not defined in the context of a system-level theory, it is difficult to design appropriate control tasks. For example, if an experiment is testing the hypothesis that MNs play a causal role in action understanding, should it control for the possibility that they instead play some role in action perception? If so, what kind of behavioral competence is indicative of action perception rather than action understanding?[5] To date, only a small number of studies (e.g., Pobric & Hamilton 2006) include control conditions designed to address this issue.

The second major challenge is that, with rare exceptions (Mukamel et al. 2010), MN activity cannot be localized precisely within the human brain. Consequently, many studies assume that activity in the ventral PMC and IPL – areas homologous to those in which MNs have been found in monkeys – is MN activity, and that behavioral changes brought about through interference with the functioning of these areas are due to interference with MNs. The results of such studies are of interest regardless of whether they relate to MNs. However, it is unsatisfactory to assume that they relate to MNs, because, in monkeys, it is likely that fewer than 20% of the neurons in these classical mirror areas are actually MNs, and because there is evidence of MNs in non-classical areas in both monkeys and humans (see sect. 2.1). Techniques such as fMRI repetition suppression and TMS adaptation (Cattaneo et al. 2011; Silvanto et al. 2007) hold some promise as means of overcoming the localization problem with human participants, by isolating behavioral effects to specific populations of neurons. Guided by system-level theory, future studies could use these techniques with a range of tasks to isolate processes in which MNs are involved.

Alongside the development of techniques such as fMRI repetition suppression and TMS adaptation for use with human participants, it would be valuable to conduct animal studies that, not only document the field properties of MNs, but also examine how those properties relate to behavioral competence. For example, are animals with MNs for actions X and Y better than other animals of the same species at behavioral discrimination of X and Y, or at imitating X and Y? Studies of this kind have been dismissed as impractical on the assumption that they would have to involve monkeys, which are demanding and expensive laboratory animals, and that between-group variation in MN activity would have to be induced via lesions or disruptive TMS. However, the associative account suggests that, in the long term, it may be possible to overcome these problems by establishing a rodent model and using sensorimotor training to induce between-group variation in the number and type of MNs present in rodent brains. If the associative account is correct, rodents are likely to have the potential to develop MNs because they are capable of associative learning. Whether or not they receive in the course of typical development the sensorimotor experience necessary to realize this potential, it could be provided by various regimes of laboratory-based sensorimotor training.

9.2. *Early signs*

Given the theoretical limitations and methodological challenges faced by research to date on the functions of MNs, it is very difficult indeed to form a consistent and potentially reliable picture of where their findings are pointing. Nonetheless, for completeness, we offer the following brief overview of research relating to the two most commonly investigated hypotheses – MN activity contributes to action understanding and to imitation. We first summarize the results of meta-analyses of functional imaging data, which, by identifying commonalities across multiple studies, highlight candidate brain areas involved in these hypothesized MN functions. Building on the fMRI studies, patient data and studies using disruptive TMS applied to classical mirror areas have the potential to identify causal, rather than purely correlational, relationships between MN activity and behavioral competence.

9.2.1. Action understanding. As discussed in section 3.1, consensus regarding the term "action understanding" has yet to be reached. In terms of the involvement of mirror areas in perceiving others' actions, a recent meta-analysis of fMRI data on action observation revealed that observation of hand movements produces responses in both premotor and parietal cortex, while face and body movements recruit premotor and parietal cortex, respectively (Grosbras et al. 2012). If, however, "action understanding" is operationalized in terms of understanding others' intentions, then the role of mirror areas is less clear: A meta-analysis of studies using mentalizing tasks concluded that classical mirror areas are not recruited unless the tasks involve action stimuli (Van Overwalle & Baetens 2009). Even when action stimuli are presented, intention understanding does not necessarily recruit mirror areas (e.g., Brass et al. 2007; de Lange et al. 2008), implying that the recruitment of mirror areas during mentalizing tasks that involve action stimuli is likely to be due to the action observation component of these tasks. Patient data indicate that components of action perception – including action detection, discrimination between observed actions, action recognition (e.g., naming observed actions), and object-action matching – may require classical MN areas (Buxbaum et al. 2005; Fontana et al. 2011; Kalenine et al. 2010; Moro et al. 2008; Pazzaglia et al. 2008; Saygin 2007; Saygin et al. 2004; Serino et al. 2010).

However, not all patients with impairments in action production are also impaired in action recognition, suggesting that motor ability may not always predict this aspect of "action understanding" (Calder et al. 2000; Negri et al. 2007), or at least that these abilities can dissociate, either prior to brain damage or via subsequent compensatory processes. Several TMS studies have demonstrated that PMC stimulation disrupts components of action perception including detection or discrimination of actions (Candidi et al. 2008; Urgesi et al. 2007b; van Kemenade et al. 2012), configural processing of bodies (Urgesi et al. 2007a), judgment of body aesthetics (Calvo-Merino et al. 2010), and motor-to-visual adaptation for observed actions (Cattaneo et al. 2011). It also impairs the ability to use information from perceived actions to judge the weight of grasped objects (Pobric & Hamilton 2006) and to initiate online predictions about ongoing actions (Stadler et al. 2012). It appears therefore that PMC may be necessary for some components of action perception, and this is an important result. However, given the current uncertainty about what is meant by "action understanding," it is not clear whether these results consistently demonstrate a role for mirror areas in "action understanding" as opposed to a more perceptual process (see sects. 3.1 and 9.1).

9.2.2. Imitation. A recent meta-analysis of functional imaging studies found consistent responses during imitation tasks in classical MN areas, suggesting a possible functional involvement of MNs in imitation (Caspers et al. 2010; but see Molenberghs et al. [2009] for inconsistent results in ventral PMC). Research investigating the effects of damage to parietal cortex supports a role for this area in imitation: for example, of mimed tool use (Halsband et al. 2001), of meaningless and object-related gestures (Buxbaum et al. 2005; Goldenberg & Karnath 2006; Tessari et al. 2007), and of phonetic detail in speech (Kappes et al. 2010). Additionally, damage to inferior frontal cortex results in impairments in imitation of finger movements (Goldenberg & Karnath 2006). Patient studies have used intentional imitation tasks that make many demands on the information processing system, in addition to the core imitation requirement to match sensory with motor representations of action (Leighton et al. 2008). Therefore, it is important that TMS studies have demonstrated that stimulation of classical mirror areas can disrupt both intentional and automatic imitation of simple finger and hand actions (Catmur et al. 2009; Heiser et al. 2003; Mengotti et al. 2013; Newman-Norlund et al. 2010).

Thus, the localization problem notwithstanding, insofar as current experimental data provide even early signs, they suggest that MN activity may make some contribution to action perception and imitation. However, the picture for action *understanding* is obscured by the fundamental problem of defining exactly what is meant by "action understanding" and how it differs from action perception. There is thus a pressing need for system-level theory to guide the design of control tasks in studies of action understanding. The picture is somewhat clearer in the case of imitation. The idea that MNs contribute to imitation was originally rejected on the grounds that monkeys do not imitate. However, guided by a leaner and more precise definition of imitation, based on system-level theory, subsequent studies have confirmed, not only that monkeys can imitate (Voelkl & Huber 2000; 2007), but also, as the associative account predicts, that distantly related species, such as budgerigars (Richards et al. 2009) and dogs (Range et al. 2011), are capable of imitation. Consistent with this, there is convergent evidence from meta-analyses, lesion studies, and TMS techniques implicating MN activity in a core component process that translates sensory input from body movement into a matching motor plan.

9.3. *Conclusion*

Like many other people, we find MNs intriguing. In Google Scholar "mirror neuron" scores some 11,000 hits, whereas "visuomotor neuron" scores 50. Some of this excitement may be ill-founded (Heyes 2010), but that is not the point of this target article. The associative account of the origin of MNs acknowledges that they were a fascinating scientific discovery, and this account is open to the possibility that MNs play one or more important roles in the control of social interaction. It differs from the received view in suggesting that (1) sensorimotor learning plays a crucial, inductive role in the development of MNs, and, because of this, (2) we will get reliable information about the function of MNs only by applying an approach based on developmental history, system-level theory, and rigorous experimentation. The first of these methodological implications underlines the fact that, relative to the genetic hypothesis, the associative account shifts the balance of explanatory power from MNs themselves to the environments in which they develop. In some ways this is inconvenient because developmental environments are much harder to study in the laboratory, but there are significant potential payoffs. As a rich source of testable predictions about when, where, and how MNs develop, associative learning theory can provide firm guidance for future research on the taxonomic distribution, typical properties, and functional roles of MNs.

NOTES

1. The present article concerns what might be described as "motor" MNs – that is, MNs that are responsive during the observation and performance of actions. There may be neurons with analogous properties involved in empathetic emotional and somatosensory responses. This interesting possibility is beyond the scope of the present article, but for discussion of how an associative framework may be applied to the origins of empathic mirroring, see Heyes and Bird (2007).

2. Infant research suggesting that tongue-protrusion "imitation" improves over trials, in the absence of visual feedback, has been taken as evidence against the view that this "imitation" effect is really a nonspecific exploratory response (Soussignan et al. 2011). However, a recent experiment showing that even adults cannot improve their imitative performance in the absence of visual feedback suggests that the trends observed in the infant data may not have been signs of improvement (Cook et al. 2013).

3. Central alpha suppression is often seen alongside attenuation of beta band (~15–30 Hz) oscillations, and beta effects are thought to reflect motor processing. The sum of the two effects is defined as "mu suppression" (Hari & Salmelin 1997), but this term is often used more liberally in the MN literature, to refer to effects observed solely in the alpha band.

4. Monkey studies reporting this information suggest that MN responses start around 250 msec after observed movement onset (di Pellegrino et al. 1992; Kraskov et al. 2009; Umiltà et al. 2001). In humans, EEG and MEG data indicate that complex visual stimuli, including actions, reach PMC and motor areas in around 300 msec (Nishitani & Hari 2000; 2002; Proverbio et al. 2009; Sitnikova et al. 2003); while muscle-specific patterns of MEP facilitation are present from 200 msec after observed action onset (Cavallo et al. 2013).

5. The need to control for "action perception" is suggested by Rizzolatti and Sinigaglia's definition of "action understanding" as understanding "'from the inside' as a motor possibility, rather than 'from the outside' as a mere visual description" (Rizzolatti & Sinigaglia 2010, p. 265). However, the potential circularity of defining perception as "merely visual" underlines the need for system-level theory.

Open Peer Commentary

The role of mirror neurons in language acquisition and evolution

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Abstract: I argue that Cook et al.'s attack of the genetic hypothesis of mirror neurons misses its target because the authors miss the point that genetics may specify how neurons may learn, not what they learn. Paying more attention to recent work linking mirror neurons to language acquisition and evolution would strengthen Cook et al.'s arguments against a rigid genetic hypothesis.

In the target article, Cook et al. claim that the genetic account of mirror neurons (MNs) is problematic and they propose an associativist alternative, arguing that "sensorimotor learning plays a crucial, inductive role in the development of MNs" (sect. 9.3). However, several models of sensorimotor learning for MNs have addressed neurophysiological findings (e.g., Bonaiuto & Arbib 2010; Bonaiuto et al. 2007; Keysers & Perrett 2004; Oztop & Arbib 2002; Oztop et al. 2013), so it seems the article is directed only to those who take MNs metaphorically and/or are unfamiliar with the primary literature.

It is true that any account proposing a rigid genetic fixation of MNs is incompatible with available evidence. Yet, Cook et al. fail to provide evidence that proponents of the genetic hypothesis are committed to such problematic accounts and some of their criticism seems to attack implausible "straw men" instead of existing accounts. For example, they claim that the "fact that these MNs respond maximally to unnatural stimuli – stimuli to which the evolutionary ancestors of contemporary monkeys could not possibly have been exposed – is hard to reconcile with the genetic hypothesis" (sect. 4.1, para. 3). The fact that "audiovisual" MNs are responding to "unnatural sounds" such as metal striking metal, plastic crumpling, or paper tearing associated with actions is allegedly problematic for the genetic hypothesis because no such sound/action connections existed for our distant ancestors and evolution could not have "acted on them." The real issue is: "What would genetics specify?" Given that natural selection can only act on present conditions and pass currently beneficial traits on to the offspring, there can be a time lag between what an organism encounters in its environment and what it has been "genetically equipped" to deal with. So if our distant ancestors encountered *any* novel sound-action combination, a rigid mechanism that encodes only correlations as specific as those mentioned by Cook et al. would be of no use. One should reasonably expect then, that it is the ability to acquire MNs adapted to changing circumstances that is genetically specified, not *what* MNs code.

Cook et al. conclude that we can "get reliable information about the function of MNs only by applying an approach based on developmental history, system-level theory, and rigorous experimentation" (sect. 9.3). Given this reasonable conclusion, it is surprising that Cook et al. failed to pay adequate attention to recent work linking MNs to language acquisition and evolution (e.g., Arbib 2005; 2010; 2011; Arbib et al. 2008; Corballis 2010; Corina & Knapp 2008; Gentilucci & Corballis 2006; Ramachandran 2000; for a skeptical view, see Bickerton 2007). Language acquisition seems to offer an excellent opportunity to gather evidence against a rigid genetic hypothesis (e.g., language acquisition accounts defended by: Chomsky 1981; 1995; 2012; Legate & Yang 2002; Lightfoot 1999; McGilvray 2006; Pietroski & Crain 2005; Pinker 1994). According to this framework, all humans possess "some innate mental state common to the species that provides the basis for acquisition of knowledge of grammar" (Chomsky 1981, p. 224). The interesting question is how the intricate details of linguistic knowledge might be genetically encoded. A healthy infant can acquire any human language. Therefore, she needs to be able to imitate both sounds that are the same as, and very different from, those her ancestors have acquired. Further, the English acquired by an infant born in 2013 differs greatly from that of an infant born in the year 848. The differences between those sounds are arguably as great as the difference between the sound of branches breaking (natural) and plastic crumbling (artificial) discussed above. It is indeed implausible that any genetically fixated mechanism could underwrite such highly flexible imitation. Such considerations lead to the abandonment of the proposal that the "innate endowment consists of a 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 (Behme 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. 18). 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→IPL→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.

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. 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 remainder of this commentary, 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. Beginning with the pioneering research of Garcia (e.g., Garcia et al. 1955), 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 eschewed 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 a mechanical pincer designed to match the movement, as well as the effect, produced by the adult.

Similarly, Longo and Bertenthal (2006) tested 9-month-old infants in an observational version of the Piagetian A-not-B search task, and showed that infants still committed 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 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 predetermined 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 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 appropriate 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 objected-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 performed in the current context regardless of reward. This model shows how mirror systems can have evolved for the purposes of monitoring one's own actions and fit within a reinforcement learning framework for action selection.

A mechanistic model of MNs with random or full connectivity and pure associative learning has never been developed. Current computational models suggest that appropriate coarse-grained connectivity and input representations are required to make the space of possible hand–object relation trajectories tractable. While the associative learning account is compatible with these models at a first approximation, it does not offer any detailed explanations as to how networks of MNs acquire their properties in development and operate in the adult. Conceptual models such as the associative learning theory of mirror neuron origins which do not provide a proof of concept in the form of a computational model, are unconvincing.

More than associations: An ideomotor perspective on mirror neurons

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Abstract: In this commentary, we propose an extension of the associative approach of mirror neurons, namely, ideomotor theory. Ideomotor theory assumes that actions are controlled by anticipatory representations of their sensory consequences. As we outline below, this extension is necessary to clarify a number of empirical observations that are difficult to explain from a purely associative perspective.

> *How often the battles of psychology have to be fought over again each time with heavier armies and bigger trains…*
>
> — William James (1890, *Principles of Psychology, Vol. 2*, p. 523, footnote)

Although William James wrote this sentence more than a hundred years ago in his ingenious paragraph on ideomotor action, it could have also have been coined in the discussion about the origin and functional role of mirror neurons (MNs). One important contribution of the associative learning account outlined in the target article by Cook et al. has been to situate the finding of MNs in the historical context of psychological theorizing on the relationship of perception and action. Moreover, associative learning provides a powerful approach to explaining the ontogenesis of MNs based on general learning principles. However, a purely associative account of mirror neurons falls short in explaining a number of important findings regarding the modulation and control of the mirror system. In this comment, we therefore outline an extension of associative learning, namely, ideomotor theory that addresses several of these problems.

While the origins of ideomotor theory can be traced back to the beginning of the nineteenth century, the most prominent proponent of ideomotor theory was William James (1890). In its modern form (Greenwald 1970), ideomotor theory assumes, just like associative learning, that learning promotes the association of sensory and motor codes. However, ideomotor theory states that in the course of learning, additional ideomotor representations are formed that resemble anticipations of the to-be-produced sensory consequences of an action (see our Fig. 1, a–c, for a model of how ideomotor representations are formed).

According to ideomotor theory, these representations primarily serve a motor control function. We control our actions by anticipating their sensory consequences. Moreover, ideomotor theory predicts a specific form of sensorimotor compatibility, namely, *ideomotor compatibility*. A stimulus that resembles the anticipation of a sensory action-effect activates the corresponding ideomotor representation (see Fig. 1d). For example, the image of another person opening their hand strongly overlaps with the representation that is used to control the hand-opening movement. Consequently, ideomotor-compatible stimuli can to some degree bypass response selection by directly activating motor programs (Brass et al. 2001).

Figure 1 (Brass & Muhle-Karbe). Acquisition of an ideomotor representation (adapted from Greenwald 1970). **(a)** A stimulus (S) triggers a specific response (R) that leads to a sensory effect (E). **(b)** After learning, the stimulus will activate an anticipation (e) of the effect that precedes the response. **(c)** This anticipation (e) becomes conditioned to the response and allows for control of the response. **(d)** Priming by action observation: a stimulus that resembles the effect of the action (S_e) primes the ideomotor representation (e) which activates the response.

As ideomotor representations are conceived as neither uniquely sensory nor motor, they should be localized in dedicated motor control structures that are distinct from primary sensory or motor areas. Such representations can be activated without necessarily leading to overt behavior and are thus likely used for motor planning and prediction (see also the commentary by Keysers, Perrett, and Gazzola for the idea of mirror neurons being involved in predictive coding). This property of ideomotor theory is consistent with human brain imaging studies showing an overlap of brain areas involved in action planning, movement observation, and motor imagery (Grezes & Decety 2001).

Another important consequence of ideomotor compatibility is that it can lead to self–other confusion. Because ideomotor-compatible stimuli directly activate representations that are used for motor control, confusion can arise between externally and intentionally triggered motor representations. Accordingly, controlling imitative behavior has been related to brain areas that are involved in the sense of agency and self–other distinction, and dissociated from brain areas involved in controlling interference from overlearned stimulus–response associations (Brass et al. 2003; 2005).

One crucial difference between ideomotor representations and simple stimulus–response associations relates to the underlying learning mechanisms. Ideomotor representations evolve from learning the relationship between responses and subsequent sensory effects (R-E learning). In contrast, classical associative learning theories, although concerned with action-outcome contingencies, primarily focus on learning the relationship of responses to those stimuli that precede them (S-R learning). Importantly, most experiments demonstrating that imitative response tendencies can be easily reversed use S-R learning paradigms rather than R-E learning paradigms (e.g., Catmur et al. 2007). From an ideomotor theory perspective, these findings may reflect that rapid learning strengthens the corresponding S-R associations to such a degree that they temporarily overrule existing ideomotor representations, leading to an advantage of ideomotor-incompatible over compatible mappings (Catmur et al. 2007).

Another difference between associative learning and ideomotor theory lies in their capacity to deal with specific forms of contextual modulation. Cook et al. outline how associative learning can explain the influence of contextual information on MN responses. In human studies, however, it has been demonstrated that the response of the mirror system is not only sensitive to contextual cues but also to high-level beliefs about the intentionality of the observed action (Liepelt et al. 2008b). Ideomotor compatibility can account for such findings, as it is based on the representational overlap between the observed event and the ideomotor representation. Therefore, stimuli that are not perceived as resulting from an intentional action will activate the ideomotor representation to a smaller degree. To our knowledge, a similarly convincing interpretation of such effects from an associative learning perspective is still lacking.

Directly testing for dissociations between associative learning and ideomotor theory proves to be very difficult, as ideomotor theory and associative learning share a common learning phase. In order to demonstrate that ideomotor theory differs from associative learning, one must reveal the anticipatory nature of ideomotor representations. Most tests of ideomotor theory, however, merely show that perceiving learned action effects activate a corresponding motor representation in the observer. This prediction is shared by both approaches. A notable exception to this is a paradigm developed by Kunde (2001). He showed that when actions are consistently followed by incompatible effects (pressing a right key that is followed by a left stimulus), participants react slower than when actions are consistently followed by compatible effects (pressing a right key that is followed by a right stimulus). In contrast to classical S-R compatibility phenomena, this effect unequivocally originates from the conflict between the previously acquired anticipatory representation of the action and the anticipation of the actual sensory consequence.

To conclude, the associative learning account by Cook and colleagues certainly provides a powerful account of the functions and origins of the mirror system. However, we propose that ideomotor theory provides an important extension of associative learning that is necessary to account for a number of phenomena that are difficult to explain from a purely associative perspective.

Reward in the mirror neuron system, social context, and the implications on psychopathology

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Abstract: Positive and negative reinforcers guide our behaviors as we interact with others in our social environment. Here, we present evidence that highlights a central role for reward in the general functioning of the mirror neuron system (MNS). We also discuss the relevance of reward-related modulation on other previous findings revealing certain properties of the MNS, and on social context and psychopathology.

The target article by Cook et al. proposes that the mirror neuron system (MNS) becomes functionally specialized through sensorimotor experience during development, and is founded upon domain-general processes similar to that of Pavlovian and instrumental conditioning. The authors acknowledge that a difference in mirror neuron (MN) responses can be influenced by the subjective value of an observed action; however, they put little emphasis on the possible role of reward in MN activity. This associative learning account particularly lends itself to the suggestion that the perceived subjective value associated with both executed and observed actions may potentially hinder or facilitate the development of the MNS and its general functioning. The differences in the subjective value associated with others' actions, just as the processing of reward is dependent on the context in which the reward is presented (Nieuwenhuis et al. 2005), may also determine the degree to which MN areas are activated, and, consequently, may temper action perception.

The neural correlates of "social rewards" are beginning to be revealed, as studies are confirming the involvement of reward-related areas in certain social scenarios (Behrens et al. 2008; Rushworth et al. 2013). It is known that the neural coding of reward is crucially involved in action selection and is therefore also intrinsic to goal-directed behavior (Schultz 2000). As the activity in the MNS has been shown to be specific only to observed actions that are goal-directed (Rizzolatti et al. 1996), it follows that reward and punishment are likely to have reciprocal effects on the neural activity associated with action observation.

Several studies have shown that the presence or absence of reward can influence the excitability of the motor cortices during both action execution and action observation, which has also been linked to motor learning (Hosp et al. 2011; Wickens et al. 2003). Reward can change the size of motor evoked potentials (MEP) as a result of inhibition of primary motor cortex (Kapogiannis et al. 2008; Thabit et al. 2011), and motor skill learning can be improved if rewarding feedback is given (Sugawara et al. 2012). Spontaneous mimicry of facial expressions can also be enhanced when the emotional face being mimicked has been associated with a high reward (Sims et al. 2012). We have also recently demonstrated that rewarding actions produced the greatest suppression in the EEG mu rhythm, an index of MNS activity in motor areas (Brown et al. 2013). These studies resonate with early work on social leaning by Bandura (1965) and others such as Liebert and Fernandez (1970a; 1970b), in which vicarious reward and punishment influenced the degree to which children tended to imitate the observed actions of adults.

There is much evidence showing that activity in the motor-related areas of the MNS can be affected by the context and "meaning" of the observed action, and here we propose that some of these findings could be accounted for by underlying differences in the subjective value associated with the seen actions. Studies demonstrating modulation of the mu suppression in the observation of painful versus non-painful action-related stimuli (Cheng et al. 2008; Perry et al. 2010) provide one clue to the influence of reward on the MNS, as pain and reward-processing are closely linked (Leknes & Tracey 2008). In terms of differences in social context, actions performed in a social interaction produce greater mu rhythm suppression than actions performed outside of an interaction (Perry et al. 2011). The mu rhythm can also be modulated by the social relevance of the observed action (Kilner et al. 2006; Oberman et al. 2007). Furthermore, the interpersonal liking between individuals can modulate MNS areas, as differences in premotor cortex activation were found when observing in-group versus out-group members' actions (Sobhani et al. 2012). Some have suggested that being in a social interaction, in itself, can be rewarding (Krach et al. 2010). If this is the case, then it would be plausible to argue that differences in motor activity seen in studies comparing social and non-social settings or stimuli may be confounded by differences in reward-processing.

The role of reward in vicarious motor cortex activity may also relate to previous studies investigating MNS function in psychopathologies that exhibit both deficits in social cognition and abnormalities in reward-processing (Gold et al. 2008; Penn et al. 2008). It has been proposed that a dysfunction in the MNS may help to explain deficits in social cognition in schizophrenia and autism spectrum disorders (ASDs) (Arbib & Mundhenk 2005; Williams et al. 2001). Some studies have found abnormal mu rhythm suppression in people with ASDs when observing actions (Bernier et al. 2007; Oberman et al. 2005; 2008), whereas others have not (Fan et al. 2010; Raymaekers et al. 2009). The findings in schizophrenia are also mixed, as one study from McCormick and colleagues (McCormick et al. 2012) found greater mu suppression in psychotic patients, whereas another found lower mu suppression (Singh et al. 2011), with both finding some relationship between mu suppression and psychotic symptoms. We suggest that these inconsistent results may have resulted from a more elementary pathological deficit in reward-processing. As reward has a substantial influence on vicarious motor activity and motor learning, then it is likely that abnormalities in the processing of reward could also have a detrimental impact on the development of the MNS, consequently leading to the apparent impairments in social cognition seen in autism and schizophrenia. This proposal is further supported by emerging evidence suggesting that problems in social functioning seen in ASDs may be founded upon an impaired response to social rewards (Dichter & Adolphs 2012).

To sum up, it does appear that reward has an influence on the motor-related areas of the MNS, which may also partially account for some of the previous findings demonstrating context-related modulation of motor cortex and MNS activity, and may help to explain some of the inconsistencies found in studies investigating MNS function in pathological groups. This proposal is well in line with the associative learning account of the MNS. Future studies looking at MNS activity may benefit from taking the potential interaction effects of reward into account.

Motor-visual neurons and action recognition in social interactions

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Abstract: Cook et al. suggest that motor-visual neurons originate from associative learning. This suggestion has interesting implications for the processing of socially relevant visual information in social interactions. Here, we discuss two aspects of the associative learning account that seem to have particular relevance for visual recognition of social information in social interactions – namely, context-specific and contingency based learning.

The proposal that motor-visual neurons are formed through associative learning is an elegant way to explain a multitude of findings about motor-visual couplings that are otherwise more difficult to reconcile. Cook et al. argue that motor-visual neurons originate from associative learning and suggest the dissociation of function from origin of motor-visual neurons. We would like to stress that this view on motor-visual associations does not dispute the involvement and the importance of motor-visual couplings in social functioning, which has been demonstrated in numerous studies (e.g., Aglioti et al. 2008; Casile & Giese 2006; Kilner et al. 2009). Rather, Cook et al. encourage us to review the function of motor-visual couplings for social functioning in past and future studies. Here, we will argue that the perspective of motor-visual couplings being a result of associative learning is able to explain some findings of social functioning in physical social interactions (e.g., handshake) that are more difficult to explain with a genetic perspective of motor-visual associations. Specifically, we will discuss two aspects of this proposal that we deem particularly important for processing of information relevant for social cognition in physical social interactions.

The associative learning hypothesis accounts for context-specific learning of motor-visual associations. Although Cook et al. mainly discussed context specificity in terms of the emergence of motor-visual linkages, we would like to point to implications of context-sensitive motor-visual associations for processing socially relevant information in social interactions. Specifically, empirical evidence indicates that context-specific processing of socially relevant information is critical for social interactions. For example, Georgiou et al. (2007) showed that the kinematic patterns for the same block stacking actions are modulated by the nature of the social context (cooperative vs. competitive context). Likewise, Streuber and colleagues (2011) demonstrated that sources of visual information about an interaction partner that allow better performance in a table-tennis task depend on the nature of the interactive context (cooperative vs. competitive play). In cooperative play, participants benefited from seeing the other person's racket, while in competitive play, participants showed performance improvements when seeing the other person's body. These and other studies (e.g., Hommel et al. 2009) demonstrate that processing of information relevant for social cognition is influenced by social context. Since there is abundant evidence for the involvement of motor-visual units in processing of socially relevant information (Iacoboni et al. 2005; Kaplan & Iacoboni 2006), motor-visual units should exhibit some sensitivity to social context. Here, the associative learning hypothesis has the potential to provide a convenient and convincing way of explaining context-sensitive processing of socially relevant information by motor-visual units.

In a similar vein, contingency-based learning of motor-visual associations could be beneficial for processing of socially relevant information in physical social interactions. Physical social interactions often consist of socially agreed (and therefore probable) action sequences, which have been learned during development (e.g., the kissing of cheeks in a certain order as a greeting in some countries). Actions are learned, therefore, not as isolated physical events but as part of an action sequence (action context). Recent observations in our lab demonstrate that processing of socially relevant visual information depends on the preceding temporal action context (de la Rosa et al. 2014), which makes one action occurring more probable than another one. In particular, we used an adaptation paradigm to examine the sensitivity of action recognition processes to temporally precursory action contexts. Previous research has shown that adaptation to one of two actions biases the perception of a subsequently presented action towards the non-adapted action (Barraclough & Jellema 2011; Barraclough et al. 2009). We investigated whether adaptation to action images is modulated by the presentation of an action context shown prior to one of the adaptors. We, therefore, created two experimental conditions that consisted of identical adaptors and test stimuli but differed in terms of a movie that was shown prior to one of the adaptors. The movies in the two conditions showed different action sequences and caused participants to differently interpret the action displayed by the adaptor. If action recognition is only based on the immediately available sensory information about the adaptors, then one would not expect any modulation of the action adaptation effect across the two conditions because the two conditions consisted of physically identical adaptor and test images. On the other hand, if action recognition is sensitive to the action context that preceded the adaptors, then the adaptation aftereffects between the two conditions should differ because both conditions were associated with different social contexts that induced a different action interpretation of the adaptor. Indeed, we found action adaptation effects to be different between the two conditions (de la Rosa et al. 2014). A control experiment showed that the presentation of the movie alone was not able to modulate the action adaptation effect between the two conditions. The results, therefore, demonstrate that action recognition does not only depend on the immediate sensory information, but also on the action context preceding an action.

We agree with the suggestion that a dissociation of function and origin of motor-visual associations is important for a better understanding of the involvement of these associations in social functioning. We think that the associative learning account provides a novel view that is able to stimulate research that improves our understanding about the ability of humans to interact, communicate, and socialize with others.

A mass assembly of associative mechanisms: A dynamical systems account of natural social interaction

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Abstract: The target article offers a *negative, eliminativist* thesis, dissolving the specialness of mirroring processes into a solution of associative mechanisms. We support the authors' project enthusiastically. What they are currently missing, we argue, is a *positive, generative* thesis about associative learning mechanisms and how they might give way to the complex, multimodal coordination that naturally arises in social interaction.

A central challenge to social cognition is in understanding how the divide between individual minds becomes bridged during social interaction. It is not surprising then that the mirror neuron system (MNS) engenders the sort of fascination it does, as it provides cortical evidence that the way we relate to others is inextricably linked to the actions of our own bodies. Importantly, as Cook et al.'s associative learning hypothesis posits, these interpersonal connections are highly attuned to changes in our social environment that mitigate (or abolish altogether) appeals to innate processes. Given the domain-general characteristics of associative learning, such a mechanism is thus well situated to account for a wide range of sensorimotor possibilities in a variety of interactional contexts. Yet, in most of the studies reviewed in the target article, movements are confined to relatively simple interactions involving repetitive and overlearned behaviors such as grasping, clasping, lifting, or flexing movements of the hands, fingers, and feet. When more naturalistic interactions are considered, such as those of professional dancers and musicians, coordination of movement is extensively structured around explicit training. These phenomena do provide valuable cases to test the associative hypotheses. But they do not yet resemble the complex, coordinated behavior of social interaction.

When two people interact, complex patterns of behavior emerge quite spontaneously. These patterns are organized across multiple types of movement that simultaneously co-occur with little to no conscious awareness. Nevertheless, they form a stable network of associations that guide how people converge on meaning and respond to higher-level communicative goals. The mechanisms proposed by Cook and colleagues surely hold great promise in better understanding how social cognition is distributed and grounded in interpersonal motor behavior. But these associative mechanisms must figure into the complex array of overt and covert processes that are present when two people interact. At present, there is no good theory of how this interleaving takes place. We have recently termed this problem the "centipede's dilemma" of interaction research (Dale et al. 2013).

One approach that seems to have promise comes from the methodological and theoretical toolbox of dynamical systems theory. Like the target article, this approach sees even human interaction as emergent from domain-general processes acting in concert – viewing human interaction as a self-organizing system. At the core of this approach is a focus on how the components of a system interact over time. Components are drawn in part from processes underlying social cognition, such as visual attention, executive control, motor priming, and many others (see Dale et al. [2013] for a more comprehensive list). These processes span a range of complexity, too, from basic biomechanical constraints of conversants, to higher-level ones such as inferences regarding knowledge and beliefs. Based on these many potential interactions, it is unlikely that any single component alone will explain the collective behavior that emerges. Instead, interaction gains its structure through a process of self-organization in which the various components mutually influence and constrain each other.

There is growing evidence that this interdependence holds across diverse processes during interaction. For example, individual frequencies of oscillatory movements, such as those generated in the way people naturally sway their bodies, spontaneously converge as stable in-phase and anti-phase rhythms (Schmidt et al. 1990), and even hold across more irregular fluctuations of movement (Shockley et al. 2003). Similar forms of coordination, albeit expressed as more subtle, global patterns of recurrence, are also evident in how people gesture, laugh and smile, touch their faces, nod their heads, and even scan a visual scene (Louwerse et al. 2012; D. C. Richardson et al. 2008). Moreover, for each behavior being coordinated, people respond to one other across unique timescales, where the near overlap of postural synchrony stands in contrast to the longer delays between head nods.

The findings just described involve interdependence, between two people, of one behavior, sometimes called "synchrony" or "alignment" (Pickering & Garrod 2004). Yet there is also interconnectivity cutting across *different* behaviors. Each behavior mutually constrains the other within and across conversational partners. Even more remarkable is that this multimodal coordination is also simultaneously modulated by social and task demands that arise in conversation. The strength of coordination increases, for example, when there is a greater possibility for misunderstanding (Louwerse et al. 2012), when people believe that they might not share common ground (D. C. Richardson et al. 2007), when two people develop a shared vocabulary (Dale et al. 2011), and even when one person is deceiving another (Duran et al., in preparation). Thus, the communicative context itself integrates those involved into a more coherent and stable two-person unit. Put differently, the associations are *doing more* than just bridging their respective behaviors. They are supporting the integration of each individual's cognitive processes and behavioral patterns into a coupled system.

We have argued that the associative approach must be supplemented with an understanding of the naturalistic dynamics of social interaction. Whatever core capacities human beings have to engage in rich social interaction, they must *act together* in order to bring it about. This is a *positive explanatory* thesis about domain-general processes and how they function to support human joint performance. Our ambitious hypothesis is that movement coordination – a mass assembly of associative mechanisms – performs the function of facilitating information transmission. Such hypotheses cannot be tested if single sparse behaviors are studied in isolation. We can't reach these phenomena by studying finger lifts and grasping. Instead, we need to measure complex spontaneous interactions between people, and capture the coordination using new integrative frameworks, such as dynamical systems theory (see M. J. Richardson et al. 2014). The methods and concepts in this framework permit the study of language, social cognition, and social interaction – the phenomena that excite supporters of the mirror neuron system – yet might also explain them with the simple mechanisms laid out in this target article.

Mirror mechanism and dedicated circuits are the scaffold for mirroring processes

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Abstract: In the past decade many studies have demonstrated the existence of a mirror mechanism that matches the sensory representation of a biological stimulus with its somatomotor and visceromotor representation. This mechanism, likely phylogenetically very old, explains several types of mirroring behaviours, at different levels of complexity. The presence in primates of dedicated neuroanatomical pathways for specific sensorimotor integrations processes implies, at least in the primate lineage, a hard-wired mirror mechanism for social cognitive functions.

The core issue of the target article is whether mirror neurons (MNs) arise by associative learning. My comments, based on neuroanatomical and electrophysiological expertise, focus on this and other related issues (mirror mechanism and action understanding) addressed by the article.

The mirror neuron mechanism. The most important aspect of MNs is their capacity to match the visual/acoustic cortical representation of a biological stimulus with its corresponding somatomotor or visceromotor representation. Thus, MNs constitute a mechanism that not only explains the automatic decoding of the motor acts of others, but also many other types of processes involved in social cognitive functions (e.g., emotion recognition, imitation, oro-facial communication). Recent studies have shown the existence of MNs active during both listening and production of species-typical song in singing birds (Prather et al. 2008), suggesting that mirror mechanisms are probably very primitive solutions evolved in different vertebrate classes to elaborate sensory information for social cognition. Furthermore, behavioural evidence suggests that other vertebrates such as rats or dogs (Range et al. 2007; Zentall & Levine 1972) or even invertebrates such as the octopus (Fiorito & Scotto 1992), could be endowed with some form of mirror mechanism.

By using the same matching mechanism, mirroring may occur, even within the same species, at different levels: in the comprehension of goals (Cattaneo et al. 2009; Fogassi et al. 2005; Rizzolatti et al 2004) or of meaningful communicative or symbolic gestures (Ferrari et al. 2003; Lui et al. 2008) (high level), and in the decoding of observed movements rather than of motor acts (Catmur et al. 2007; Fadiga et al. 1995) (low level).

Mirror neurons and sensorimotor associative learning. Cook et al. claim that MNs are the result of associative learning rather than an adaptation selected by evolution for action understanding genetically coded in humans and ancestors. Following the authors' reasoning, if we knew the experience of every monkey since birth, we could predict the formation, in monkeys living in different developmental environments, of different types of MNs. Furthermore, many of the typical primate behavioural functions of daily life would be the result of associative learning, and therefore we should observe a large inter-individual behavioural variability. However, it is well known that, for example, object- or space-related sensorimotor transformations for reaching-grasping actions are grounded on dorsal cortical circuits (Rizzolatti & Matelli 2003) that are phylogenetically very old and, in the primates' lineage, very similar among different species. Just as there are these dedicated circuits, linking specific parietal and premotor areas (Rizzolatti & Luppino 2001), so there is also a dedicated *mirror circuit* for hand actions observation, linking anterior superior temporal sulcus (aSTS)↔inferior parietal cortex (PFG)↔ventral premotor cortex (area F5c) (Nelissen et al. 2011, p. 3754). It is evident that such selected circuits cannot re-build every time. They provide, rather, the neuroanatomical scaffold for both hard-wired and newly-learned sensorimotor transformations. In these circuits, pre-existing and new motor representations are matched with their corresponding sensory representations.

As an example of an anatomo-functional circuit in which the mirror matching mechanism operates, a series of recent works (Bonini et al. 2010; Fogassi et al. 2005) has shown that the discharge of purely motor and MNs of monkey premotor (area F5c) and parietal (area PFG) cortex is modulated, during grasping observation/execution, depending on the behavioural goals of specific executed or observed action sequences (grasp-to-eat or grasp-to-place). Furthermore, the percentage of MNs tuned for the hard-wired action (grasp-to-eat) is much higher than that of MNs tuned for the learned action (grasp-to-place). Overall, these and other data suggest that the mirror mechanism, deeply rooted in primate evolution, also plays a strong role in the extension of action understanding capacity to new actions, in motor skill consolidation (Cross et al. 2006) and in observation-based rehabilitation (Ertelt et al. 2007). These processes could also benefit from associative learning.

Action recognition and action understanding. Cook et al. claim that there is no consensus on the concept of action understanding and on its distinction from action perception and recognition. If the objective of the nervous system were to simply ensure action recognition, probably the visual system would be enough: some sectors of aSTS would be the best candidate for recognizing the actions of others. However, if we assume that the motor system is crucial for cognition because it provides information about motor goals, aSTS areas alone are not able to support action understanding because they do not show motor responses (Perrett et al. 1989). Thus, we can hypothesize that the reciprocal neuroanatomical links between high-order visual areas and motor areas endow individuals with two main abilities: (1) to interpret the vision of a hand approaching an object in terms of goal; (2) to better perceive the details of the observed actions.

Two recent studies support these two functions. The first (Caggiano et al. 2009) shows that in half of recorded MNs the intensity of the visual response is different depending on whether the observed grasping is performed within or outside the peri-personal space of the monkey, and this effect can be further modulated by the possibility for the monkey to act or not in its peri-personal space. The second (Caggiano et al. 2011) shows that 75% of the recorded MNs discharge more strongly when the monkey sees the action either from an egocentric or a third-person perspective. These results can be interpreted as the demonstration that MNs, although always encoding, in their output, the goal of a motor act (they are basically motor neurons), can, at the very same time, in conjunction (through feedback projections) with high-order visual areas sensitive to biological stimuli, provide information on specific details of the observed action, by enhancing the activity of the sensory neurons that are more selective for those details.

Understanding action with the motor system

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Abstract: We challenge Cook et al.'s claim about the vagueness of the notion of action understanding in relation with mirror neurons. We show the multidimensional nature of action understanding and provide a definition of motor-based action understanding, shedding new light on the various components of action understanding and on their relationship. Finally, we propose an alternative perspective on the origin of mirror neurons, stressing the necessity to abandon the dichotomy between genetic and associative hypotheses.

The role of the mirror mechanism (MM) in social cognition is still a matter of debate. Much disagreement is primarily due to different notions of action and of action understanding. On the standard view, an action is directed to a goal in virtue of the action's being appropriately related to some high-order mental states (e.g., beliefs, desires, and intentions) representing this goal. The relation between actions and their goals is traditionally assumed to be largely independent of the motor processes and representations underpinning action execution. These processes and representations allegedly concern motor features such as joint displacements or muscle contractions only. However, two decades of cognitive and neuroscientific research on the cortical motor system has repeatedly challenged this view. Neurophysiological and behavioral evidence (Rizzolatti & Sinigaglia 2010) has demonstrated that motor processes may involve motor representations of action goals (e.g., to grasp, to place, etc.), and not only kinematic or dynamic components of actions. This suggests that beliefs, desires, and intentions are neither primitive, nor the only bearers of intentionality in action. Indeed, motor representation is enough to ground the directedness of an action to its goal (Gallese 2000; Butterfill & Sinigaglia 2014).

The MM indicates that this holds not only for action execution, but also for action observation. The activation of the MM can be selectively related to the observed action goal regardless of its kinematics, dynamics, and the body effector involved (Gallese & Sinigaglia 2011; Rizzolatti & Sinigaglia 2010). This supports the claim that the MM may play a role in action understanding. By recruiting her own motor representation of the goal to which the observed action is directed, the observer may understand what the agent is doing without needing any high-order processing.

Claiming that the MM plays a role in action understanding of course does not imply that action understanding is overall solely explained by the MM. Understanding an action is a complex process. It involves at least representing to which (proximal and distal) goals the action is directed; identifying which beliefs, desires, and intentions specify reasons explaining why the action happened; and realizing how those reasons are linked to the agent and to her action. The MM enables the representation of the goals of others' actions by taking advantage of one's own motor cognition. The richer a person's own motor cognition is, the greater her sensitivity to another's action and the better her ability to grasp the goal to which that action is directed. Consistently, action understanding deficits occur following specific impairments in the recruitment of the motor representation of action goals (for a review, see Gallese & Sinigaglia 2011).

The fact that a motor-based action understanding doesn't match any "established category of psychological functioning" (target article, sect. 9.1) is not per se a good reason to reject it. On the contrary, it provides a new empirically and theoretically sound framework to investigate basic aspects of social cognition. Furthermore, differently from what Cook et al. maintain, it enables us to shed new light on the various components (e.g., perceptual, motor, and mentalizing) of action understanding, as well as on their relationship. To this extent, it is worth noting that even high-order purely sensory mechanisms, like those characterizing extrastriate cortices such as the Superior Temporal Sulcus (STS) region, are insufficient to represent the goal of a given action at the same general level as the MM does. In addition, there is no evidence to date that the STS responds both to proximal goals (e.g., grasping a piece of food) and to distal action goals (for eating or for throwing away), as the MM does (Gallese & Sinigaglia 2011; Rizzolatti & Sinigaglia 2010).

Pertaining to the relationship between the motor components of action understanding and mentalizing, many studies have demonstrated that the MM kicks in when people have to understand to which goal an observed action is directed (de Lange et al. 2008; Liepelt et al. 2008a). When people must determine the reasons why an agent performed a given action, additional activations of cortical regions such as the mesial anterior frontal cortex, the anterior cingulate cortex, and the temporo-parietal junction – typically considered to belong to the so-called mentalizing network – are detected (de Lange et al. 2008; Liepelt et al. 2008a; Van Overwalle 2009). In spite of many theoretical attempts to integrate these different components of action understanding, so far there is neither convincing evidence about the mentalizing specificity of these activations, nor a theoretically coherent and empirically motivated explanation of how the "mentalizing network" might work. Ironically, such controversial aspects of the neurobiological bases of mentalizing have not attracted so much debate, certainly not as much as the role of the MM in social cognition.

Finally, the functional properties of the MM and its involvement in action understanding are not captured by either a strictly genetic or a purely associative account about its origin. We hypothesize (Gallese et al. 2009) that an innate rudimentary MM is already present at birth, which can then be flexibly modulated by motor experience and gradually enriched by visuomotor learning. Indeed, such a system could be an ideal candidate for the neural underpinning of neonatal facial imitation in humans and nonhuman primates. Recent neurophysiological evidence also suggests there is an inborn rudimentary form of action mirroring in neonate rhesus macaques (Vanderwert et al. 2013). Differently from the associative account proposed by Cook et al., our hypothesis entails a primacy of motor experience in the development of the MM and its contribution to understanding others' actions. This primacy is supported by several studies showing a causal link between the ability to produce an action and the ability to understand it (see, among others: Cannon & Woodward 2012; Kanakogi & Itakura 2011).

Evolution after mirror neurons: Tapping the shared manifold through secondary adaptation

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Abstract: Cook et al. laudably call for careful comparative research into the development of mirror neurons. However, they do so within an impoverished evolutionary framework that does not clearly distinguish ultimate and proximate causes and their reciprocal relations. As a result, they overlook evidence for the reliable develop of mirror neurons in biological and cultural traits evolved to work through them.

Cook et al. have done a great service by marshaling the mounting evidence that experience influences the operation of mirror neurons (MNs). This work reinforces other recent calls (e.g., Henrich et al. 2010) to study the effects of variable environments, both in humans (across cultures) and in nonhuman primates (across rearing and field settings), on the development of neural and psychological systems. Cook et al. advance this issue with the hypothesis that specific aspects of developmental environments influence the ontogeny and functions of MN systems. Encouragingly, anthropologists have documented relevant population variation, including in adult interactions with infants (e.g., Ochs & Schieffelin 1984), and in interactive practices across cultural domains (Fiske 1992). Primatologists and comparative psychologists have also increasingly catalogued variation in social behaviors across natural populations (Whiten et al. 2001) and captive environments (Call & Tomasello 1996; Russell et al. 2011). While the painstaking comparative groundwork is just beginning, it is hard to dispute Cook et al. on the value of the enterprise.

However, Cook et al. rely on a curiously impoverished evolutionary framework that likely hinders the empirical project they advocate. The authors do not clearly distinguish and relate types of biological causation (Laland et al. 2011). To be sure, they do clearly propose both a proximate/ontogenetic and an ultimate/functional explanation of MNs – MN development is driven by action-perception contingency learning, and is a by-product of associative learning mechanisms that bear no evidence of adaptive specialization for MNs. However, Cook et al. develop alternative approaches to this "associative" account that are arbitrary conjunctions of ultimate and proximate explanations. Their "genetic" account weds a nativist ontogenetic explanation to a specific ultimate function, "action understanding." That this account is said to "combine" questions of origin and function, while the associative account "dissociates" them, is an artificial consequence of the "genetic" hypothesis as presented. The authors are mistaken when they state that, "If MNs were a genetic adaptation, it is likely that their properties would be relatively invariant across developmental environments" (sect. 9.1.1). Natural selection operates on developmental systems through the phenotypes they produce, and MN development could be largely experience-dependent while having a specific evolved function (see Barrett 2012). Likewise, MNs could be highly canalized and reliably developing, yet could have evolved for functions other than "action understanding," including empathy (Gallese 2003; Preston & de Waal 2002) – a widely discussed and investigated ultimate hypothesis that the target article relegates to a footnote. The "genetic" hypothesis is at best an arbitrary hypothesis, and at worst a straw man.

In addition, contrasting "canalization" and "exaptation" as Cook et al. do has the unfortunate effect of obscuring interesting phylogenetic questions. While the authors argue that "the motivation for invoking exaptation is not compelling" (sect. 8.2, para. 1), they advocate the purest possible exaptation hypothesis – an ancient adaptation was coopted for producing MNs without any "secondary adaptation" (Gould & Vrba 1982). The authors go on to argue that any species capable of associative learning should be capable of developing MNs, and they predict controlled training regiments will produce MNs in lab rats. Intriguing, but this raises a question: Why do humans and macaques (and likely other species: Mancini et al. 2013; Mui et al. 2008; Range et al. 2011) "naturally" develop mirror neurons, while rats apparently do not? Is this a happy accident of variation in early developmental environments? Or has there been varying selection pressures across species for secondary adaptations that facilitate MN development (such as mother–infant face-to-face interaction; Ferrari et al. 2009b)?

In general, the target article is overly restrictive in discussing such canalizing mechanisms. Cook et al. discuss only one attention bias, infant self-observation of reaching. They overlook other biases, both in infants and in adults, that could facilitate MN development. For example, in humans the properties of infant-directed speech (Bryant & Barrett 2007) and adult encouragement and imitation (Bornstein et al. 1992) show evidence of invariance across cultures, while infants show perceptual preferences for faces (Valenza et al. 1996) and infant-directed motion (Brand & Shallcross 2008). In addition, no mention is made of mounting evidence that associative learning mechanisms often evince domain-specific design features, such as preparedness to learn particular fitness-relevant contingencies (Barrett & Broesch 2012; Garcia & Koelling 1966).

Cook et al. also fail to appreciate the likely evolutionary consequences of MNs reliably developing in a species. Although ultimate and proximate explanations are classically considered orthogonal, they can be reciprocally related, such as when proximate mechanisms become part of the selective environment (Laland et al. 2011). Selection for behaviors and capacities that exploit MNs would be a clear case of this. Expressions of emotion may be a case in point. There is strong evidence that emotional contagion and mimicry of expressions are mediated by MNs (Carr et al. 2003; Kircher et al. 2013; Wicker et al. 2003) and have significant consequences for social competencies (Pfeifer et al. 2008) and relationships (Lakin et al. 2003). Given both mirror neurons and selection for empathy and/or emotional coordination, evolution could well craft emotional expressions for facilitating shared emotion. For example, we have argued that laughter evolved as a medium for playful emotional contagion that taps MNs to facilitate mutually beneficial social play (Gervais & Wilson 2005; see also Davila-Ross et al. 2011). To the extent that human expressions of emotion are elaborated homologues of ancestral ape expressions (Parr et al. 2007), one might implicate uniquely human selection pressures that attended ratcheting interdependence (Tomasello et al. 2012). Further, the emergence of cultural evolutionary processes in humans (Boyd et al. 2011) may have created an additional consequence of MNs – selection for cultural practices (e.g., religious rituals; Atkinson & Whitehouse 2011; Fiske 1992) that facilitate MN development and build social bonds through them.

Even if mirror neurons develop through associative learning, they may be reliably developing adaptations. Evidence of secondary adaptation, including biological and cultural traits designed to exploit MNs, would be evidence of a history of such reliable development. The investigation of such derived traits should thus be integral to the mirror neuron enterprise.

Mirror representations innate versus determined by experience: A viewpoint from learning theory

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Abstract: From the viewpoint of pattern recognition and computational learning, mirror neurons form an interesting multimodal representation that links action perception and planning. While it seems unlikely that all details of such representations are specified by the genetic code, robust learning of such complex representations likely requires an appropriate interplay between plasticity, generalization, and anatomical constraints of the underlying neural architecture.

Mirror neurons (MNs) have stimulated extensive discussions in cognitive neuroscience and related disciplines, often based on relatively limited empirical data. The article by Cook et al. provides an excellent overview of an ongoing discussion concerning the possible origins of MNs, and, especially, about the question whether their properties are innate or learned.

Mirror neurons, originally found in premotor and parietal cortex, represent an interesting representation that links the perceptual processing of actions with motor planning (Rizzolatti et al. 2001; Rizzolatti & Sinigaglia 2008). Meanwhile, MN-like sensory-motor representations have been found in a large variety of systems, for example, at different sites in the primate brain (Mukamel et al. 2010; Shepherd et al. 2009; Tkach et al. 2007), and even in non-primates such as birds (Prather et al. 2008), that is, substrates that are not homologous to the primate mirror neuron system (MNS). Following the arguments of Cook et al., this suggests that MN-like properties might emerge from mechanisms that apply to brains in general, instead of being pre-programmed in detail by the genetic code or evolutionary processes that changed a particular subsystem in the brain.

From the viewpoint of pattern recognition, MNs seem jointly to encode equivalent classes of perceived actions, and fragments or primitives of motor programs relevant for the control of action execution. Also, MNs have also been associated with the encoding of "semantic properties" of actions (Arbib 2008; Kemmerer & Gonzalez-Castillo 2010; Pulvermüller 2005), where the precise mathematical definition of action semantics or the critical underlying features remains an open problem. Although it seems likely that MNs represent certain aspects of actions that are invariant, and specifically useful for motor planning, the principles of the neural encoding of such properties within populations of MNs are completely unknown. For example, a recent experiment shows that many mirror neurons are view-dependent, contradicting the interpretation that MNs encode abstract semantic properties, invariant with respect to visual stimulus parameters such as the view (Caggiano et al. 2011). Even less is known about neural mechanisms supporting the efficient learning of such representations and their critical invariance properties.

In the domain of sensory pattern recognition, substantial progress has been made with respect to the understanding of computational and neural principles of the learning of complex sensory patterns, e.g., in vision (Poggio & Edelman 1990; Tarr & Bülthoff 1998; Ullman 1996). Sensory pattern recognition is based on learning, and the efficiency of such learned representations is essentially dependent on maintaining a balance between their selectivity (the accuracy with which individual complex features are encoded) and the invariance against unimportant, semantically irrelevant details of encoded patterns (Vapnik 1998). For object as well as action recognition, it has been shown that this problem can be solved by hierarchical architectures of learned detectors, or classifiers, that increase feature complexity and invariance along the hierarchy, and such architectures have been used to account for visual properties of mirror neurons (Fleischer et al. 2013). The same problem of balancing selectivity versus invariance applies equally for the encoding and recognition of motor behavior (Poggio & Bizzi 2004), and thus also for the encoding of sensorimotor patterns in the MNS. However, it is much less clear how selectivity and generalization in spaces of complex and goal-directed motor patterns can be appropriately defined. Recent work has started to explore which learned structures might enable generalization between different motor tasks, and how expected reward might interact with the control of motor behavior (Wolpert et al. 2011). The influence of expected reward is likely important for the understanding of the function of MNs, since many of them are encoding the expected amount of reward (Caggiano et al. 2012).

Extensive research in visual pattern recognition has investigated how hierarchical representations with good generalization properties can be learned. Whereas initial approaches optimized intermediate feature detectors by learning, often using large amounts of training data (Olshausen & Field 1996; Serre et al. 2007; Ullman 2007), more recent approaches, often referred to as "deep learning," try to learn whole hierarchical recognition architectures in an unsupervised manner, enabling generalization even from very limited datasets (Bengio & Le Cun 2007; Hinton 2007). To make such architectures work, it is essential to constrain the local learning processes, the overall learning strategy, as well as to choose general network architectures with bottom-up and top-down connections that ensure an efficient information transfer through the network during learning. Recent work suggests that similar hierarchical architectures might be suitable also for the encoding and recognition motor patterns (Taylor et al. 2011; Yildiz & Kiebel 2011), and it has been postulated that hierarchical predictive architectures might be essential in the MN system (Grafton & Hamilton 2007; Kilner et al. 2007a).

Although we are still quite far from an understanding of the principles of the robust learning of flexible representations for action encoding, the lessons learned from sensory pattern recognition suggest a slightly different view of the debate as to whether MNs are learned or innate. Efficient learning in mirror representations likely will depend on an interplay between anatomical constraints (e.g., basic connectivity patterns between specialized areas, specific local circuitry principles, or "canonical microcircuits"; Bastos et al. 2012; Douglas & Martin 2004) that ensure sparse encoding and dynamic network stability, and potentially suitable forms of bottom-up top-down connectivity (e.g., Bastos et al. 2012). These principles might in fact be genetically encoded. In addition, an appropriate control and scheduling of relevant plasticity processes (e.g., ensuring local and layer-wise learning vs. closed-loop optimization of larger parts of the representation exploiting top-down predictions) might be critical. This factor might also depend additionally on ontogenetic factors, for example, how sensorimotor patterns are acquired and trained during human development. Beyond these factors, as stressed by Cook et al., the efficient context- and attention-dependent control of the activity of MNs and related plasticity processes is critical to avoid spurious learning, and such control seems compatible with recent electrophysiological results from mirror neurons (Caggiano et al. 2009; 2012).

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Higher-level processes in the formation and application of associations during action understanding

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Abstract: The associative account described in the target article provides a viable explanation for the origin of mirror neurons. We argue here that if mirror neurons develop purely by associative learning, then they cannot by themselves explain intentional action understanding. Higher-level processes seem to be involved in the formation of associations as well as in their application during action understanding.

Cook et al. present an elucidative perspective on how mirror neurons (MNs) could emerge in the human brain. By clarifying the conceptual distinction between questions about the function of MNs and questions about the origin of the matching properties of these neurons, their article makes an important contribution to the field of MN research. With respect to the origin of MNs, we think that the associative account put forward by Cook et al. provides a strong theoretical framework by which experimental findings can be assessed. In this commentary, we would like to elaborate on the potential function of MNs in action understanding, assuming that the associative account put forward by Cook et al. is correct.

Cook et al. note that if MN activity can be understood as arising from associative learning, then its function, if any, in action understanding remains an open question. We would like to take their proposal one step further and argue that if MN activity indeed is a purely associative phenomenon, then there are strong theoretical reasons to believe that MN activity itself cannot be constitutive of genuine action understanding, in the sense of understanding the "why" of actions (e.g., the goals and intentions underlying actions). Our argument consists of two parts. First, we argue that, at least in humans, higher-level cognitive processes can guide the formation of appropriate associations, and that such guidance seems necessary for forming associations that code for the "why" of actions. Second, we argue that even if such appropriate associations have been formed successfully, higher-cognitive processes seem required for selecting which of many possible associations codes the "why" in a particular situation.

Cook et al. review evidence showing that in order to build an associative connection between two events, it is sufficient that the two events occur around the same time and that one reliably predicts the other. This suggests that associative learning is a low-level process where no reasoning is involved. The fact that even basic organisms that are unlikely to have higher-order reasoning ability (e.g., invertebrate sea slugs; Walters et al. 1979) are sensitive to classical conditioning suggests that cognitive processing is indeed not necessary for the formation of associations. However, there is evidence that suggests that the degree to which any two events are associated can be guided by beliefs about the causal structure of the world and other prior knowledge. For instance, in a trace conditioning paradigm, Clark and Squire (1998) found that participants could be conditioned to blink their eyes when hearing a tone, but only if they were aware of the relation between that tone and a puff of air to the eye that caused them to blink. A similar influence of causal beliefs on association seems operational in the well-known "blocking" effect in conditioning. This is the effect that the association of an event A with event Y is prevented if A is presented together with another event B that has previously been associated with event Y. Notably, Waldmann (2000) found that this effect is modulated by whether the participants were led to believe that A and B were either possible causes or possible effects of Y. Findings such as these provide strong evidence that, at least in humans, which types and degrees of associations are formed is partly shaped by higher-level cognitive processes. If MNs indeed code for associations, as Cook et al. suggest, then the degree to which they can be supposed to support action understanding, if at all, will depend on the degree to which the associative processes that guide the MN matching properties are in turn guided by relevant higher-level processes involving beliefs about the causal structure of actions. In other words, if associations are formed without consideration of the causes of actions, including mental causes such as goals and intentions, then they cannot come to code for the "why" of actions.

Admittedly, it is conceivable that the associations coded by the MN system are shaped in part by higher-level processes and thereby could form associations in a way that is sensitive to the causal structure of actions. But even then, for the interpretation of newly observed actions, the MN system can probably not interpret these actions without the involvement of higher-level cognitive processes. This leads us to our second point. There are many possible intentions that may explain an observed action, as well as many possible actions that result from an intention. This many-to-many mapping implies that any given observed action can activate – for example, in the MN system – many possible intentions that have been previously associated with that action. To select which of these associations applies to the current situation, we need some other, context-sensitive process. For reasons that have been detailed elsewhere (Uithol et al. 2011), this process most plausibly involves some form of (possibly implicit, unconscious) reasoning that takes into account some form of knowledge of the world and how actions interact with intentions and contexts. This idea is supported by studies showing that when people consider why an action was performed, for example, when they observe novel actions (Brass et al. 2007) or when they are instructed to attend to the intentionality of an action (de Lange et al. 2008), areas other than MN areas are recruited. Hence, it seems that, if MN associations play a functional role in action understanding at all, these associations need to be integrated with prior knowledge and beliefs in areas outside the MN system for a full appreciation of the intentionality of actions.

In summary, we agree with Cook et al. that the associative account of MN activity is viable. The properties of MNs seem indeed explainable by associative learning. We go one step further than Cook et al. by proposing that a purely associative account implies that MNs cannot explain genuine action understanding, including understanding of the "why" of actions. Higher-level processes are important in the formation of appropriate associations that may code the intentions of actions, as well as in the application of learned associations during intentional action understanding.

Associative and sensorimotor learning for parenting involves mirror neurons under the influence of oxytocin

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Abstract: Mirror neuron–based associative learning may be understood according to associative learning theories, in addition to sensorimotor learning theories. This is important for a comprehensive understanding of the role of mirror neurons and related hormone modulators, such as oxytocin, in complex social interactions such as among parent–infant dyads and in examples of mirror neuron function that involve abnormal motor systems such as depression.

We agree with Cook et al. that sensorimotor associative learning takes place pervasively in the brain, as well as among mirror neurons (MNs) in particular. However, many associative learning theories stress the importance of cognitive representations in Pavlovian and instrumental conditioning (Balleine & Dickinson 1998; Berridge & Robinson 2003). Without consideration of the roles of cognitive representations, MNs end up being the action-executing motor neurons (the primary motor cortex), as opposed to the neurons responsible for action-planning (Schubotz & Von Cramon 2003) an issue recognized by Cook et al.

We recommend that the "cardinal feature" of MNs – sensorimotor matching properties – should be best understood in a way no different from that to understand how the unity of conscious perception is brought about by integrating distributed activities in the brain, known as the "binding problem" (Revonsuo & Newman 1999). This issue applies to a range of brain functions including perception (Treisman & Gelade 1980), volitional emotion regulation (Phan & Sripada 2013; Swain et al. 2012), and social cognitive emotional interaction (Ho et al. 2012). For example, the Theory of Event Coding (TEC) by Hommel et al. (2001) suggested that a domain-general binding process can generate "event files," that is, cognitive representations (memory) of events, which can be any to-be-perceived or to-be-generated incident in the environment. Interestingly, there is evidence that such "event files" can be formed after a single sensory-motor encounter and represented by a network of loosely linked nodes rather than a master file (Hommel 1998). Because TEC has been linked to MNs (Hommel 2004), a direct comparison and contrast of TEC and the account presented in the target article should be performed.

One specific example of MN activity is in the parent–infant dyad. Neuroimaging studies are beginning to explore this in mothers (Mayes et al. 2005; Swain 2011). Recent findings (Atzil et al. 2011; 2012) have demonstrated brain activations in response to baby-videos that constitute a social network involved in mentalization, action representation, simulation, mirroring, and attention functions (Dodell-Feder et al. 2011; Iacoboni & Dapretto 2006; Keysers & Fadiga 2008). These neuro-hormonal networks underpin social interactions among kin and non-kin members of society (Decety 2011; Swain et al. 2004; 2011; 2012), as they have been demonstrated to respond according to minute-by-minute interactive synchrony between mother and infant (Atzil et al. 2011). Such social brain responses involve the integration of higher-order cognitive functions implicated in mentalization and empathy, as well as more basic functions of perception (lingual gyrus) and action representation (motor areas). Possibly, when perception–action regions are co-activated with mentalization regions, they have a social-attentive function that enhances the salience of the social context and the planning of adequate action – such as in parent's ability to understand the intentions and desires of her infant and to respond with a synchronized conduct (Atzil et al. 2011).

These parental social-brain functions have been shown to be under close regulation of oxytocin (OT) (Gordon et al. 2010). The brain–OT correlations may provide additional support to the notion that mothering is guided by greater motivational–emotional focus. Recent pharmaco-imaging study suggests that plasma OT levels significantly correlated with limbic–emotional brain areas among mothers and fathers (Atzil et al. 2012). Oxytocin is central for the formation of social bonds in general and parenting in particular, and is critical for maternal behavior (Shahrokh et al. 2010) in animal models. In human studies, oxytocin has been established as important for many social competencies, including trust, "mind-reading," and empathy (Bartz et al. 2011). In parenting, oxytocin was differentially related to limbic and cortical activations in mothers and fathers for whom arginine vasopressin may play a related role in modulating social brain circuits (Atzil et al. 2011) through motivation enhancement or cognitive modulation.

Perhaps, then, the "laboratory" of the parent–infant dyad will be useful in exploring the importance of MNs for parents, as well as the development of related systems. One example that has received no attention so far is the development of MNs in humans who either have no experience of motion or have the experience of impaired motion. For example, for babies where motor function is impaired, would MNs not develop? In this case, their leg-related sensorimotor cortex would neither be capable of action "understanding," and so forth, nor significant neural activity in areas commonly accepted as MNs when witnessing leg movements, because they would have never been able to associate the visual experience with the motor experience and thereby never have developed MNs. A less extreme example may be to study MN development in children of parents with depression – in which psychomotor retardation may be a significant mediating factor in the detrimental effects of postpartum depression on infant development (Tronick & Reck 2009).

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The alluring but misleading analogy between mirror neurons and the motor theory of speech

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Abstract: Speech is commonly claimed to relate to mirror neurons because of the alluring surface analogy of mirror neurons to the Motor Theory of speech perception, which posits that perception and production draw upon common motor-articulatory representations. We argue that the analogy fails and highlight examples of systems-level developmental approaches that have been more fruitful in revealing perception–production associations.

Cook et al. make the case that sensorimotor learning plays an important role in the origin of mirror neurons (MNs) and that it is therefore essential to pay careful attention to an organism's developmental history and to couple this understanding with rigorous systems-level theory and experimentation. The putative role of MNs in speech perception offers both a cautionary tale of making too much of a surface analogy and a demonstration of the fertility of a systems-level developmental approach to human behavior.

Speech perception is one of the many phenomena claimed to be related to MNs. This link is most commonly made through the Motor Theory (MT) of speech perception, an influential theory that posits that humans perceive speech not as sounds, per se, but as the intended phonetic gestures of the speaker. The central claim is that speech production and perception share common processes and representation, drawn from a linguistic module evolved specifically for communication (Liberman et al. 1967; Liberman & Mattingly 1985). One virtue of MT is that it provides an explanation for how listeners bridge the gap between the variable, continuous acoustic speech signal and discrete, relatively invariant linguistic representations. Another virtue is that it explicitly provides a common representation for production and perception – phonetic gestures (or articulations). Empirical tests of MT's predictions have provided mixed support, at best (e.g., Kluender et al. 2005; Lotto & Holt 2006; Massaro & Chen 2008), but the discovery of MNs has led to a rebirth of MT, influencing research in the neuroscience of speech and language processing, speech development, and language evolution (Fogassi & Ferrari 2007; Galantucci et al. 2006).

Mirror neurons have been taken as evidence for MT because they provide neural confirmation of a perception–production link, leading to proposals that "mirror neurons represent the link between sender and receiver that Liberman postulated" (Rizzolatti & Arbib 1998, p.189), and that the MN "system mediates … speech perception" (Rizzolatti & Craighero 2004, p. 186). Given the importance of common representations for perception and production in a communication system – what Liberman and Mattingly (1985) called "parity" – the temptation to attribute MNs with a central role in speech is understandable. However, as cautioned against more generally in the target article, the link between MNs and MT has been based largely on analogy and on the similarity of rather coarse descriptions of MNs and MT.

This alluring analogy fails for several reasons. We have previously argued (Lotto et al. 2009) that it is critical to be clear that MT is much more than just the proposal that there is a link between speech perception and production, or that processes of speech perception and production interact in some manner. There is no debate about these tenets. Auditory cortical regions are activated during speech production (e.g., Price et al. 2011), and motor regions are activated during speech perception (e.g., Wilson et al. 2004). However, the nature of the production–perception link and its significance for either production or perception are not well established. In particular, it is not clear how these links or MNs would solve the problems of mapping variable acoustics to linguistic representations, which first motivated MT. Like the authors of the target article, we argue that the analogy between MN and MT is counterproductive in that it directs research endeavors away from systems-level research that might provide explanations for these mappings.

Nonetheless, there are examples of empirical research and computational modeling in speech perception that provide excellent illustrations of the kinds of systems-level approach taking into account developmental history that can move theories away from analogy and toward explanatory power. Imada et al. (2006), for example, used magnetoencephalography to examine passive listening among newborns, 6-month-olds and 12-month-olds. Across all ages, they observed activation localized to the left superior temporal cortex, responsible for auditory analysis. However, whereas regions localized to left inferior frontal cortex (Broca's area) consistent with speech motor analysis were active among 6- and 12-month-olds passively listening to speech, no inferior frontal activation was observed among newborns. This suggests that cortical regions associated with speech perception and production are not intrinsically linked. Rather, links may emerge with experience. Intriguingly, the developmental timeline of this emergence fits with the onset of imitation and canonical babbling, consistent with a sensorimotor association interpretation.

The target article makes the case that the associative hypothesis suggests that correlated sensorimotor experience drives the development of MN through contiguous, but also contingent, association. Speech is an especially rich stimulus for developing such relationships; by and large, the sounds we utter, we also hear and so there are meaningful correlations among auditory, motor, and somatosensory signals with which to learn perception-action relationships. In the fields of speech perception and production, computational models have been constructive in delineating systems-level theories for how such relationships may be learned. The DIVA (Directions Into Velocities of Articulators) model (Guenther & Vladusich 2012) includes an articulatory control system that is trainable by feedback from auditory and somatosensory control systems. Predictions of the model concerning effects of auditory input on speech motor acquisition and control have been extensively tested, and many of the aspects of the model have been related to plausible neural structures. This is exactly the kind of explanatory developmental model called for by Cook et al. in the target article. Whereas the "neurons" in DIVA are active both during perception and production, this is a consequence of the model's architecture and the nature of the feedback. Nothing is gained in the theory by referring to these neurons as MNs. Likewise, a more recent computational-neural model of sensorimotor integration in speech by Hickok et al. (2011) provides a theoretical foundation for understanding perception–production interactions arising from a feedback-feedforward system with no explicit need for neurons genetically specified to respond to action and perception. These types of models provide strong theoretical bases for the development of neurons with "mirror"-like properties as a result of correlations in perceptual-production experience and the demands of communication.

Hebbian Learning is about contingency, not contiguity, and explains the emergence of predictive mirror neurons

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Abstract: Hebbian Learning should not be reduced to contiguity, as it detects contingency and causality. Hebbian Learning accounts of mirror neurons make predictions that differ from associative learning: Through Hebbian Learning, mirror neurons become dynamic networks that calculate predictions and prediction errors and relate to ideomotor theories. The social force of imitation is important for mirror neuron emergence and suggests canalization.

There is much to like about Cook et al.'s article. Asking how mirror neurons (MNs) emerge is indeed different from asking what MNs are good for. The authors' richness of stimuli argument is well made. Their experimental evidence shows that experience can have an effect on sensorimotor associations. Unfortunately, it also presents the Hebbian Learning account of MNs (Keysers 2011; Keysers & Perrett 2004) as an inferior alternative to Associative Sequence Learning (ASL) based on contiguity alone. Here, we argue instead that Hebbian Learning and ASL represent different levels of description – neural and cognitive, respectively – by showing that (a) Hebbian Learning is sensitive to contingency and causality, and (b) Hebbian Learning generates valuable predictions about the neural properties of mirror neurons.

Psychology and physiology. ASL was proposed from a psychological perspective to explain the "causes and consequences of imitation" (Heyes 2001). In contrast, the Hebbian Learning account was independently developed from a neurophysiological perspective to explain the emergence of mirror neurons. Single cell physiologists, Keysers and Perrett (2004), unaware of ASL, recorded neurons in the superior temporal sulcus (STS) and the premotor (PM) cortex. The unexpected similarity in the sensorimotor properties encountered in these two regions begged for a mechanistic explanation of how neurons acquire such action sensitive responses, and they harnessed a modern understanding of Hebbian Learning, based on the known physiology of Spike Timing Dependent Plasticity, to explain how such neuron sensitivities could be wired up, because, when you hear/see your actions or others imitate you, STS and PM neurons have the firing statistics to become interconnected (Keysers & Perrett 2004).

Hebbian Learning is not simply contiguity. Cook et al. depict the Hebbian account of MN development as one of "contiguity," that is, when neurons "fire together" (see target article, sect. 3.2, para. 3, point 3). However, this is not accurate. The Hebbian Learning account of mirror neurons draws on our *contemporary* understanding of Spike Timing Dependent Plasticity (Caporale & Dan 2008). Hebb (1949) stated that synapses become stronger "when one cell repeatedly assists in firing another" (p. 63), emphasizing causality, and neuroscience shows synapses are potentiated if the presynaptic input precedes but not follows postsynaptic activity (Fig. 1a). Additionally, intermixing trials in which postsynaptic spiking occurs without presynaptic input prevents synaptic potentiation (Bauer et al. 2001). In summary, physiologists and neuromodellers (http://lcn.epfl.ch/~gerstner/SPNM/node70.html) understand Hebbian Learning to depend on *contingency/causality*, not simple *contiguity*. Cook et al.'s critique of Hebbian Learning in this and other articles is a misunderstanding of what physiologists and modellers understand it to mean. Ironically, the authors' new attempt to define ASL in neural terms – "The kind of learning that produces MNs occurs when there is correlated […] excitation of sensory neurons and motor neurons […that] increases the strength of the connection between them […] when we observe our own actions" (sect. 3.2, para. 2) – is thus actually an adoption of a Hebbian Learning account of mirror neurons.

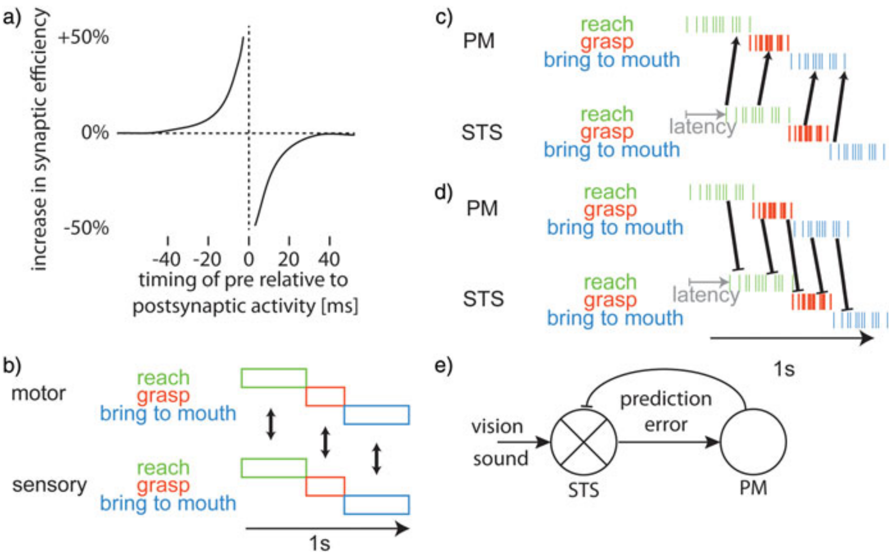

Figure 1 (Keyers). (a) Temporal asymmetry in Hebbian Learning. (b) ASL predicts associations between corresponding phases of an action sequence. Hebbian Learning predicts associations between subsequent phases, that is, predictions (c), and utilizes inhibitory feedback (d) for prediction errors (e).

Hebbian Learning and ASL are not "synonyms." According to Cook et al., the "canalization" hypothesis posits "Hebbing Learning" and "associative learning" as synonymous terms (sect. 8.1, para. 1). Again, this isn't accurate. ASL takes a holistic, systems perspective. When I reach for a peanut, grasp it, and bring it to my mouth, I have three separate episodes of correlated sensorimotor experiences. ASL predicts associations within action phases (Fig. 1b and their Fig. 1c and vertical connections in Heyes 2001). In contrast, Hebbian Learning takes the microscopic perspective of individual neurons and their spiking (Fig. 1c). STS neurons start firing ~100 msec after their favorite stimulus (Keysers et al. 2001), and hundreds of milliseconds lapse between PM spiking and overt movement (and even more before imitation by others); the assumption that sensory and motor representations are simultaneous is therefore an approximation (Keysers 2011) – STS activity occurs ~250 msec after PM activity for the same action (gray arrows in Fig. 1c). With synaptic plasticity temporally asymmetric (Fig. 1a and 1c), Hebbian Learning, unlike ASL, predicts that synaptic plasticity will also occur between action phases, connecting reach-STS to grasp-PM neurons, and grasp-STS to bring-to-mouth-PM neurons. Viewing reaching should then activate grasp-PM neurons. Predictive coding (Keysers 2011; Keysers & Perrett 2004) and active inference (Friston et al. 2011) are fascinating outcomes of Hebbian Learning. Indeed, predictive coding is apparent: Still images of reaching increase the excitability of muscles involved in grasping (Urgesi et al. 2010) and grasping mirror neurons respond to the sight of reaching behind an opaque screen (Umilta et al. 2001).

Connections from PM to STS also exist and have a net inhibitory influence. The Hebbian Learning account suggests the information flow from PM back to STS may cancel predicted sensory consequences and thereby compute action prediction errors (Fig. 1d) (Keysers & Perrett 2004). Indeed, we showed that as people increasingly predict the gestures of others, the flow of activation indeed shifts from STS -> PM to PM -> STS (Schippers & Keysers 2011).

Hence, unlike ASL, Hebbian Learning predicts the dynamic details of the neural circuitry that emerge during self-observation and imitation. The Hebbian Learning account matches modern theories of predictive coding or active inference (Fig. 1e). While ASL refers to sensory or motor representations, Hebbian Learning describes a flow of information between STS and PM with both coming to contain hybrid sensorimotor representations. This opens intriguing parallels with ideomotor theories (Hommel et al. 2001) (see also the commentary by Brass & Muhle-Karbe in this *BBS* issue).

ASL and Hebbian Learning are descriptions at different levels, and arguing that ASL accounts for mirror neurons better than Hebbian Learning seems as idle as arguing that psychology is better than neuroscience. Instead, asking how the circuitry-level predictions of contemporary Hebbian Learning relate to, implement, and inform the systems-level predictions of ASL are more fruitful approaches.

Finally, Cook et al. argue that MNs are not a social adaptation because domain-general mechanisms suffice to explain them – yet, parents' peculiar motivation to imitate their child's facial expressions, a domain-*specific social* behavior, is argued to be essential for, hence to canalize (Del Giudice et al. 2009) mirror neurons. This social force merits more analysis before accepting the argument against hybrid models.

Deciphering mirror neurons: Rational decision versus associative learning

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Abstract: The rational-decision approach is superior to the associative-learning approach of Cook et al. at explaining why mirror neurons fire or do not fire – even when the stimulus is the same. The rational-decision approach is superior because it starts with the analysis of the intention of the organism, that is, with the identification of the specific objective or goal that the organism is trying to maximize.

Cook et al. argue that the proper entry-point to decipher mirror neurons (MNs) is the associative-learning hypothesis. They argue that the standard "genetic" hypothesis implicitly suggests that MNs are adaptive, that is, favored by natural selection. Instead, they argue that MNs exist as a by-product of associative learning – where the genetic component is rather learning as domain-general capability. Put differently, there are no genetic blueprints specific for the MNs phenotype. MNs are simply the by-product of the broader learning mechanism: When the spectator's sensory and motor neurons are excited as the spectator watches another organism doing action X, it is because the same neurons got excited when the spectator, in the past, has undertaken a similar action, say X^+. That is, MNs fire as a result of learning, when X^+ is judged to be close enough to X. So, to put it plainly, the spectator's MNs fire mainly because of "remembrance": One can relate to the observed action because it reminds one of one's own experience, whether it is joy or suffering. So, MNs are ultimately the outcome of a self-centered mechanism, where one can reach out to others only if one has undergone the same situation.

Despite its many insightful payoffs, the associative-learning hypothesis leaves two blind spots. First, it cannot, at first approximation, explain how the spectator could understand the action of another, where the spectator has never been in a similar situation. That is, how could there be "action understanding" in cases where X and X^+ are far apart? For instance, men can normally understand the pain of women in labor, although they could not have entered such an experience. Adam Smith (1976b, p.317) mentions this example to repudiate Hobbes' "selfish" theory of sympathy. For Smith, when one sympathizes with another person, it is not because of "remembrance" of his or her joy or suffering – but rather because of the ability to view matters from the station of the other.

Second, if MNs are about learned response, how could MNs fire in some cases and fail to fire in other cases – in cases where the observed actions, X and X^+, are very close? For instance, while a spectator's MNs fire when the spectator sees a hand reaching for a cup, they do not fire if the spectator witnesses the same motion, but no cup in sight. The reason for this is MNs usually fire when the action has *meaning*, that is, there is a goal to reach. As also noted by the Cook et al., the spectator's MNs do not fire when the spectator watches object-absent or pantomimed motion of the hand, even when the motion is very similar to the motion of trying to grasp a cup (see Gallese et al. 1996).

Actually, these two cases raise the same question: What is the link between MNs and "meaning" or "action understanding"? To see the link, we have to move beyond the associative-learning approach. To introduce the issue of context, á la Cook et al., is merely ad hoc. A more promising way to decipher MNs is through the anatomy of decision making (Khalil 2011). It seems that MNs fire when the spectator intends to "understand" the intention of the observed actor and, in fact, does understand it. As such, the spectator places himself or herself in the station of the observed actor and imagines what it would be like. Such switching of stations, emphasized long ago by Smith (1976a), amounts to the spectator looking at the matter not from his or her own self-centered station, but rather from the station of the observed. In such case, the objective of the spectator is knowledge or understanding. If the spectator cannot make sense of the observed action, MNs would not fire. However, if the organism can make sense of the observed action, MNs would fire.

The situation is different if the organism's objective is not knowledge but rather self-enjoyment (utility). In this case, the neurons would fire or not fire irrespective of understanding. Actually, in this case, the neurons in question differ from what is technically called MNs (Khalil 2011). The spectator here uses the observed action as a stimulus – similar to what Cook et al. argue – to remember his or her own experience. In this case, the organism here simply wants to indulge itself in the observed sensation. It does not care to find out "why" or "how come" the observed sensation has risen. It simply takes the observed reaction, without any regards to the observed reaction in relation to its cause, as a way to indulge in self-enjoyment. In this case, the organism does not place itself in the station of the observed, but rather stays in its own station.

To decipher this minute, but intricate difference between the two objectives – understanding as opposed to utility – we need to identify at the entry point what is the objective of the organism (see Khalil 2013). But such a set-up is the hallmark of rational-decision hypothesis. Namely, to understand the function of any trait, we must first identify the actor and the actor's objective.

Relating the "mirrorness" of mirror neurons to their origins

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Abstract: Ever since their discovery, mirror neurons have generated much interest and debate. A commonly held view of mirror neuron function is that they transform "visual information into knowledge," thus enabling action understanding and non-verbal social communication between con-specifics (Rizzolatti & Craighero 2004). This functionality is thought to be so important that it has been argued that mirror neurons must be a result of selective pressure.

The central hypothesis put forward by Cook et al. is that mirror neurons (MNs) are not the direct result of a genetic adaptation per se, but rather, they are a result of associative learning between visual and motor modalities. Within this framework, it is the mechanism underlying associative learning that has been selected for – not MNs. One of the crucial differences between the genetic adaptation account and the associative account is that the adaptation account assumes that the origin and function of MNs are co-dependent, whereas the associative account dissociates the questions about origin and function, such that they can be treated as independent processes. Any discussion about the ontogeny of MNs, therefore, depends inextricably upon their proposed functional role. Cook et al. adopt the view that the function of MNs is to encode the goal of an observed action. They then go on to argue that the neurophysiological data do not clearly support this functional role and should be considered as evidence against the genetic adaptation account.

Another possibility though, is simply that the mirror neurons do not encode the "goal" of the observed action – rather than encoding the goal of an action, MNs may be part of a distributed network that predicts the sensory (exteroceptive and proprioceptive) consequences of an action (Clark 2013; Kilner et al. 2007b). Within this framework, MNs discharge during action observation not because they are driven by the visual input, but because they are part of a generative model that is predicting that input. In this predictive coding account, the motor system is active when observing an action because it is the best model of the observed action. The generative model entails a representation of – or probabilistic belief about – the goal or intention of an observed action. Given this belief, MNs, in concert with other brain areas, generate a prediction of the sensory consequences of the most likely action that would achieve the goal or intention: for example, the kinematics of the action. By comparing the predicted sensory information with the actual sensory information, the system can infer the goal of the observed action by minimising prediction error. Crucially, in this framework MNs play the same role during both action execution (active inference) and action observation (predictive coding) (Friston et al. 2011). In predictive coding, neuronal representations are used to make predictions, which are optimised during perception by minimizing prediction error. In active inference, action tries to fulfill these predictions by minimizing sensory (e.g., proprioceptive) prediction error. This enables intended movements (goal-directed acts) to be prescribed by predictions, which action is enslaved to fulfill. In this framework, the "mirrorness" of MNs simply reflects the fact that the content of the representations, the action, remains the same in action execution and observation. What changes is the context, or agency – whether the action was produced by the self or another. Therefore, whatever account, genetic or associative, best explains the ontogeny of mirror neurons, it must hold for both action observation and action execution. Within the active inference framework, any selective pressure must operate at the level of agency (self or other) and not at the level of the mirror neurons.

Cook et al.'s article highlights the important point that it is incredibly hard to disambiguate the genetic and associative contributions to the ontogeny of a specific neuronal population. This is because all neurons show associative plasticity, and their response profiles can be modified through interactions with the environment – where these modifications depend upon heritable (genetic) synaptic (associative) plasticity. For example, orientation-tuned responses in neurons in primary visual cortex can be elicited in kittens as soon as they open their eyes – suggesting that the orientation maps are innate. However, depending on the environment, the orientation-tuning can be optimised during development to reflect the observed world (Blakemore & Mitchell 1973). If a kitten is raised in an environment with only vertical stripes, the response properties of the kitten's neurons in the primary visual cortex will reflect this and responses to horizontal stimuli will be lost. In addition to this, many responses of neuronal populations that we think of as being a result of evolutionary adaptations – for example, binocular disparity responses and direct cortico-motoneuronal cells – are not present at birth but develop postnatally. This is in distinction to the formal phenotypes that contextualise the function of these neurons; for example, having two eyes and opposable thumbs. Indeed, for visual responses, the consensus view is that the primary repertoire of connections that underlie vision are present at birth and are fundamentally refined by early postnatal experience. In other words, it is not the neurons that are the genetic adaptation, but rather, how they form connections. In this light, it is tempting to propose the same for the visuomotor responses of MNs. In other words, mirror neurons arise as a result of domain-general mechanisms of associative learning, as proposed by Cook et al., but in the context of cortical connections between visual and motor systems selected by genetic adaptation. From this point of view, with respect to the ontogeny of MNs, perhaps we should consider that no neuron is an island?

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A developmental perspective on action and social cognition

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Abstract: The target article argues that developmental processes are key to understanding the mirror neuron system, yet neglects several bodies of developmental research that are informative for doing so. Infants' actions and action understanding are structured by goals, and the former lends structure to the latter. Evaluating the origins and functions of mirror neurons depends on integrating investigations of neural, social-cognitive and motor development.

Cook et al. articulate two conclusions with which we wholeheartedly agree: (1) The functions of mirror neurons (MNs) cannot be determined based only on patterns of neural activation during action observation. Independent measures of the putative social-cognitive functions of MNs are needed and have, so far, not been sufficiently integrated with neural measures; and (2) understanding the developmental origins of MNs and the broader systems in which they are situated is essential for understanding their functional significance.

Given the centrality of developmental processes to Cook et al.'s arguments, we find it surprising that they do not engage the developmental literature more fully. They propose a relatively simple learning process – the formation of contingency-based associations between visual and motor experience – to account for the existence of MNs. For example, they propose that MNs reflect repeated experiences with reaching for objects and seeing the resulting hand movements. This kind of learning seems very likely to occur, but without a fuller consideration of motor and social-cognitive development, it is difficult to see how any important social-cognitive functions could arise from motor experience. In fact, several bodies of experimental work with human infants indicate that much richer connections exist between motor experience and social cognition.

Developmental research shows that infants' actions are prospectively goal-directed from very early in infancy (von Hofsten 1980; 2004), and during the first year, manual skills become increasingly well-organized (Thelen et al. 1996; von Hofsten & Ronnqvist 1988). For example, Claxton et al. (2003) demonstrated that infants reach for objects differently depending on what they intend on doing next: They are faster to reach for a ball if they are going to throw it versus place it into a container. Further, over the course of the first year of life, infants begin to systematically anticipate the shape, size, and orientation of the objects that they grasp (von Hofsten & Ronnqvist 1988). This body of work shows that motor competence even in young infants involves abstract action plans, as it does in adults (Rosenbaum 1991). This fact about infants' actions has implications for the role that action experience might play in infants' perception of others' actions as organized by goals.

In fact, converging research has shown that infants also view others' actions as structured by goals. Infants encode others' actions in terms of the relation between agent and goal (e.g., Brandone & Wellman 2009; Luo & Johnson 2009; Sodian & Thoermer 2004; Sommerville & Woodward 2005; Woodward 1998), selectively imitate the goals of others' actions (Gerson & Woodward 2012; Hamlin et al. 2008; Meltzoff 1995), and anticipate the outcomes of others' actions based on their goals (Cannon & Woodward 2012; Gredebäck et al. 2009; Kanakogi & Itakura 2010; Krogh-Jespersen & Woodward, under review). Moreover, across these findings, matched comparison conditions and fine-grained analyses of infants' attention during the tasks have shown that infants' responses reflect more than simply attention to physical movements or low-level associations between hands and objects. Instead, this body of evidence shows that infants analyze others' behavior in terms of the abstract relational structure that organizes goal-directed actions.

Importantly, infants' action understanding is related to and shaped by their action experience. The emergence of goal-directed actions in infants' own motor repertoires correlates with their analysis of these actions in others (e.g., Brune & Woodward 2007; Cannon et al. 2012; Kanakogi & Itakura 2011; Loucks & Sommerville 2012; Sommerville & Woodward 2005). Critically, interventions that change infants' own actions render changes in their analysis of others' action goals. For example, 3-month-old infants are not yet efficient at reaching, but, given training to use Velcro "sticky" mittens to apprehend objects, they subsequently demonstrate an understanding of others' reaches as goal-directed (Sommerville et al. 2005). Matched training that involves passively observing others' reaches does not have this effect (Gerson & Woodward 2014; for related findings, see Libertus & Needham 2010; Sommerville et al. 2008). Thus, this body of work shows that infants' own experience producing goal-directed actions informs their understanding of the goals that structure others' actions.

Nevertheless, studies of infants have made only preliminary progress in the domain in which the MN hypothesis originated – neural processes. We agree with Cook and colleagues that a systems approach is needed to evaluate the functional relations that may be signaled by the firing properties of MNs. In human infant research, we have neither the precision of single-cell recordings nor (yet) an analysis of connectivity among potential components of the mirror neuron system (MNS). Even so, infants evidence neural activity in the motor system during observation of others' actions (Marshall et al. 2011; Nyström et al. 2011; Southgate et al. 2009). Critically, changes in infants' motor experience modulate this neural response to others' actions. Developments in infants' motor skill affect the motor system's response to others' actions (Cannon et al., under review; van Elk et al. 2008), and short-term manipulations of motor experience in infants generate similar effects (Marshall et al. 2013; Paulus et al. 2012). Yet, as Cook et al. point out with regard to the adult work, the critical connection between the MNS and social understanding has not been made for infants. Establishing this connection requires integrating neural techniques with behavioral methods for investigating social cognition in infants.

Cook et al. use a developmental framework to argue against over-interpretation of MN findings. While we see merit in their argument that many open questions still exist concerning the MNS, we also advise against throwing out the baby with the bathwater. Rather than using developmental arguments to minimize the potential significance of MNs for social cognition, the field should be pushing forward to understand the links between neural systems, social cognition, and motor skill. Because each of these systems undergoes rapid and dramatic change during early ontogeny, a developmental approach is likely to shed the most light on the links between them.

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The origin and function of mirror neurons: The missing link

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Abstract: We argue, by analogy to the neural organization of the object recognition system, that demonstration of modulation of mirror neurons by associative learning does not imply absence of genetic adaptation. Innate connectivity defines the types of processes mirror neurons can participate in while allowing for extensive local plasticity. However, the proper function of these neurons remains to be worked out.

The article by Cook et al. addresses the question whether mirror neurons (MNs) are a genetic adaptation for action understanding. The authors argue that if this were the case, one might predict that their functioning would be protected against "environmental perturbations" (sect. 7.1, para. 1). They make the further claim that if it could be demonstrated that the functioning of MNs can be modulated by associative learning, such an outcome could be taken as evidence against the genetic adaptation hypothesis.

One may question the prediction that if mirror neurons were "designed by evolution" for action understanding, their response properties should likely be protected against experience-based modulations. There are numerous examples in the literature demonstrating innate neuronal machinery that is modulated by experience (e.g., experience-based modulations of ocular dominance columns in V1: Wiesel & Hubel 1965; activation of primary visual cortex during Braille reading in early blind participants: Buechel et al. 1998; enlargement of the cortical representation of neighboring digits after deafferentation of single digits: Merzenich et al. 1983). Such plasticity, while constrained by the innate connectivity pattern of cortical and subcortical areas, enables the brain to flexibly adjust to a dynamic environment and to both permanent and temporary changes of the input. It is far from obvious why one should assume that a function that is innate would be protected from such plasticity. Thus, although Cook et al. convincingly demonstrate that the properties of MNs can be modulated by experience, the studies discussed in their article are inconclusive regarding the question whether the capability to match visual and motor representations of actions is innate.

We have argued, in another context, that the observed object category-specific organization in the visual ventral stream is driven primarily by distinct long-range connections to downstream processes (Mahon & Caramazza 2011). Different domains of objects are associated with different types of processes. For example, animate but not inanimate objects involve computing affective/social responses. The different processes that characterize different object domains involve distinct, even distant, areas of the brain that must be connected to function effectively as domain-specific networks. On this view, then, visual cortical organization is determined in part by the need to satisfy innate connectivity constraints. The innateness of these constraints is revealed by the fact that the large-scale, domain-specific organization of visual cortex remains invariant in congenitally blind subjects, that is, in the absence of visual input (e.g., Mahon et al. 2009). However, in these subjects the properties of the neurons in "visual" areas have undergone extensive modification: they now respond to completely different sensory inputs even as they retain their domain-specificity. This shows that plasticity does not imply absence of innate neural organization. Likewise, it seems reasonable to assume that the capacity of MNs to match visual and motor representations is made possible by the innate connectivity between ventral premotor cortex/macaque F5 and parietal cortex (AIP [anterior intraparietal], PFG [parietal] areas), which receives visual input from areas IT (inferotemporal cortex), STS (superior temporal sulcus), and MTG (middle temporal gyrus) (Borra et al. 2008; Luppino et al. 1999; Matelli et al. 1986; Muakkassa & Strick 1979; Petrides & Pandya 1984; Webster et al. 1994). This innate connectivity defines the types of processes MNs can participate in while allowing for extensive local plasticity.

In our view, the fundamental question that needs asking is not whether specific associations between visual and motor representations of actions are present at birth – which we take as a given – but whether the link between visual and motor representations takes the form proposed by mirror neuron theorists. A mechanism specialized for connecting visual and motor functions is fundamental for any cognitive function, or otherwise we would lack the ability to react appropriately to sensory input. It seems reasonable to assume that such a basic mechanism should be genetically determined. What remain to be worked out are the anatomical and functional structure of the innate connections between visual to motor representations and the precise nature of the representations involved in this process. In the context of the latter issue, figuring out the role played by MNs in action understanding is key, but as Cook et al. note, the role of these neurons remains poorly understood.

One source of difficulty is the fact that even granting that MNs are involved in matching visual and motor aspects of actions, this does not imply that they are required for action understanding. It is typically argued that (mirror) neurons that code the abstract "goal" of an action (e.g., "grasping food," irrespective of the type of grip and the effector involved) should be involved in action understanding. It is less clear, however, what is "motor" about such abstract representations, and how these differ from conceptual representations outside the macaque mirror neuron system. What is needed is evidence that MNs are necessary for comprehension as opposed to being activated as a consequence of action understanding, for example, to react appropriately to the observed action, or to coordinate our actions with those of other people. Unequivocal evidence demonstrating a causal link between the functioning of MNs and the ability to understand actions has not been presented thus far. We believe that the answer to this question is unlikely to come from investigation of modulation of MNs by associative learning alone, important as this might be for a full characterization of these neurons, but through the investigation of the impact of temporary and permanent lesions to areas containing mirror neurons and their connections.

Reconciling genetic evolution and the associative learning account of mirror neurons through data-acquisition mechanisms

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Abstract: An associative learning account of mirror neurons should not preclude genetic evolution of its underlying mechanisms. On the contrary, an associative learning framework for cognitive development should seek heritable variation in the learning rules and in the data-acquisition mechanisms that construct associative networks, demonstrating how small genetic modifications of associative elements can give rise to the evolution of complex cognition.

In promoting the associative learning account of mirror neurons (MNs), Cook et al. have chosen to adopt an extreme version. Not only have they argued that the matching properties of MNs (the coupling of perception and action) are learned, but they also claim that this learning process did not evolve beyond a domain-general, all-purpose associative learning mechanism. Although we are strongly in favor of the first, more general associative argument (which is also clearly supported by Cook et al.'s review of the scientific evidence), we find their second claim less convincing, theoretically problematic (in terms of evolutionary theory), and somewhat counterproductive. Instead, we shall argue that a more realistic and productive associative account of MNs (and of similar advanced cognitive traits) should be based on identifying the genetically variable mechanistic details on which the associative process is based, and on which selection can operate in the course of evolution.

Cook et al.'s second claim that precludes genetic evolution is not as parsimonious as it may first appear. It implies that associative learning mechanisms acting in the construction of MNs for thousands of generations were not affected by selection in any way that was related to their role in producing MNs. This argument is difficult to test and is also evolutionarily unlikely. Unless it is clear that a trait is fairly recent (such as reading, typing, driving a car, etc.), a possible effect of natural selection on this trait cannot be precluded and is even to be expected. For example, although it is possible that our ability to use our hands for handling tools is merely a by-product of their adaptive design for climbing trees, we cannot preclude the possibility that our hands were also modified by natural selection as a result of their tool-making activity during the past ~3 million years. Moreover, the functionality and the conserved nature of associative learning mechanisms (highlighted by Cook et al.), suggest that they are under strong stabilizing selection. This stabilizing selection, however, is unlikely to be identical across multiple species and populations. It is both plausible and supported empirically that despite general similarity, associative learning mechanisms may differ in their parameters or mechanistic details as a result of different selection pressures. Many forms of learning, from imprinting to taste aversion, are increasingly recognized as different forms of associative learning that have adapted to different tasks (e.g., Bateson 1990; Shettleworth 2010). There is also evidence for fine-tuning of associative learning mechanisms by different selection pressures imposed by alternative behavioral strategies (Mery et al. 2007). Why, then, should associative learning mechanisms acting in the construction of MNs be different?

Paradoxically, the extreme version of the associative learning account weakens our ability to use associative learning to explain cognitive phenomena. If indeed all it takes to construct MNs (or similar associative networks) is to have the same basic domain-general associative learning ability, then all animals and all individuals should construct such networks equally well. Ignoring for the moment whether this is the case, adopting this view implies that heritable variation or species-specific differences in cognitive abilities cannot be explained by the associative account. Thus, the extreme version of the associative learning account may still explain MNs but cannot explain heritable variation in intelligence or social skills (Baron-Cohen et al. 2003; Gray & Thompson 2004), cannot address genetically based cognitive disorders (e.g., Crespi et al. 2010), nor can it be used as a framework for cognitive evolution.

Alternatively, allowing associative learning mechanisms to vary genetically may offer a much more powerful account. We have recently proposed such a framework (Lotem & Halpern 2012) based on earlier work (Goldstein et al. 2010; Lotem & Halpern 2008) and their recent implementation (Kolodny et al. in press; 2014). In our framework, MNs may be viewed as no more than a specific instance of a much wider set of associative networks that represent contingencies or contiguities in time and space, which is consistent with Cook et al.'s general view. However, contrary to Cook et al., we predict that different species or individuals may construct different associative networks as a result of genetic differences in (a) their data-acquisition mechanisms (the attentional and motivational mechanisms directing them to process the relevant data) and in (b) the memory parameters (weight increase and decrease) of their associative learning rules. Most importantly, our model emphasizes the coevolved coordination between these two genetically variable components, coordination that determines learning dynamics and therefore the content and the structure of the network. Our data-acquisition mechanism is in fact similar to Heyes's idea of "input mechanisms" by which associative learning may be tuned to acquire data about the actions of others in order to facilitate social learning (Heyes 2012c). But we also go a step further by proposing that acquiring the relevant data is not sufficient. Memory parameters possessed by the learner must also fit the distribution of acquired data, as they presumably evolved to test the statistical significance of patterns and associations, given the natural distribution of the data. We used these principles to explain a range of phenomena in language acquisition and cognitive development (Lotem & Halpern 2008; Goldstein et al. 2010; Kolodny et al. in press) and to propose an associative framework for cognitive evolution (Lotem & Halpern 2012; Kolodny et al. 2014). Although our model may eventually turn out to be inaccurate or even incorrect, it certainly suggests that allowing associative principles to evolve is a much more useful exercise than dismissing their genetic evolution. We thus call the readers to adopt Cook et al.'s general endorsement of associative accounts (see also Heyes 2012b;

2012c), but not to the point of neglecting the genetic evolution of their underlying mechanisms.

Understanding the role of mirror neurons in action understanding will require more than a domain-general account

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Abstract: Cook et al. propose that mirror neurons emerge developmentally through a domain-general associative mechanism. We argue that experience-sensitivity does not rule out an adaptive or genetic argument for mirror neuron function, and that current evidence suggests that mirror neurons are more specialized than the authors' account would predict. We propose that future work integrate behavioral and neurophysiological techniques used with primates to examine the proposed functions of mirror neurons in action understanding.

In their target article, Cook et al. argue that mirror neurons (MNs) did not evolve to support action understanding. Instead, they argue that MNs emerge through a domain-general associative mechanism: Neurons that are contingently activated by observing and performing a particular action ultimately become selectively activated by either observing or performing that action. We agree with the authors that it is premature to conclude that MNs have the specific adaptive function of subserving action understanding (and that the term "action understanding" itself is typically ill-defined). Nevertheless, while we think Cook et al. are right that we know little about the function and origin of MNs, we think they may be right for the wrong reasons.

The first problem concerns the fact that Cook et al. use evidence that MN responses can change with experience to support their domain-general association account. Unfortunately, the finding that MNs are tuned by experience does not in principle mean that MNs are not innate and do not have an adaptive function. Instead, MNs may be responsive to goal- or object-directed actions more abstractly, perhaps starting out prepared to represent a fixed set of canonical actions that are phylogenetically ancient and then through experience becoming more finely tuned such that non-canonical actions can be represented as goal-directed (e.g., using a grasping tool to reach an object). For these reasons, we don't see the fact that MNs respond to a broader set of stimuli to which the "evolutionary ancestors of contemporary monkeys could not possibly have been exposed" (sect. 4.1, para. 3) to be difficult to reconcile with an innateness account. The idea that mirror neurons may start with a fixed set of prepared representations that gradually expand through experience seems to fit well with how many domain-specific cognitive mechanisms work.

Indeed, the science of the mind has several examples of abstract innate biases that are tuned by specific experiences. To take a classic example, rats have an innate bias to connect nausea with what they have eaten, but they must also use associative learning to identify which specific foods are to be avoided after different experiences (Garcia & Koelling 1966). As this case illustrates, showing that MNs change with experience does not necessarily mean that they result in domain-general learning mechanisms that can take in any sort of inputs. Instead, MN representations could still emerge from *domain-specific* processes, ones that allow only certain kinds of experiences to act as inputs but become tuned to new inputs across experience.

A second set of reasons to doubt the target article's claim that MN learning is domain-general concern (1) the *rarity* of these neurons (according to one study, only about 17% of neurons sampled from a common monkey F5 region; Gallese et al. 1996), and (2) their seeming *specificity* to only particular types of visual-motor contingencies (e.g., grasping). If MNs develop through domain-general processes whenever there is contingent stimulation, Cook et al. should expect any and all neurons to develop "mirror" properties, and thus should expect to observe MNs for a variety of contingencies all over the brain. A domain-general account of MN learning should predict that species would develop mirror-like neurons that respond to Pavlovian contingencies, such as a neuron that fires both when a bell rings and when the subject salivates. If neurons are truly domain-general associative learners as the authors contend, then it is hard to explain why only *some* kinds of associations are represented by MNs to the exclusion of others and why only a small subset of neurons turn into MNs over the course of development. Even if MNs do acquire mirror properties through experience with contingent activation, this only pushes the question of specialization back to why these neurons change in response to contingencies while the majority of neurons in the brain do not.

Finally, the target article attempts to marshal evidence that human learners receive enough of the necessary types of inputs to create MNs through associative learning, stating that "much of the sensorimotor experience required for MN development comes from being imitated, synchronous action, and exposure to action words" (sect. 3.2., para.3). Unfortunately, this account of MN formation would likely not predict the existence of MNs in nonhuman primates, who rarely imitate (see Lyons et al. 2006) and do not have language at all (eliminating two of the proposed routes to MN formation). Thus, the experiential account proposed by Cook et al. to account for their proposed origin of MNs seems incomplete given the data.

For all these reasons, we believe that the target article's approach of searching for MNs' developmental origin before their function may not be the best way to examine or falsify an adaptive argument for these neurons. In order to falsify the hypothesis that MNs are involved in action understanding, we recommend that MN researchers instead directly test the role that MNs play in action understanding empirically – through experiments investigating the level at which actions are represented by these neurons. Since most of what we know about MNs comes from single-cell recording in monkeys, we propose to integrate neurophysiological recording techniques with behavioral methods that allow us better insight into the types of actions that monkeys understand (e.g., Umiltà et al. 2001). Primate cognition researchers have recently developed a number of new behavioral methods in which monkeys appear to represent others' object-directed actions (Rochat et al. 2008), perceptions (Flombaum & Santos 2005; Santos et al. 2006), and knowledge (Marticorena et al. 2011). We argue that recording monkey MN activity while subjects perform these action understanding tasks could provide unique insight into the specific ways that action is represented in these neurons. Cook et al.'s article points us in the right direction by questioning the current accounts of the role MNs play in "action understanding," but we believe that careful empirical work will be needed to test these accounts going forward. A domain-general association account is an inadequate replacement.

Vocal coordination and vocal imitation: A role for mirror neurons?[1]

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Abstract: Some birds and mammals have vocal communication systems in which coordination between individuals is important. Examples would include duetting or antiphonal calling in some birds and mammals, rapid

exchanges of the same vocalization, and vocal exchanges between paired individuals and other nearby pairs. Mirror neurons may play a role in such systems but become functional only after experience.

A possible role for mirror neurons in human speech has been raised by others (e.g., Hickok 2010). Here, I propose that mirror neurons (MNs) may play a role in other forms of vocal communication, specifically wherever imitative or responsive vocalization is found. In humans, examples would include contagious laughing or crying, and synchronized singing in duets or choral groups. In more general terms, I wish to raise the possibility that mirror-like neurons exist to foster vocal communication between individuals, where rapid exchange of information is required. Communication of this type exists in nature in duetting birds and mammals, and in rapid vocal exchanges between two individuals, where the appropriate response to a particular vocalization is a vocal response given after a brief interval. I further propose that neurons that serve this function are part of inherited neural circuitry that mediates a communication system, but become active only through experience.

There are numerous species of birds and mammals that engage in rapid and frequent vocal exchanges. These may be referred to as "duetting," "antiphonal calling," or simply vocal exchanges. In birds and some primates, duetting seems to serve to maintain or strengthen the pair-bond. In some cases, the duetting pair call in such rapid synchrony that it is often difficult to determine which partner is performing which part (e.g., Geissmann 2002; Müller & Anzenberger 2002).

Such synchronization obviously requires a neural system that can manage this behavior, and, presumably, also mediate the learning processes that lead up to the performance of this behavior (Brenowitz et al. 1985. I propose that a "mirror-neuron–like" system may be central to the performance of this behavior. Such an ensemble of neurons would, in each partner, monitor both the immediately ensuing component and trigger the expected output. How such an ensemble becomes activated in an individual may depend on associative learning, but there also must be a genetically derived program that puts together the components of the ensemble in the first place.

While Cook et al. propose that experimentation in the lab is needed to demonstrate the essential role of associative learning in MN formation, most of the behaviors I am addressing are probably not likely to occur in lab settings. However, some primates widely used in laboratory settings engage in vocal exchanges that can be observed while they are in captivity, and for which an established history in behavioral neuroscience exists. In squirrel monkeys (*Saimiri*), females who are affiliative partners (as determined by their close association during foraging and rest periods) produce "chuck" vocalizations in rapid exchanges of no more than a few hundred msec (Newman & Bernhards 1997). Each affiliative partnership exchanges chucks with each other, and each individual makes chucks that are sufficiently distinct acoustically so that their partner can recognize them on the basis of their vocalizations alone. Experimentation has shown that one particular part of the chuck (referred to as the "flag") is essential for accurate recognition and response (Soltis et al. 2002). This behavior starts out during development as a more general "contact call," in which young females respond indiscriminately to the chucks of other females. Gradually, over a year or two, a female learns to distinguish, and differentially respond to, the chucks of its mother and other affiliating females (McCowan & Newman 2000). The genetic component of this behavior is in the tendency to make chucks in the first place. The associative learning component comes from a young female gradually learning to restrict her chuck responses to the chucks of affiliative partners. While MN-like populations of neurons need not be necessary for this behavior, I propose that ensembles that regulate the production, monitoring, and subsequent response (and hence "MN-like") would be more efficient (and likely favorably selected for) over populations of neurons that might be engaged in a variety of behavioral activities.

Another primate vocal communication system that might be mediated by a MN-like system is antiphonal calling in the common marmoset (*Callithrix jacchus*). Here, members of a mated pair exchange loud "phee" calls with other mated pairs within an interval of 5 sec or less (Miller & Wang 2006). This behavioral system requires that a vocalizer recognizes when its partner calls, and when a member of another pair calls, and responds only to the latter with less than a 5-sec delay. No one knows how the brain mediates this behavior, but a study (Miller et al. 2010) using immunocytochemistry of c-fos gene expression has identified areas of the cortex that show neural activity to hearing a phee, to producing a phee, and to the production and hearing of a respondent's phee. No one, as yet, has recorded from single units in the identified frontal cortical areas in the marmoset, so it would be interesting to learn if MN-like activity was found there. Such specialized activity would likely occur both when the vocalizer called and when there were responses.

To summarize, ensembles of neurons that possess mirror-neuron–like properties are likely to exist in a wide range of birds and mammals, so that a correspondingly broad approach to identifying and learning more about these systems is needed. Cook et al. suggest that experiments in the lab would be needed to reveal the MNs emerging during associative learning. My suggestion that MN-like systems exist widely in nature implies that behavioral tests performed in a lab setting would be insufficient to explore the full extent of their role in communication. Some species are too vulnerable in nature or otherwise protected from invasive experimentation, but, with the improving technology to record neural activity in freely moving animals, it might be possible to study these systems. Some work being done on European Starlings (*Sturnus vulgaris*) has potential here (George et al. 2010).

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NOTE

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Associative learning alone is insufficient for the evolution and maintenance of the human mirror neuron system

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Abstract: Cook et al. argue that mirror neurons originate from associative learning processes, without evolutionary influence from social-cognitive mechanisms. We disagree with this claim and present arguments based upon cross-species comparisons, EEG findings, and developmental neuroscience that the evolution of mirror neurons is most likely driven simultaneously and interactively by evolutionarily adaptive psychological mechanisms and lower-level biological mechanisms that support them.

In the target article, Cook et al. suggest that the evolutionary origins and maintenance of the mirror neuron system (MNS) lie in "domain-general processes of associative learning in the course of individual development, and, although they may have psychological functions, their psychological functions do not necessarily have a specific evolutionary purpose or adaptive function" (target article, Abstract). We agree that the excitement surrounding the discovery of mirror neurons (MNs) has led to an inordinate focus on their role in social-cognitive functions and how these functions might play a role in the evolution of the MNS. However, we strongly disagree with the authors' claims that the known social-cognitive roles the MNS plays in primate cognitive and behavioral functioning have not and do not affect the MNS in an evolutionary context and that the associative account "separates questions about their origin and function" (sect. 1, para. 4).

The target article describes a lower-level biological mechanism (associative learning) that, as Cook et al. argue, fully accounts for the phylogenetic and ontogenetic development of mirror neurons. We assert that the initial evolution, further evolution, and evolutionary maintenance of the MNS is likely jointly influenced by such lower-level biological mechanisms *and* by the well-documented role that the MNS plays in social-cognitive functions. One example of this joint influence can be observed in individuals with an intact versus an impaired MNS who are more able to attract reproductive partners, reproduce, and protect and provide for their offspring within the complex social structures of primate societies (e.g., Howlin & Moss 2012).

We agree that associative learning is likely a critical mechanism for both the development and the evolution of mirror neurons. However, given that associative learning mechanisms exist in species that do not have a MNS, some alternative mechanism *must* interact with associative learning in order to produce the evolutionary pressure required for the origin and maintenance of the MNS in humans. To avoid directly addressing the evolutionary advantages the social-cognitive functions of the MNS confer, Cook et al. use a "straw man" argument. They attack the most extreme proposal of the role of social-cognitive functions in the evolution of the MNS – evolutionary selection via action understanding. The "associative learning in vivo" and "evolutionary selection based upon action understanding" accounts represent polar extremes, both of which are unlikely to reflect reality. Simultaneously, however, the adaptive advantages of the social-cognitive capacities (e.g., action perception, processing, and prediction) ascribed to the MNS enhance individuals' reproductive fitness, creating precisely the evolutionary pressure that the authors propose has not, and does not, exist.

Cook et al.'s depiction of the role of developmental research in elucidating biological/genetic versus environmental/learning influences on the MNS is concerning. We agree that evidence for neonatal imitation is limited and, even if it is present, is unlikely to be driven by MNS mechanisms since cortical regions that contain MNs are not fully developed at birth. However, the postnatal developmental timeline of the MNS neither rules out genetic/biological and evolutionary processes nor demonstrates the role of associative learning. It is well known that frontal and association cortices that house MNs undergo striking synaptic development and myelination between 8-months and 3-years of age (Huttenlocher 2002; Imada et al. 2006; Locke et al. 1995). Developmental EEG evidence similarly indicates protracted cortical development in these regions (Hagne 1968; Southgate et al. 2009), with continuing maturation until late childhood or adolescence (Martineau & Cochin 2003). Therefore, biological factors may explain protracted MNS development.

Cook et al. also dismiss EEG mu suppression as an index of MNS functioning too quickly. The strong relationship between the mu rhythm and action observation/execution can be traced back to 1954, when Gastaut and Bert reported that the mu rhythm was consistently reduced when stationary subjects "identified themselves with an active person represented on a screen" (see also Pineda 2005). We also recently published a re-analysis of pooled data from four published studies, including a total of 66 individuals with autism spectrum disorders (ASD), demonstrating that, across the age-span from 6–17 years, there was significantly less mu suppression in individuals with ASD compared with matched controls during action observation, but not during self-movement (Oberman et al. 2013). Although source estimation indicates that the generator of the mu rhythm is in the postcentral gyrus rather than premotor or primary motor cortex (Hari & Salmelin 1997), the possible downstream modulation of motor cortex by the MNS is tangential to their mirror properties. Cook et al. also ignore recent studies showing that the same stimuli that elicit mu suppression also activate MN regions (as indicated by BOLD response; Perry & Bentin 2009) and modulate a TMS-induced motor evoked potential (Lepage et al. 2008), suggesting that all three indices are likely capturing the same underlying cortical mechanism.

In summary, we argue, contrary to Cook et al., that the origins and evolution of mirror neurons are unlikely to be driven by associative learning alone, but, rather, to be a consequence of a combination of evolutionary, biological, developmental, social-cognitive, and experience-based influences. Indeed, we speculate that the MNS is not functionally fixed, but rather a currently evolving, flexible, semi-modular neural network that interacts with multiple other neural systems, including the motor and social-motivation systems (Oberman et al. 2008). The functioning of such a system at any point in development should be viewed as a snapshot of a dynamic system that is constantly modulated by these influences and interactions with other systems (Johnson 2011; Johnson et al. 2002). Environmental and biological influences unfold simultaneously and interactively, not separately and sequentially, and their relative roles can only be disentangled with careful measurement and calculation (Dobkins et al. 2009; Smit et al. 2012). Cook and colleagues attack theories that argue for the evolution of the MNS based upon its proposed role in action understanding (Rizzolatti & Fadiga 1998; Rizzolatti et al. 1996), but we believe that the theory proposed by Cook et al. arguing that associative learning mechanisms alone can account for the origins and development of the MNS is equally as unlikely. Both models ignore the reciprocal relationships between evolutionarily adaptive psychological mechanisms and the lower-level biological mechanisms that are required for their existence.

Testing key predictions of the associative account of mirror neurons in humans using multivariate pattern analysis

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Abstract: Cook et al. overstate the evidence supporting their associative account of mirror neurons in humans: most studies do not address a key property, action-specificity that generalizes across the visual and motor domains. Multivariate pattern analysis (MVPA) of neuroimaging data can address this concern, and we illustrate how MVPA can be used to test key predictions of their account.

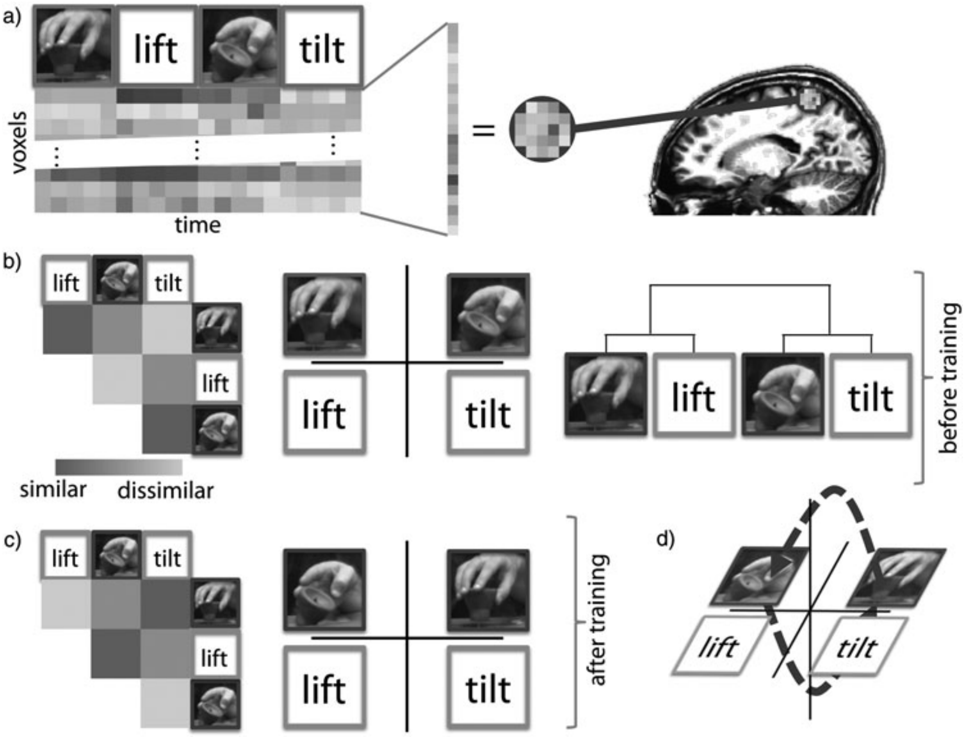

Figure 1 (Oosterhof). Hypothetical example illustrating neural effects of visuomotor "counter-mirror" training. (a) Neural responses are measured in a region of interest using fMRI while participants observe (red boxes) or are instructed to perform (green boxes) two actions (lifting or tilting a cup-shaped object). Each trial is associated with a spatially distributed pattern of responses over voxels. (b) Before training, congruent actions across the visual and motor domain are represented more similarly, as illustrated by a similarity matrix (higher pattern similarity indicated in dark orange; left), multi-dimensional scaling in two dimensions (more similar patterns depicted nearer in space; centre), and a dendrogram ("leaves" representing patterns are connected by shorter paths if patterns are more similar; right). (c) After counter-mirror training, where participants learn to lift (or tilt) the object after observing a tilt (or lift, respectively) action, the neural similarity structure might have changed, where non-matching actions are represented similarly across the visual and motor domain. (d) When visualized using multi-dimensional scaling, here in three dimensions, the similarity "trajectories" (dark purple arrows) during learning and unlearning of the associations can be visualized, allowing for assessment of the temporal dynamics of changes in visuomotor associations. A color version of this image is available at http://dx.doi.org/10.1017/S0140525X13002434.

The discovery of mirror neurons (MNs) in macaques has undoubtedly had a major impact on the field of social neuroscience by providing a potential mechanism for associating visual and motor aspects of actions, which could be a core component in action understanding. The timely article by Cook et al. addresses one of the fundamental questions on this topic, namely, how such visuomotor associations emerge in the first place.

While we agree with much in Cook et al.'s article, our concern is that some of the interpretations and conclusions the authors draw about mirror neurons in humans generally, and in favour of the associative account specifically, risk being overstated based on the evidence reviewed. Specifically, most inferences (but see Mukamel et al. 2010) about MNs in humans are based on a combination of proposed homologies between macaques and humans, and on studies employing less invasive methods to study the brain, including transcranial magnetic stimulation, magneto- and electroencephalography, and most notably, functional magnetic resonance imaging (fMRI). The former approach assumes a mapping between brain regions across monkey and human species, but this homology is imperfect (Sereno & Tootell 2005). The latter ostensibly provides a wealth of evidence for human MNs; for example, numerous fMRI studies have shown common areas demonstrating an increased response during observation and execution of actions (compared to a baseline condition), but such effects could be explained by task engagement or attention processes (Oosterhof et al. 2013).

In contrast, we would argue that stricter requirements are needed to infer that a brain region may contain mirror neurons. In macaques, MNs have been shown to code specific, individual manual actions that generalize across the visual and motor domains. In contrast, most fMRI studies with humans do not test for this key property: action-specificity. To demonstrate action-specificity in the human brain, the same action, whether observed or executed, should elicit more similar neural responses than dissimilar actions (Oosterhof et al. 2013).

In our view, the most promising approach addressing this limitation is the application of multivariate pattern analysis (Edelman et al. 1998; Haxby et al. 2001; Haynes & Rees 2005; Norman et al. 2006), which considers neural responses across a group of voxels. The logic behind this method is that the spatially distributed pattern, across voxels, of a specific observed (or executed) action should be more similar to the pattern associated with executing (or observing, respectively) the same action than a different action. Although fMRI cannot be used to measure individual neurons, MVPA complements single-cell recording approaches by considering spatially distributed responses at a system level. Importantly, this sensitive approach allows for dissociating responses of spatially overlapping neural populations (Peelen & Downing 2007).

Relevant to the topic of the present article, the human mirror system, recent MVPA studies have provided evidence for cross-modal action-specific representations of manual actions in anterior parietal and lateral occipito-temporal cortex (Oosterhof et al. 2010; 2012). These findings, together with evidence from single-cell recordings in humans (Mukamel et al. 2010), indicate that regions consistent with MN properties can also be found outside the canonical fronto-parietal network, consistent with Cook et al.'s associative account.

Particularly relevant for the target article is that MVPA – in particular, representational similarity analysis (RSA; Kriegeskorte 2009; Kriegeskorte et al. 2008) – can be used to test key predictions, at a neural population level, of the associative account of the human mirror system. Cook et al. write "the properties of MNs can be changed in radical ways by relatively brief periods of sensorimotor experience" (sect. 3.4, para. 4), based on evidence from several behavioural studies showing that priming effects (e.g., automatic imitation effects) can be reduced or even reversed after counter-mirror training. Although we agree that these findings are interesting and consistent with an associative learning account, we do not believe that results from such studies alone provide strong evidence to support the authors' claim, as the neural correlates of these effects were not measured in fine detail. We believe that MVPA enables such detailed measurement and can be used to characterize where and when such changes occur at a neural population level.

To illustrate this, we provide a hypothetical example based on associative account predictions brought forward by Cook et al. of how counter-mirror learning can be adapted to study the changes in neural representations using MVPA (cf. Catmur et al. 2007; Press et al. 2007). Patterns of responses can be measured in the brain when participants observe or execute two different manual actions (Fig. 1a). Before training, observing and executing actions congruent across the visual and motor domain are represented similarly (Fig. 1b). After counter-mirror training, where actions incongruent across the visual and motor domain are associated with each other, this situation is reversed: manual movements incongruent across the visual and motor domain might now be represented similarly (Fig. 1c).

The application of MVPA provides other advantages. First, unlike TMS studies, MVPA does not require defining regions of interest a priori through the use of "searchlight" analyses (Kriegeskorte et al. 2006; Oosterhof et al. 2010; 2011). Second, MVPA enables the study of temporal dynamics of learning and unlearning new visuomotor associations of specific actions across the brain (Fig. 1d). Third, MVPA can be used to test generalization to other experimental factors such as viewpoint and different grasps. Fourth, MVPA allows for comparisons of neural representations across species (macaques and humans) and brain measurement methods (fMRI and neurophysiology), allowing for more detailed comparisons of (dis)similarities across species (Kriegeskorte 2009).

In conclusion, we agree that the existing evidence of a human mirror system is compatible with an associative learning account. However, we argue that the current evidence is not strong enough to fully support all the claims made by Cook et al. in the target article. We believe that the application of MVPA, in particular RSA and information mapping techniques, offers a promising avenue to more fully characterize the human mirror system, and thus provide evidence to support or falsify the associative learning hypothesis. We predict that these methods will be crucial for future fMRI studies if they are to advance our understanding of the human mirror system.

The mirror system in human and nonhuman primates

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Abstract: The description of the mirror neuron system provided by Cook et al. is incomplete for the macaque, and incorrect for humans. This is relevant to exaptation versus associative learning as the underlying mechanism generating mirror neurons, and to the sensorimotor learning as evidence for the authors' viewpoint. The proposed additional testing of the mirror system in rodents is unrealistic.

Cook et al., in the section on mirror neuron basics (sect. 2), provide an incomplete description of the mirror system in the macaque, ignoring some recent developments. Using monkey fMRI, Nelissen et al. (2005) visualized the frontal regions involved in action observation. This study is extremely important as it makes a point which has escaped most researchers in the human imaging field: In order to activate F5c, where mirror neurons (MNs) are housed, in fMRI, the actor has to be in view in the videos. Simply showing an isolated hand preforming an action is insufficient. Cook et al. also ignore the subsequent study (Nelissen et al. 2011), combining fMRI experiments with anatomical tracer studies. This later study revealed that the visual signals conveying action observation travel from the superior temporal sulcus (STS) to F5c over two parietal way stations: cytoarchitectonic PFG and the anterior intraparietal (AIP) area. Thus, this report indicates that, contrary to the assertion in section 3.2 (para. 2), STS neurons need not be linked to premotor neurons for the MNs to be generated, but rather, that visual and motor signals have to be associated in only a few parietal areas: PFG and AIP. This latter area, while not a classical mirror area, also houses MNs, according to fMRI (Nelissen et al. 2011) and unpublished single-cell results from studies conducted in Parma and Japan. Although this restricted association in parietal cortex is compatible with a genetic/evolutionary as well as an associative learning origin, it suggests that a domain-general mechanism such as associative learning may not be needed and that a more specialized hybrid mechanism, such as exaptation (sect. 8.2), might be more relevant than Cook et al. indicate. The sentence "there is no evidence that the sensorimotor learning involved in MN development is modified or constrained relative to the associative learning that occurs in standard conditioning experiments" (sect. 8.2, para. 1) may thus require serious revision.

The other development regarding monkeys concern two recent studies from the Lemon group showing how the mirror signal is "extinguished" by the addition of suppressed MNs among cortico-spinal neurons in F5 or M1 (Kraskov et al. 2009; Vigneswaran et al. 2013). Any account of how mirror neurons acquire their intriguing properties should take into account this transformation from purely excitatory to mixed excitatory/suppressed populations of MNs along the motor hierarchy. This point is again unaddressed, and it may well be that a genetic or hybrid mechanism can account for this range of responses more easily than an associative learning process. The data from monkeys concerning suppressed MNs also bear upon the interpretation of the Mukamel et al. (2010) data, suggesting that these human recordings may have been made in areas situated at a level of the motor hierarchy other than the planning level of the classical mirror areas (PFG/AIP and F5c).

In the section discussing mirror neuron basics, the authors also claim that the human mirror system is known. Ironically, the only mirror area for which the homology is known is the least documented in monkeys: AIP. There is indeed excellent evidence for the existence of this homologue, a combination of dorsal intraparietal sulcus anterior (DIPSA) and the so-called putative human AIP (phAIP) in anterior IPS (Durand et al. 2009). In contrast, most evidence for human areas cited by Cook et al. is weak or inexistent. Overlapping activations for action observation and execution are by no means proof for the existence of MNs, as the voxels contain thousands of neurons (Dinstein et al. 2008). Similarly, the repetition suppression studies have yielded contradictory results, unsurprisingly so, given that repetition suppression overestimates selectivity (Sawamura et al. 2006) and visual responses of premotor neurons do not adapt (Caggiano et al. 2013). That imitation constitutes an argument supporting the existence of a mirror system in humans is debatable, and that the inferior frontal gyrus (IFG) comprises a classical mirror area is unlikely, since it is not activated by action observation in well-controlled studies (Abdollahi et al. 2013; Jastorff et al. 2010). Finally, the direct evidence of Mukamel et al. (2010) is also very disputable, because for technical reasons the so-called mirror neurons were, unlike the monkey MNs, recorded outside the areas involved in the planning of grasping. Indeed, so far it has been possible to record single neurons only in the medial regions of the hemispheres of epileptic patients undergoing pre-surgical physiological evaluation, preventing any exploration of anterior IPS or ventral premotor cortex. Given the recent evidence that medial fronto-parietal areas are involved in the observation of climbing and locomotion (Abdollahi et al. 2013), it is likely that Mukamel et al. (2010) tested neurons with far from optimal actions. The absence of clear evidence for human MNs and areas reduces the value of all the sensorimotor learning experiments that are cited in support of the authors' viewpoint (sects. 7.1 & 7.2), as they have been performed only in humans.

Finally, Cook et al. appear relatively uninformed about the value of rodent experiments, which they propose as an alternative to monkey studies (sect. 9.1, experimentation, para. 3). Even if rats do grasp with their forepaws, this behavior differs markedly from human grasping, reducing the relevance of proposed experiments for understanding the origin of human MNs. In general, given the immense difference in cortical surface area between the two species (for mice, the ratio is 1/1,000 [Rakic 2009], compared to 1/9.2 for macaque [Van Essen et al. 2012]), the value of rodents as a model for the human brain may be overrated. Given the importance of the the posterior parietal cortex (PPC) for an extended mirror system, suggested by recent studies (Abdollahi et al. 2013; Filimon et al. 2007), its limited development in rodents might further devaluate the rodent model in the present context. In fact, it may be the case that the most dorsal parts of the human superior parietal lobule (SPL) are evolutionarily the oldest parts of PPC (which we may share with rodents), whereas the more ventral regions of the inferior parietal lobule (IPL) are the most evolutionarily novel (Mantini et al. 2013). Given the limitations of the rodent model, lesion or reversible inactivation experiments in monkeys would be more relevant than asserted by Cook et al.

Contagious behavior: An alternative approach to mirror-like phenomena

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Abstract: Contagious behaviors such as yawning and itching/scratching have mirror-like properties and clearly defined stimulus and motor parameters; they are also relatively easy to study and should be part of the debate about mirror neurons and the neurological mechanisms of social behavior. The broadly tuned, multimodal stimuli of contagious behavior challenge present accounts of mirror mechanisms that focus on specific, mirrored acts.

The range of mirror-like processes under investigation should be broadened to include contagious behavior, a class of social behavior that is largely neglected by mirror neuron (MN) researchers. The study of contagious behavior offers the highly desirable properties of identifiable stimuli and motor responses. In contrast, mirror neurons (MNs) seem lost in thought, like disembodied computers not hooked up to printers – full of potential, but short on demonstrated function. Once the relation between the brain's inputs and outputs are defined, we will be well on the way to understanding the mechanism of mirror-like behavior. The study of contagious behavior also offers an economic incentive; it can be a low-budget affair that requires only behavioral observation, not the pricey technology of neurophysiology labs or fMRI machines.

Upon first hearing about MNs, students often ask about their involvement in contagious yawning, laughter, and the like. They are surprised to learn that what seems obvious to amateurs is often ignored by professionals, including the authors of the target article. My present comments focus on yawning and itching/scratching, representative contagious behaviors. These and other contagious acts – laughing, coughing, nausea/vomiting, and vocal crying – are reviewed and contrasted in my recent book, *Curious Behavior: Yawning, Laughing, Hiccupping, and Beyond* (Provine 2012).

Yawns are propagated, being passed from one person to another, in a behavioral chain reaction. This mindless connectedness involves social behavior of the most primal sort. When you yawn contagiously, you do not consciously decide to imitate the observed yawn – it happens automatically. The rippling of yawns through a group is heritable, neurologically programmed social behavior that synchronizes the physiological and behavioral state of the group. Details about the mechanism of this contagion, its evolution, and its development are still being worked out. However, it is clear that the motor act of yawning is phylogenetically ancient, characteristic of most vertebrates, and develops early in prenatal life. Contagious yawning, in contrast, is phylogenetically more modern, confined in various degrees to great apes and, perhaps, dogs and other highly social mammals, and develops several years after birth (see reviews in Provine 2005; 2012; Walusinski 2010).

One of the most striking features of adult human yawning is its extreme contagiousness. Almost anything associated with yawning can be a vector for the contagious response, including viewing yawning faces, hearing yawn-related sighs, thinking about yawning, or even reading about yawning, as you are now doing. Given the broad, multimodal spectrum of yawn stimuli, the involvement of a single, narrowly tuned detector or MN sensitive to a specific aspect of a yawning person seems unlikely. Instead, contagion is probably mediated by a variety of detectors of yawn-related stimuli, each capable of producing a yawn. In the pre-MN research era, I proposed that an ethological releasing stimulus was responsible for triggering the stereotyped motor act of contagious yawning (Provine 1986; 1996). Although the stereotypy of yawning is unchallenged, the detector activated by the releasing stimulus is much more broadly tuned than I had anticipated.

Itch and associated scratching, like yawning, are highly infectious, and the stimulus vector for their contagion is broadly tuned and multimodal (Provine 2012). Although eczema, contact dermatitis, and other skin irritation can trigger itch, so can such abstract stimuli as hearing a lecture about itch, viewing itch-causing parasites, or seeing someone else scratching, especially among individuals with pre-existing dermatological conditions (Holle et al. 2012). The itch/scratch complex provides intriguing research opportunities because it has more potential response variability than stereotyped behaviors such as yawning. For example, Ward et al. (2013) investigated how the behavior of a model influences the specific site of itchiness and scratching of an observer. When participants in their study viewed a movie depicting scratching, they were more likely to scratch themselves, but the hand that they used to scratch (left or right) and the site of scratching did not necessarily match the model. Although the model scratched only the arms and chest, the majority of participants viewing the video directed their scratching upward toward their face and hair. The authors concluded, "contagious itchiness may be more driven by vicarious perception of the feeling state (itchiness/unpleasantness) than contagion of the motor act or bodily target" (Ward et al. 2013, p. 2).

Many questions about contagious behavior and MNs remain. Building on the above results for contagious yawning and itching/scratching, should we conclude that the sufficiency of a variety of multimodal stimulus triggers is evidence against the behavioral involvement of MNs, instances of broadly tuned or multiple MNs, or examples of a different class of mirror-like acts that do not involve MNs? Do environmental contingencies influence the tuning of stimulus triggers or MNs, possibly contributing to the acquisition of multimodality? And what about other contagious behaviors? To what extent does the contagiousness of nausea/vomiting, coughing (but not sneezing), vocal crying, laughing, and yawning involve shared feeling states or another, more specific trigger (Provine 2012)? The answers to these questions may come from developmental, comparative, and perceptual studies that are now underway. Whatever the outcome, such research will broaden our understanding of the neurological basis of sociality.

Experiential effects on mirror systems and social learning: Implications for social intelligence

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Abstract: Investigations of biases and experiential effects on social learning, social information use, and mirror systems can usefully inform one another. Unconstrained learning is predicted to shape mirror systems when the optimal response to an observed act varies, but constraints may emerge when immediate error-free responses are required and evolutionary or developmental history reliably predicts the optimal response. Given the power of associative learning, such constraints may be rare.

Cook et al. present a compelling case that mirror neurons (MNs) have a developmental origin in associative learning. Moreover, they legitimately argue that empirical testing is required to determine whether MNs and mirror systems have evolutionary origins as adaptive specializations, echoing criticism of adaptationist "just-so" stories in other fields (Pigliucci & Kaplan 2000). Here, I discuss whether work on mirror systems can be informed by, and inform, the fields of social information use and social learning. I leave aside discussion of communicative signals, by definition adaptive specializations.

Many animals use social information (information provided by other individuals) and social learning (learning from this information; Reader & Biro 2010). Debate over mirror system origin and function can be viewed as part of a broader debate over the origins of a reliance on social cues and of the mechanisms underlying social information use, a debate Heyes (1994; 2012a; 2012c) has also championed. Besides the fact that mirror systems utilize social information, there are numerous points of intersection between the two research fields. Mirror systems have been proposed to underlie various forms of social learning, including stimulus enhancement, emulation, and imitation learning (Byrne 2002; Keysers & Perrett 2004), and such systems could potentially associate personal and conspecific location and thus also underlie local enhancement. Social learning propensities, biases, and processes have been proposed to be products of general learning processes, in a similar fashion to the Cook et al. proposal (Church 1957; Heyes 1994; 2012c; Keysers & Perrett 2004; Laland & Bateson 2001; Leadbeater & Chittka 2007; Miller & Dollard 1941). Furthermore, like mirror systems, the assumption that social learning is an adaptive specialization has been questioned, as has whether any such adaptive specialization would involve input systems rather than the learning mechanisms themselves (Caldwell & Whiten 2002; Heyes 2012c; Lefebvre & Giraldeau 1996; Reader et al. 2011). These points of intersection suggest the two fields may usefully inform each other.

Experiential effects on the propensity to use and learn from social information have been demonstrated in several species (Kendal et al. 2009), supporting the idea that responses to social cues can be learned. However, flexibility alone is insufficient to demonstrate that the value and meaning of social cues are acquired by learning, since flexibility could be genetically encoded. For example, individuals could follow evolved unlearned rules-of-thumb of when, where, and how to employ social information (Rendell et al. 2011). Direct manipulation of the benefits of social information provides superior evidence for learned biases in social information use. For example, sparrows raised with an artificial parent that had reliably indicated food were more likely to approach feeding conspecifics than if the parent had not reliably indicated food (Katsnelson et al. 2008). Similarly, in finches manipulation of the net benefits of attending to others resulted in changes in individual tendencies to use social information, with lags that suggested the birds were learning the optimal response on the basis of received rewards (Mottley & Giraldeau 2000). Perhaps the most compelling current evidence for associative learning shaping social information use involves the acquisition of matching and nonmatching responses during social learning. Dawson et al. (2013) trained bumblebees in a feeding array where conspecific "demonstrators" indicated either the presence of sweet sucrose or bitter quinine. Bees thus readily learned to approach or avoid conspecifics. Later, the bees observed demonstrators at one color of flower in a two-color array. Bees previously rewarded for approaching conspecifics were more likely to choose the same color as demonstrators, whereas the reverse was true in the quinine-trained bees. Such data strikingly parallel mirror and counter-mirror effects observed in budgerigars and dogs (Mui et al. 2008; Range et al. 2011).

Although these examples provide evidence that experience can shape reliance on social cues, interpreting all individual and between-species variation in social information use as the result of prior learning would risk telling *associationist* "just-so" stories. Studies of the evolution of learning provide useful insights into when an evolutionary account may explain variation in social information use (e.g., Boyd & Richerson 1985; Dunlap & Stephens 2009; Johnston 1982). When opportunities for learning are limited, learning or errors are costly, or the optimal response to a social cue is highly predictable, natural selection could shape genetically encoded predispositions to respond in a certain manner to particular social cues. Similarly, if experiences in early life predict later payoffs of social information, and there are costs to learning, early life experience may result in fixed social learning tendencies during adulthood (Lindeyer et al. 2013).

There are several instances where responses to social cues appear fixed. Cases such as humans copying the most successful individual even when this is suboptimal (Offerman & Schotter 2009), birds ignoring reliable asocial information to copy conspecifics (Rieucau & Giraldeau 2009), and the aforementioned counter-mirror effects taking longer to develop than mirror effects could all be the result of the extensive social experience individuals have prior to testing. However, other examples are more difficult to explain in terms of experiential effects. For example, several avian species use conspecific and heterospecific nesting or breeding success during their own habitat selection without clear opportunities to learn to use these cues (although experience can shape later choices; Morand-Ferron et al. 2010). Restrictions on the stimuli monkeys and warblers socially learn about are also consistent with an adaptive specialization account (Davies & Welbergen 2009; Mineka & Cook 1988, but see Heyes 1994). Such predispositions would reduce errors during social learning, rather like predispositions to attend to conspecifics protect young birds from errors during filial imprinting (Horn 2004).

Given that predispositions are expected for certain forms of social information use, the unconstrained flexibility of mirror systems that Cook et al. note raises two possibilities, assuming that mirror system efficiency is a determinant of fitness. Either (1) mirror system flexibility is vital to their adaptive function, suggesting that social cues have variable meanings that must be learned, or (2) evolved alternatives to associatively acquired mirror systems are constrained, perhaps by their cost. The broad affordances of associative learning may mean that beneficial mirror systems come virtually “for free,” reducing the likelihood of alternate evolved solutions.

If mirror systems and social learning tendencies are the products of general learning processes, the evolution of social and general intelligence may be closely entwined (Brown & Brüne 2012; Dunbar & Shultz 2007; Reader et al. 2011). Furthermore, because associative learning and social information use are phylogenetically widespread, mirror systems could be studied in species such as insects, where evolutionary studies could examine the related but separate questions of adaptiveness and adaptive specialization. Particularly informative would be studies of species where deviating from group behavior carries strong costs, such as certain fish (Bates & Chappell 2002). Studies of links between mirror system efficacy and behavioral competence are essential, ideally by measuring costs and benefits for fitness in “real-world” group situations to establish when individuals out-compete or interact more effectively with others. Cook et al. present a parsimonious model that inspires broad application and testing of mirror system concepts.

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Confounding the origin and function of mirror neurons

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Abstract: Cook et al. argue that mirror neurons originate in sensorimotor associative learning and that their function is determined by their origin. Both these claims are hard to accept. It is here suggested that a major role in the origin of the mirror mechanism is played by top-down connections rather than by associative learning.

The characterizing feature of the primary visual cortex of primates is the presence of neurons sensitive to stimulus orientation. Regardless of whether the orientation-sensitive neurons are determined genetically or acquired by experience, or both, they are at the basis of the functional organization of primates’ visual system (Hubel & Wiesel 1998; Marr 1982). The same is true for mirror neurons (MNs). Regardless of whether their properties are determined genetically, acquired by experience, or both, they represent the neural substrate of a fundamental mechanism that transforms sensory information into a motor format (the mirror mechanism). The functions of the mirror mechanism vary from action understanding, to imitation, to empathy, and even, in birds, to song recognition (Rizzolatti & Sinigaglia 2010). Their function depends on their anatomical location. Thus, contrary to the view advanced in the present target article, the problem of how MNs originate is utterly irrelevant as far as their *function* is concerned. It is an interesting problem, but it has little to do with the function of the mirror mechanism.

The claim that mirror neurons are just “another type” of association neurons misses their characterizing, unique property, which is that of giving a motor format to sensory stimuli. This misunderstanding can be also found in an interesting paper on mirror neurons by Damasio and Meyer (2008). They claimed that the parieto-frontal mirror neurons are neural ensembles included in higher-order association areas called “non-local convergence-divergence zones” that collect information from lower-order visual, auditory, and somatosensory association areas, and signal back to those areas. Action understanding depends on the activation of this network. This proposal had the merit of highlighting the role of top-down connections in action understanding. It overlooked, however, as done in the present target article, the fact that parieto-frontal mirror neurons are *motor* neurons. When MNs discharge, they “ignite” motor schemata similar to those endogenously activated during motor imagery and, within limits, during actual motor act execution. In other words, *my* motor schemata are activated during the observation of similar motor schemata of *others*. This provides a neurophysiological account of the mechanism underlying action understanding “from inside” (Rizzolatti & Sinigaglia 2010): “a *first person process*, where the self feels like an *actor*, rather than a *spectator*” (Jeannerod 1997, p. 95; emphasis added). This appears to be a function that only the mirror mechanism is able to mediate.

Mirror neurons have top-down effects (Damasio & Meyer 2008, see also Kilner et al. 2007b). In other words, following MN activation, signals go not only toward other motor areas, but also backwards to lower-order visual, auditory, and somatosensory areas. This top-down activation *binds* the understanding of what a person is doing (e.g., grasping), encoded in the motor cortex, with the visual details of that action. An interesting possibility is that the top-down mechanism also has another function, which is: to be the neural substrate of a learning mechanism that starts from motor centers rather than from the environment. An elegant experiment by Van Elk et al. (2008) illustrates this point well. EEG was recorded during observation of action videos in 14- to 16-month old infants. Desynchronization of the movements-related rhythms (e.g., mu rhythms) was found for the observation of crawling, but not for the observation of walking. Furthermore, the size of the effect was strongly related to the infant’s own crawling experience. The authors concluded that experience of one’s own actions is closely related to how actions of others are perceived.

Cook et al. dismiss the experiments showing that human neonates are able to copy actions done by others (Meltzoff & Moore 1977). Their argument is the following. The best-documented imitative action is tongue protrusion, but even this act “lacks the specificity … of imitation” (target article, sect. 6.1, para. 1). In addition, this behavior can also be elicited when infants observe a mechanical “tongue” or disembodied mouth. It is hard for me to conceive how the mirror mechanism of a neonate might have a neurological maturity such as to provide a precise copy of tongue protrusion. Occasionally this could happen, but the potential act encoded in a newborn must be, for maturational reasons, just “protruding.” Note also that grasping MNs generalize across the observed actions having the same goal. For example, in both monkeys and humans the observation of a grasping robot arm is effective in triggering mirror neurons (Gazzola et al. 2007, Peeters et al. 2009; Rochat et al. 2010), exactly as does the “mechanical tongue” in the example mentioned above. My hypothesis is that tongue protrusion in newborns is an effect mediated by a mirror mechanism similar to that described for crawling by Van Elk et al. (2008). Action comes first and links motor centers with sensory centers. Once these connections are established (or reinforced), the external information can flow in a forward direction, from stimuli to actions. Hence the imitation.

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The emergence of mirror-like response properties from domain-general principles in vision and audition

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Abstract: Like Cook et al., we suggest that mirror neurons are a fascinating product of cross-modal learning. As predicted by an associative account, responses in motor regions are observed for novel and/or abstract visual stimuli such as point-light and android movements. Domain-specific mirror responses also emerge as a function of audiomotor expertise that is slowly acquired over years of intensive training.

The discovery of mirror neurons (MNs) proffered a tempting solution for the difficult theoretical and neurocomputational problem of linking self and other (Barresi & Moore 1996). MNs were regarded in some quarters as a neuroscientific silver bullet, one providing the evolutionary and neural basis of social cognition, empathy, theory of mind, language, and civilization. After this period of MN-Mania, inevitably there has been a fierce counter-MN-reformation, with some acolytes vociferously denying the mere existence of MNs. By pleasant contrast to either extreme, the target article offers a sober and reasoned framework for thinking about the origins and emergence of the Mirror Neuron System (MNS). Here, we offer additional evidence that may be explained with an associative MN account, but are problematic to account for via specific innate mechanisms. First, the human MNS seems capable of abstraction and generalization, as evidenced by its involvement in processing novel visual stimuli that have not existed through evolution and are thus hard to square with built-in, genetically coded MNs. Second, a straightforward associative model of early speech production accurately predicts the existence of MN-like responses for speech; and domain-specific mirror-like responses emerge in response to intensive training in producing and perceiving instrumental sounds.

Abstraction and selective tuning for conspecifics (lack thereof). In both correlational and causal studies, human MNS has been linked to the processing of point-light biological motion stimuli, which depict actions through motion cues (Gilaie-Dotan et al. 2013; Saygin et al. 2004; van Kemenade et al. 2012). In contrast, macaque MNs do not even respond to videos of actions (Ferrari et al. 2003), except possibly after extensive training (Caggiano et al. 2011). Although differences between humans and nonhuman primates could also have cross-methodology sources (e.g., firing rates, vs. LFPs, vs. BOLD fMRI), contrasting the ease with which human observers process point-light stimuli, with the daunting undertaking of getting nonhuman primates to perform even the simplest tasks with them (Vangeneugden et al. 2009), it appears there may be cross-species differences. The ability of the human MNS to extrapolate to such abstract representations is difficult to explain with a specific genetic adaptation, but fits rather well as a natural by-product of the human ability to effectively use abstractions in associative learning (cf. language, see next), itself an emergent outcome of domain-general aspects of primate evolution.

Consider also whether the MNS is adapted specifically for conspecifics. Although one study has claimed the human MNS is "mirror only for other humans," further studies have reported that human MNS also responds to robot actions (e.g., Cross et al. 2012; Gazzola et al. 2007; Oberman et al. 2007), as do subdivisions of F5 in the macaque (Nelissen et al. 2005). EEG and fMRI studies involving highly human-like androids indicate that the human MNS is not straightforwardly tuned to human motion or human appearance (Saygin et al. 2012; Urgen et al. 2013). Overall, in terms of response properties, it appears that MNS is not highly selective to conspecifics, or even living things. Such data, and more generally, the oft-noted insensitivity of MNs to perceptual factors, are much more consistent with an adaptationist account than a genetic account of MNs. For why should the brain have a specially evolved system for understanding the actions of others that is also responsive to stimuli that did not exist in the natural environment until very recently, such as twentieth century point-light displays and twenty-first century Japanese androids?

Notes from speech and language. Language has been one of the most paradigmatic areas in which nature versus nurture and domain-specific versus domain-general debates took place (Elman et al. 1996). We have long held that language is best viewed as a complex skill that emerges from adaptations of domain-general sensorimotor neural systems (Dick et al. 2004; 2007; Saygin et al. 2003), nicely summarized by the late Elizabeth Bates as "language is a new machine built out of old parts" (Bates et al. 1988).

The field of speech and language has lived through decades of the "poverty of the stimulus" argument regarding the purported necessity for innately specified, special mechanisms and representations (see commentary by Holt & Lotto, this *BBS* issue). But if anything, the emerging consensus is that language has parasitized a remarkably plastic yet determinedly primate brain that is organized along sensorimotor and not domain-specific lines. We suggest that the continuing saga of mirror neurons may follow a similar dramatic arc.

The domain of speech provides a compelling example of how MNs might develop in a simple "fire together wire together" learning mechanism with simple (yet realistic) anatomical constraints. In a computational model of infant babbling, Westermann and Miranda (2002; 2004) showed that a network that produces babble (permutations of muscle movement combinations), and simultaneously "hears" its acoustical output, will spontaneously form MNs for speech. Once the computational baby has babbled sufficiently, when it then hears a vowel, the auditory representation map of this vowel will activate the motor representation that has been linked up to it via Hebbian learning.

A strong prediction of this early associative model of the emergence of MNs for speech was found in an fMRI study: Enhanced activation for passively heard syllables was observed in a premotor region that was strongly activated during production of the same syllables (Wilson et al. 2004). Although this finding was taken by some as confirmation of the motor theory of speech perception, subsequent studies have shown that mirror-like responses can emerge in motor regions as a product of more general audiomotor expertise, as would be predicted by associative accounts. When listening to dramatic speech and solo violin playing, professional actors show considerably more activation for speech in premotor areas, including that reported in Wilson et al. (2004). Conversely, violinists listening to the same stimuli show the opposite pattern – much greater activation for listening to violin excerpts than for speech (Dick et al. 2011).

Overall, mirror-like responses, rather than being specific genetic adaptations, are more likely to be evidence for the remarkable functional plasticity that allows primates – especially humans – to learn and master complex contingencies via domain-general mechanisms.

Neonatal imitation and an epigenetic account of mirror neuron development

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Abstract: Neonatal imitation should not exclusively be considered at the population-level; instead, we propose that inconsistent findings regarding its occurrence result from important individual differences in imitative responses. We also highlight what we consider to be a false dichotomy of genetic versus learning accounts of the development of mirror neurons, and instead suggest a more parsimonious epigenetic perspective.

A number of lines of evidence support the notion that neonatal imitation is a real phenomenon. Although we realize our commentary is unlikely to settle this debate, we believe that Cook et al. fail to consider the importance of individual differences in neonatal imitation. Neonatal imitation has been demonstrated using more than one gesture (which is critical because it shows specificity in matching) in more than two-dozen studies. In fact, recent work – not reported by Cook et al. – refutes the notion that neonatal imitation is simply an arousal effect (Nagy et al. 2013). Similarly, neonatal imitation is not a reflex-like behavior, as newborns appear to remember, after a delay, both the particular gesture (Paukner et al. 2011) and person (Simpson et al. 2013) with whom they interacted and initiate interactions. Moreover, nursery infant monkeys, who have no exposure to contingent behaviors from caregivers, and therefore have no opportunities to learn to imitate, still show neonatal imitation (Ferrari et al. 2006). Given that neonatal imitation occurs in a variety of primates, it may be a shared behavioral adaptation (Paukner et al. 2013a).

Critically, neonatal imitation may reflect activity of the nascent mirror neuron system (MNS), as it is associated with suppression of specific electroencephalogram (EEG) frequency band activity (Ferrari et al. 2012). This work is consistent with a recent study based on simultaneous EEG and functional magnetic resonance imaging (fMRI) in human adults showing activity of the parietal and premotor/motor cortex (i.e., mirror neuron areas) linked to EEG suppression within the alpha band (i.e., mu rhythm) (Arnstein et al. 2011). And, there is EEG evidence of a functioning MNS from birth in neonate macaques that lack any early face-to-face contingent experience with social partners (Ferrari et al. 2012).

Inconsistent neonatal imitation findings (e.g., Cook et al.'s Fig. 2) may be the result of variation among infants in imitation, indicating significant individual differences in infants' abilities to learn contingent behavior, upon which critical cognitive and social skills are based (Reeb-Sutherland et al. 2012). In support of this idea, recent findings reveal that individual differences in neonatal imitation in monkeys are correlated with visual attention to social partners (Simpson et al. 2014; similar findings in humans: Heimann 1989), person recognition (Simpson et al. 2013), face viewing patterns (Paukner et al. 2013b; under review), deferred imitation (Paukner et al. 2011), and goal-directed movement (Ferrari et al. 2009c). Therefore, rather than dismissing neonatal imitation – as Cook et al. appear to do – we argue that one should focus on the causes and consequences of individual differences in neonatal imitation through longitudinal (Suddendorf et al. 2012) and comparative (de Waal & Ferrari 2010) studies of newborns. We suggest that it would be insightful to examine neonatal imitation in infants who have siblings with autism spectrum disorder, a high-risk population (e.g., Chawarska et al. 2013), or examine effects of early experiences on neonatal imitation, including behavioral (e.g., Sanefuji & Ohgami 2013) and pharmacological (e.g., Tachibana et al. 2013) interventions.

In addition to questioning their view of neonatal imitation, we, like others (e.g., Casile et al. 2011; Del Giudice et al. 2009), believe that Cook et al. are mistaken in opposing genetic and learning views on MNS development. Instead, as with any developmental phenomenon, it is important to consider gene expression in different environments, and in different species, in order to understand how evolution produced predictable, functional, and species-specific phenotypes. Using this approach, we can examine how mechanisms of learning evolved to produce adaptive specializations through epigenetic mechanisms (Domjan & Galef 1983). Epigenetics is the study of changes in gene expression as a consequence of an organism's response to different environmental stimuli; genes can be temporally and spatially regulated, and epigenetics is the study of these reactions and the environmental factors – including the prenatal environment – that influence them. Countless examples emerging from the field of epigenetics demonstrate that genetic and epigenetic inheritance is not indicative of innateness, nor are phylogenetically inherited traits insensitive to experience (e.g., Jensen 2013; Roth 2012). Indeed, epigenetic models now focus on the origins of complex behaviors; we propose that such models should be considered along with associate learning mechanisms in predicting developmental trajectories, within and between species. We agree that it is misleading to think that natural selection selects only specific "good" genes. Instead, natural selection acts on phenotypes, which are the result of complex interactions, including environmental effects on gene expression. Therefore, it is more fruitful to identify epigenetic regulatory factors responsible for the emergence of predictable developmental brain/behavior trajectories, than to search for genes that produce specific phenotypes. For example, in macaque infants, we are now beginning to understand the epigenetic mechanisms that can explain how early social adversity increases the risk of disease and disorder (e.g., Provençal et al. 2012).

We also agree with Cook et al. that learning likely shapes the development of the mirror neuron (MN) network in the brain, but learning occurs differently as a function of individual characteristics and context. Selection pressures operate not only on the final phenotype, but also on the interactions between genes and the environment and the interactions between molecular factors and the environment (Blekhman et al. 2008). It is possible that MNs evolved to support learning of basic functions of sensorimotor recognition of others' behavior, essential, though not specifically an adaptation for, higher-order cognitive functions, as well as sensorimotor learning (Bonini & Ferrari 2011). The interaction of genes and experience through learning can only occur if the basic neural circuitry is there to support such learning. We contend that MNs may provide the scaffolding for these interactions early in life, having themselves been remodeled by epigenetic processes across evolution.

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Authors' Response

Mirror neurons: Tests and testability

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Abstract: Commentators have tended to focus on the conceptual framework of our article, the contrast between genetic and associative accounts of mirror neurons, and to challenge it with additional possibilities rather than empirical data. This makes the empirically focused comments especially valuable. The mirror neuron debate is replete with ideas; what it needs now are system-level theories and careful experiments – tests and testability.

R1. Introduction: Types of challenge

The target article ("Mirror neurons: From origin to function" – henceforth "O2F") called for a new approach to research on mirror neurons (MNs): a shift in priorities from "ideas" to rigorous, theory-based experimentation. Reflecting current priorities, the commentators have offered many more conceptual than empirical challenges; more in principle possibilities than testable hypotheses. In some respects this is disappointing, but it makes the empirically grounded commentaries especially precious; and, since many of the possibilities are very interesting, it does not detract from the liveliness of the discussion.

We will respond to all substantive comments in roughly the order in which the relevant issues arose in O2F. The major exception is section R2, which deals with comments relating to sections 3 and 8 of the target article. Section R3 relates to section 4, R4 to section 5, and R5 to section 6. Breaking the rhythm, section R6 focuses on commentaries that offered convergent evidence in support of the associative account or extensions of our approach, and R7 relates to section 9 of O2F. Those who are quick on their feet will notice that there is no partner for section 7 of O2F, in which we presented experimental evidence in support of the associative account. That is because this evidence has not been challenged. Some commentaries, discussed in section R2, say that it does not show all that we think it shows, but no one has denied that the properties of MNs can be changed radically by sensorimotor experience.

R2. Nature *and* nurture: Five false claims

Perhaps it is human nature to dichotomize nature and nurture (Linquist et al. 2011)! Maybe we humans have such a powerful tendency to split nature and nurture – to think of biological form as a product of internal *or* external factors, genes *or* environment, evolution *or* learning – that we imagine others are doing it even when they are not. Such a cognitive bias would help to explain why many commentators mistook our genetic-associative distinction for a nature-nurture dichotomy. To put the record straight, here are five claims that we did *not* make in O2F because, like the commentators cited in this list, we think these claims are false:

1. Associative learning is sufficient for the development of MNs (**Bertenthal**; **Bonaiuto**; **Giese**; **Oberman, Hubbard, & McCleery** [**Oberman et al.**]).
2. The genetic account assumes that learning does not contribute to the development of MNs (**Behme**; Bertenthal).
3. Genetically inherited traits are insensitive to experience (Bertenthal; **Kilner & Friston**; **Lingnau & Caramazza**; **Martin & Santos**).
4. Genetically inherited traits are insensitive to associative learning (Bertenthal; Bonaiuto; Kilner & Friston; Lingnau & Caramazza; **Newman**).
5. Associative learning cannot be adaptively specialized (Behme; Bertenthal; **Gervais**; Martin & Santos; **Simpson, Fox, Tramacere, & Ferrari** [**Simpson et al.**]).

R2.1. Associative learning is sufficient for the development of MNs

Taken at face value, this claim is so obviously false that no one could imagine it was the thrust of our article. Even when one takes "the development of MNs" to be shorthand for "the development of the matching properties, or mirrorness, of MNs" – as we did throughout O2F – it is clear that the developmental system draws on a multitude of resources in addition to associative learning, starting with basic nutrients and the genetically inherited potential to develop neurons at all. The useful version of the "associative learning is sufficient" claim is laid out by **Bonaiuto**, who suggests that the associative account assumes "every neuron is either directly or indirectly connected with every other neuron in the brain." This is useful because it gives us a new and clearer way of saying: "The associative hypothesis assumes that gene-based natural selection has played a significant background role with respect to the development of MNs; for example, in shaping the anatomy of visual and motor cortex for visual guidance of action" (O2F, sect. 3.2, para. 1). With Bonaiuto's help, we can now rephrase this: The associative hypothesis does *not* assume complete or random connectivity between visual and motor cortex. Rather, it assumes that gene-based natural selection has produced partial connectivity as an adaptation for the development of visual control of actions, not for mirroring. For example, visual areas detecting highly action-relevant properties of objects may have the potential to be more richly or readily connected with premotor cortex than visual areas processing less action-relevant properties of objects. It is also possible that genetic evolution has produced some preferential connectivity between visual areas processing observed action and motor areas. However, the associative account suggests that, if this is the case, these predispositions do not favor mirror over non-mirror or counter-mirror connections. Therefore, the issue that separates the associative account and Bonaiuto's view from the genetic account (e.g., **Fogassi**) is whether the pattern of partial connectivity, or "primary repertoire" (**Kilner & Friston**), was favored by natural selection because it tends to produce sensorimotor neurons that are good for guiding instrumental action or because it produces MNs that are good for action understanding or another social cognitive function.

R2.2. The genetic account assumes that learning does not contribute to the development of MNs

According to **Behme** (see also **Martin & Santos**), our discussion of MN responses to unnatural stimuli – such as plastic crumpling and paper tearing – made clear that, although we *said* that "the genetic hypothesis does not necessarily assume that experience plays a minimal role" (O2F, sect. 3.1, para. 4), the genetic account is *really* a straw man who insists that learning does not contribute to the development of MNs. By reaffirming its basic tenets, **Fogassi**'s commentary confirms that the genetic account is not a straw man. More specifically, we agree with Behme that the mere fact that some MNs respond to unnatural stimuli is problematic only for the starkest version of the genetic account. However, as we emphasized (O2F, sect. 4.1), many MNs do not merely respond, they respond *maximally*, to unnatural stimuli. This is hard to reconcile even with versions of the genetic hypothesis that assign important roles to sensory and/or motor learning, because these assume that links among sensory neurons, or among motor neurons, account for responses to unnatural stimuli. In contrast, maximal responding to unnatural stimuli implies that the learning that produces tool-use and audiovisual MNs is sensorimotor; it connects sensory neurons coding unnatural stimuli directly with motor neurons coding action (Cook 2012).

R2.3. Genetically inherited traits are insensitive to experience

We are grateful to **Kilner & Friston** and **Lingnau & Caramazza** for mentioning some of the classic studies showing unequivocally that genetically inherited traits are sensitive to experience.

R2.4. Genetically inherited traits are insensitive to associative learning

The fourth claim deserves closer scrutiny. Several commentators assumed not only that we are making this claim, but also that, without it, the evidence that sensorimotor learning can radically change MNs does not support the associative over the genetic account (**Bertenthal**; **Bonaiuto**; **Gervais**; **Kilner & Friston**; **Newman**). This misconception is largely our fault. The argument underlying our tests of the associative account has been explained previously (Heyes 2010), but was not made explicit in the target article. To rectify this, here is a short, focused version of the argument: Our training experiments (reviewed in O2F, sect. 7) indicate that (A) counter-mirror sensorimotor experience (e.g., moving an index finger whenever you see little finger movement) reverses the matching properties of MNs, and (B) sensorimotor experience with inanimate objects (e.g., making a fist whenever you see a certain shape) induces MNs to respond to inanimate objects.[1] As predicted by the associative account, effects A and B show that sensorimotor experience perturbs but does not damage MNs: it prevents MNs from selectively encoding similar observed and executed actions, but does not stop them from encoding systematic relations among stimuli and responses. This is hard for the genetic account to accommodate because (1) if a trait is a gene-based adaptation, its development tends not to be perturbed by environmental variations that were present when the trait evolved, and (2) sensorimotor experience of the kind that reverses and induces MN activity is likely to have been present in the period when, according to the genetic account, MNs evolved. Specifically, it is likely that the common ancestors of extant monkeys and humans experienced contingencies between observation and execution of nonmatching actions (e.g., when one individual countered a blow from another) and between objects and actions (e.g., when distinctive actions were made on distinctive objects).[2] Thus, our key assumption is not that "genetically inherited traits are insensitive to associative learning," but that "if a trait is a gene-based adaptation, its development tends not to be perturbed by environmental variations that were present when the trait evolved."

R2.5. Associative learning cannot be adaptively specialized

Several commentators have suggested that we were wrong to contrast the genetic account with the associative account because associative learning can be adaptively specialized (aka "canalized" and "exapted") (**Behme**; **Bertenthal**; **Gervais**; **Giese**; **Keysers, Perrett, & Gazzola** [**Keysers et al.**]; **Lotem & Kolodny**; **Martin & Santos**; **Simpson et al.**). For example, as indicated by Garcia's classic experiments on food aversion learning (e.g., Garcia et al. 1955), genetic evolution can alter input mechanisms or learning rate parameters so that contingencies between some pairs of events (e.g., flavor and illness) are learned more readily than others (e.g., flavor and shock), a phenomenon known as "selective association" (Gemberling & Domjan 1982; Heyes 2003; Pearce 2008). To be clear: We have no doubt that associative learning can be adaptively specialized. Indeed, if we had any doubts, we would not have put so much effort into experiments that were explicitly designed to test for signs of adaptive specialization in the development of MNs. We have tested for adaptive specialization – for example using counter-mirror and induction training (O2F, sect. 7) – and failed to find it. That is why the associative account is not a hybrid model; why it is "extreme" (Lotem & Kolodny) in suggesting that MNs are forged by domain-general processes of learning that have not been specialized by genetic evolution for the development of MNs.

The associative hypothesis would be less plausible if it had been shown that adaptive specialization of associative learning is not merely possible, but normal or typical (**Lotem & Kolodny**). However, the evidence does not support typicality. There are quite a few examples of selective association, but selective association can be due to prior learning (Mackintosh 1973) rather than genetic processes – "ontogenetic inflection" rather than "phylogenetic inflection" (Heyes 2003) – and in many cases it has merely been assumed that the source of selective association is phylogenetic; that it constitutes adaptive specialization.

The commentaries on our article offer a rich array of hybrid genetic-associative possibilities. For example, commentators point out that MNs could be built by a form of associative learning that is adaptively specialized for empathy (**Gervais**) or self-monitoring (**Bonaiuto**) rather than action understanding; via epigenetic as well as genetic processes (**Simpson et al.**); by the modification of memory parameters as well as input mechanisms (Bonaiuto; **Keysers et al.**; **Lotem & Kolodny**); and where the modified input mechanisms involve mother-infant face-to-face interaction, infant-directed speech, imitation by adults, and the face preference (Gervais; Keysers et al.). We agree that these are all logical possibilities and that there is "no a priori reason" (**Behme**), such as lack of parsimony (Lotem & Kolodny), to reject hybrid models. Indeed, as we said in the target article, we see hybrid modeling as "a promising direction for future research" (O2F, sect. 8.2). We just want to see some evidence. It is not enough to generate hypotheses; they also need to be tested.

Reader's commentary confirms that it is possible to test adaptive specialization hypotheses by discussing research on social learning, rather than MNs, in which this has been done successfully. In contrast, very few commentators have identified empirical research on MNs that, in their view, supports a hybrid, adaptive specialization model over the associative and genetic accounts. **Oberman et al**. cite a study by Howlin and Moss (2012) which reported that people with autism spectrum conditions (ASC) are at a disadvantage, compared with neurotypical controls, in relation to employment, social relationships, health, and quality of life. To count this as evidence for a hybrid model, it would be necessary to make three unjustified assumptions: that people with ASC have abnormal MNs; that their disadvantages are due to this abnormality; and that the disadvantages would not occur if MNs developed in the manner described by either the genetic or the associative account.

Similarly, citing Meltzoff (1995), **Bertenthal** suggests that infants more readily imitate human than mechanical movements and that this animacy bias supports a hybrid model over the associative account. However, a replication of Meltzoff's (1995) study found evidence that his results were due to stimulus enhancement – a phenomenon that does not implicate MNs – rather than imitation (Huang et al. 2002). More broadly, animacy bias in imitation – which has been reported in other studies – is fully compatible with the associative account. Human developmental environments typically offer many more opportunities to associate the observation of human action, than the observation of mechanical action, with action execution (Press 2011). Therefore, one does not need to invoke adaptive specialization to explain animacy bias. Furthermore, as predicted by the unadorned associative account, animacy bias is abolished when action execution is correlated with observation of mechanical movements (Press et al. 2007).

Taking a broader approach, **Gervais** (see also **Martin & Santos** and **Oberman et al.**) suggests that hybrid models are better able to explain why monkeys and humans, but not rats, have MNs. The first problem with this argument is that we do not know whether rats or free-living monkeys have MNs; they have not been tested. The second problem is that the associative account predicts species differences based on the amount and kind of sensorimotor experience received in the course of typical development, and – borrowing **Bonaiuto**'s terminology again – the pattern of partial connectivity between sensory and motor areas that has been favored by genetic evolution for visual guidance of action.

We hope our article will encourage those who back hybrid models to test them against the genetic and associative accounts in carefully designed experiments. This was, to a large degree, our purpose in writing O2F. The resulting experiments may well show that the associative account is wrong or needs to be augmented (Heyes, in press). For example, in common with **Gervais**, we have suggested elsewhere that cultural evolution, rather than genetic evolution, may have favored social practices that facilitate the development of imitation and MNs through associative learning (Heyes 2012a; 2013). But even if future experimental research shows that the associative account is plain wrong, in our view it would be a good result. It would mean that research on MNs has moved from exciting speculation to exciting experimentation: from ideas to tests and testability.

R3. "Goals" and the field properties of MNs

In section 3 of O2F, we argue that research on the field properties of MNs does not support the claim that they selectively encode action "goals," a central plank of the case for the genetic account. Several commentators explicitly endorse our view that MNs do not selectively encode goals (**Giese**; **Heil, van Pelt, Kwisthout, van Rooij, & Bekkering** [**Heil et al.**]; **Kilner & Friston**). Others repeat the claim that MNs selectively encode goals, but do not engage with the evidence we have presented (**Brown & Brüne**; **Fogassi**; **Gallese & Sinigaglia**; **Khalil**; **Martin & Santos**). They do not explain how the goal-encoding claim can be reconciled with the evidence that MNs are responsive to intransitive as well as transitive actions, and to low-level features of action such as the path through space, effector used, and observer's viewpoint.

Orban mentions four studies that we did not discuss in O2F, two using fMRI and two using single-unit recording in monkeys. The first fMRI study (Nelissen et al. 2005) reported that area F5c was active during action observation when the actor's body was in full view but not when the monkey could see only parts of the actor's body. This finding does not warrant the general claim that a full view of the agent is necessary for MN firing in monkeys. For example, audiovisual MNs discharge when the monkey hears paper tearing and can see only the experimenter's static, disembodied head and arms (see Figure 1b in Keysers et al. 2003). However, in those cases where MN activity is sensitive to the visibility of the actor's body, the associative account makes the testable prediction that this is due to either generalization decrement or contextual learning of the kind discussed in section 5 of O2F. The second fMRI study (Nelissen et al. 2011) confirmed that signals travel from STS to F5c over two parietal way stations, which is entirely compatible with our statement that some sensory neurons in STS are "connected, directly or indirectly, to motor neurons in PMC … and parietal cortex" (O2F, sect. 3.2, para. 2).

The third and fourth studies reported "suppression MNs," neurons that discharge when a focal behavior is executed and show below baseline activity when a similar behavior is observed (Kraskov et al. 2009; Vigneswaran et al. 2013). These results are very interesting indeed, but it is not clear why **Orban** believes that they support a genetic or hybrid account over the associative hypothesis. Indeed, at first blush, suppression MNs seem to be troublesome for any account suggesting that evolution designed MNs to promote action understanding. If standard "excitation MNs" were designed to promote action understanding, it looks as if suppression MNs must have been designed to prevent action understanding. This is implausible, and therefore supporters of a genetic or hybrid account have appealed to an untested auxiliary hypothesis – that the specific and presumably unique function of suppression MNs is to allow self-produced and other-produced actions to be distinguished (Mukamel et al. 2010).

Given that associative learning can be both excitatory and inhibitory, there is no reason to doubt that suppression MNs are compatible with the associative account. However, a good deal more will need to be discovered about suppression MNs before the associative account, or any other hypothesis, can offer a clear and specific explanation of their properties. For example, we need to know how suppression MNs are related to MNs that show below baseline activity during *both* action execution and observation (di Pellegrino et al. 1992), about the source(s) of inhibitory input (frontal executive regions, parietal cortex, and/or other F5 neurons), and about the developmental history (e.g., the training received by the animals prior to recording) of the monkeys in which suppression MNs can be found.

Fogassi suggests that two observations favor the genetic account, which postulates goal encoding, over the associative account: The activity of some MNs covaries with the outcome of the observed movement (grasp-to-eat versus grasp-to-place), and "the percentage of MNs tuned for the hard-wired action (grasp-to-eat) is much higher than that of MNs tuned for the learned action (grasp-to-place)." We discussed the first of these observations in O2F (sect. 5.2), showing that the pattern of covariation can be explained by contextual associative learning. We cannot see how the second observation bears on the distinction between the genetic and associative accounts as they were described in the target article or why the commentator identifies grasp-to-eat as "hard-wired" and grasp-to-place as "learned," but it should in any case be clear that the associative account predicts varying proportions of MNs as a function of the differential contextual sensorimotor experience received by the animal.

R4. Still the right kind of learning

In section 5 of O2F we argued that domain-general principles of associative learning, including contingency sensitivity and contextual modulation, provide a unified explanatory framework for the field properties of MNs. While many commentators agree that associative learning plays a significant role, some argue that a special kind of associative learning is involved in the development of MNs. In section R2 we have responded to commentaries which suggest that it is special in being adaptively specialized. In this section, we turn to commentaries which suggest that the development of MNs depends on associative learning that is more "Hebbian," more "ideomotor," and more "high-level" than that which has been revealed by research on conditioning in animals.

R4.1. Hebbian and/or associative?

In O2F we offered two interpretations of what **Keysers et al**. describe as the Hebbian hypothesis: On one reading, it is "identical in substance to the associative hypothesis [and] helpful in providing a more detailed neuronal model of how sensorimotor experience makes MNs out of motor neurons" (sect. 8.1, para. 1), and on the other reading – which we thought "less likely to represent the authors' intentions" – "'Hebbian learning' differs from 'associative learning' in depending on contiguity alone, rather than both contiguity and contingency" (sect. 8.1, para. 2). In their commentary, Keysers et al. seem to confirm that our first interpretation was correct. They certainly emphasize the neuronal specificity of their model, and stress that, however Hebbian learning may have been understood in the past, Keysers et al. understand it to be a process that depends on contingency. However, if, as they suggest, the associative and Hebbian accounts are merely "descriptions at different levels," and it is "idle" to argue that one is better than the other, it is not clear why Keysers et al. also suggest that the two accounts make different predictions; that the Hebbian account would, and the associative account would not, predict the formation of associations between as well as within action phases – for example, between "reach-STS" (observation of reaching) and "grasp-PM" (execution of grasping), as well as between "grasp-STS" (observation of grasping) and "grasp-PM" (execution of grasping). Two theories are either equivalent, and it is idle to ask which is correct, or they make different empirical predictions, and it is the basic stuff of science to test them against one another.

In this case, we think that **Keysers et al.** are right about the equivalence rather than the differential predictions. Tracking of predictive relationships between events (rather than event co-occurrence), via prediction error, is at the heart of the formal models of learning that underwrite the associative account (e.g., Rescorla & Wagner 1972; Schultz & Dickinson 2000). Therefore, the associative account is wholly compatible with "sensory prediction" (Keysers et al.), "predictive coding" (**Brass & Muhle-Karbe**; **Kilner & Friston**; Press et al. 2011), and, most specifically, with the formation of associations between, as well as within, action phases. The challenge for both the associative and the Hebbian views – assuming they are equivalent in substance – is to define the conditions in which learning produces "classical" MNs, which fire during the observation and execution of the same action (e.g., grasping), and those in which it yields nonmatching MNs such as logically related MNs, that may encode relations between successive components of an action sequence. The advantage of the associative/Hebbian account over the genetic account is that it can readily accommodate both kinds of MNs because associative learning is all about prediction rather than matching. However, because associative learning does prediction on a variety of timescales, those who support an associative account need to work on predicting the timescale on which it will operate for different types of action and of sensorimotor experience.

R4.2. Ideomotor and/or associative

In their thoughtful commentary, **Brass & Muhle-Karbe** suggest that MNs are a neural substrate of ideomotor representations, established through the formation of response-effect associations, and contrast this with our associative account, which identifies MNs as "sensorimotor" representations and refers to "sensorimotor" learning (see also **Ho, MacDonald, & Swain** [**Ho et al.**]). They may well be right. There may be a real, empirically testable difference between their ideomotor account and our associative model. But, as with **Keysers et al.**, where Brass & Muhle see conflict, we see harmony. We suspect that the two views *seem* to be different because what we call "stimuli" they call "response effects," but the two accounts are in fact united in suggesting that the critical associations – the associations that give MNs their cardinal properties – link neuronal representations of "R" and "E," not "S" and "R," in their diagram (see Fig. 1 in Brass & Muhle-Karbe's commentary). If this is correct, our training experiments (O2F, sect. 7.1) contain the right ingredients for the ideomotor account – they expose participants to contingent relationships between R and E, execution and observation of action – but not in the order in which these events are typically experienced in everyday life. In each trial of our training regimes, participants observe an action and then execute an action. We have used this kind of regime because it is easier to control the contingencies experienced by participants when the observed action comes first, and because there is compelling evidence that associative learning is bidirectional (Ayres et al. 1987; Elsner & Hommel 2001; 2004; Mahoney & Ayres 1976). It is important to note that, confirming the bidirectionality assumption, other groups have replicated and extended our findings using training regimes in which response execution precedes action observation (e.g., Wiggett et al. 2011).

Of course, the proof of the ideomotor/associative pudding will be in the testing, but the examples mentioned by **Brass & Muhle-Karbe** do not yet convince us that it will be possible to generate differential predictions. They suggest that two empirical findings are inconsistent with the associative account. In the first, Kunde (2001) found that responses were executed faster when followed by compatible, rather than incompatible, sensory effects – evidence for anticipatory excitation of the sensory consequences of action. However, as discussed in the previous paragraph, the associative account is compatible with predictive motor-to-sensory propagation, following exposure to either S-R or R-E contingencies. In the second study, Liepelt et al. (2008b) found a larger index/middle automatic imitation effect when fractional finger movements were presented inside, rather than alongside, metal clamps. Applying the associative account, Heyes (2011) agreed with the view (proposed by Brass previously and given by Brass & Muhle-Karbe in their present commentary) that this could be described as an effect on mirroring of "high-level beliefs about the intentionality of the observed action," but suggested that the effect was mediated by enhanced attention to the clamped movements (see also **Heil et al**. and **Brown & Brüne**).

R4.3. Reasoning and/or association

The associative account identifies the learning processes involved in the development of MNs with those that produce conditioning in a variety of animal species. However, **Heil et al.** argue that this type of "low-level" associative process is ill-suited to producing MNs. Appealing to evidence that beliefs about causal structure can modulate human associative learning, Heil et al. raise the possibility that another type of associative process is responsible for the development of MNs, one that is shaped by and integrates higher-level cognitive processes. This is an interesting but, in its current form, largely speculative hypothesis. To make it testable, Heil et al. would need to say more about the kind of high-level processes they take to be involved in the development and online control of MNs (e.g., the processes that yield contingency awareness may or may not be reasoning processes) and about the way in which the high- and low-level processes are supposed to interact. In humans, language-mediated high-level processes can certainly influence associative learning by modulating input mechanisms – for example, task instructions can direct participants' attention towards or away from the computer screen on which stimuli are presented – but this kind of interaction is entirely compatible with our associative hypothesis (e.g., **Lotem & Kolodny**). To motivate their hypothesis, Heil et al. would also need to cite findings from the MN literature that they regard as consistent with a high-level associative process, but inconsistent with a low-level mechanism. At present they suggest only that a high-level process would be needed if MNs are to mediate action understanding. This may be so, but it is not a compelling argument in favor of a high-level process given the ambiguity of the term "action understanding" (O2F, sect. 3.1), and the corresponding lack of clear evidence that MNs mediate action understanding (O2F, sect. 9.2).

In section R4 we have argued that both the associative and Hebbian accounts are compatible with predictive coding; that the associative account is complementary to, not in conflict with, ideomotor theory; and that there are currently no data from MN research suggesting that their development or operation is guided by a "higher-level" associative process. We therefore maintain that phylogenetically ancient associative processes are "the right kind of learning" to yield the field properties of MNs.

R5. Poverty of the poverty argument

In section 6 of O2F we argued that human developmental environments typically contain multiple sources of the kind of correlated sensorimotor experience necessary to build MNs; each of these sources is rich; and the mechanisms of associative learning can make swift and efficient use of these sources. No commentary queried the evidence in support of this "wealth of the stimulus" argument. We also suggested that imitation and EEG data from human and monkey neonates do not support a complementary "poverty of the stimulus" argument; they do not show that MNs develop too soon to be built by associative learning. Some commentators have concurred with this view. For example, **Oberman et al.** agree that the evidence for neonatal imitation is limited, and suggest that, even if the evidence were stronger, it is unlikely that neonatal imitation would reflect MN activity because the cortical areas containing MNs are not fully developed at birth. Similarly, **Rizzolatti** finds it hard to "conceive how the mirror mechanism of a neonate might have a neurological maturity such as to provide a precise copy of tongue protrusion." However, two commentaries have opposed our view of the neonatal imitation literature: **Gallese & Sinigaglia** do so implicitly, by simply stating that neonates imitate, but **Simpson et al.** cite evidence that, in their view, shows that neonatal imitation is a "real phenomenon."

There are, in our view, several problems with **Simpson et al.**'s survey of the literature on neonatal imitation. First, in pointing out that neonatal imitation has been demonstrated "in over two-dozen studies," it focuses on positive effects and disregards the greater number of published studies reporting negative effects; failure to find evidence of neonatal imitation (see Fig. 2 in O2F). Second, the vast majority of the positive findings cited by Simpson et al. come from studies that incurred a high risk of Type I error because they did not use the standard, "cross-target" or "double-dissociation" procedure. This procedure reduces the risk that nonspecific effects of a movement stimulus will be mistaken for imitation (production of a specific, matching response) by comparing the frequency of action A following observation of A and B, *and* the frequency of B following observation of A and B; that is, looking for an interaction between stimulus and response. The only evidence of such an interaction cited by Simpson et al. (Ferrari et al. 2006) could have occurred by chance; it appeared to be present on only one of four test days and across only the lip-smacking–tongue-protrusion comparison. Consistent with this possibility, the effect appears not to have been replicated in a subsequent study by the same authors (Paukner et al. 2011; see O2F for discussion). Finally, Simpson et al. do not offer compelling reasons to believe that the mixture of positive and negative findings, illustrated in Figure 2 of O2F, is due to individual differences in neonatal imitation rather than a general lack of imitative capacity in newborns. Yes, it is possible that neonates vary in their ability to imitate, and they are certainly difficult to test. But in humans the tongue-protrusion effect has been replicated many times, suggesting that current procedures are good enough to detect a signal when a signal is there to be found.

We argued in O2F that the tongue-protrusion signal is reliable but indicative of an oral exploratory response rather than imitation (Jones 1996; 2006). Contesting this view, **Simpson et al.** cite a new study (Nagy et al. 2013) indicating that observation of tongue-protrusion does not induce arm and leg movement. Appendage movements are unlikely to be part of oral exploration, and therefore this study does not bear on our point.

Turning from imitation to EEG measures, **Simpson et al.** and **Oberman et al.** argue on two grounds that alpha suppression during action observation is a valid indicator of MN activity in neonatal monkeys: (1) When human adults observe action, alpha suppression has been found alongside BOLD responses in premotor cortex, and (2) some studies have found that when people with autism spectrum conditions (ASC) observe action, they show less alpha suppression than neurotypical controls. The first of these observations does not establish alpha suppression as a valid index of motor, rather than somatosensory, activity, because alpha effects correlate with both premotor and somatosensory BOLD responses (Arnstein et al. 2011); MEPs during action execution correlate with beta, but not with alpha, suppression (Lepage et al. 2008); and in adults the source of alpha suppression during action execution has been traced to somatosensory cortex (Hari & Salmelin 1997). It is likely that, because of the high connectivity between somatosensory and motor areas, motor activity sometimes contributes to alpha suppression. However, even if a motor contribution could be demonstrated in studies of action observation in infants, it would remain an open question whether the motor contribution represented mirroring – activation of motor programs corresponding to the actions observed – or a generalized readiness to act. The force of the second observation – that people with autism show less alpha suppression than controls – rests on the highly controversial assumption that people with autism have abnormal MNs (Bird et al. 2007; Press et al. 2010; Southgate & Hamilton 2008).

Research on mirroring in neonates faces formidable methodological challenges. Unless or until these are overcome, it cannot support a compelling poverty of the stimulus argument.

R6. Convergent evidence and extensions of the associative account

Many commentators have presented convergent evidence supporting the associative account. **Oosterhof, Wiggett, & Cross** (**Oosterhof et al.**) report multivariate pattern analyses (MVPA) of fMRI data that indicate mirror – sensorimotor matching – responses in brain areas outside the classical parietal-frontal mirror circuit. As Oosterhof et al. note, the finding that mirror responses are widespread across the brain is in line with the predictions of the associative account. It also therefore counters those commentators who argue that the associative account must be wrong because MNs are only found in restricted brain areas (**Bonaiuto**; **Fogassi**; **Martin & Santos**; **Orban**).

Saygin & Dick discuss evidence indicating that mirror responses are not solely responsive to biological stimuli, being present also for point-light displays and robotic or android movements. As they note, and particularly in the light of evidence that some MNs respond maximally to unnatural stimuli (see R2.2 and Cook 2012), such findings fit more closely with an associative than with a genetic account of MN matching properties.

Presenting further convergent evidence for the associative account, several commentators mention data demonstrating experiential effects, both on social behavior more generally and on mirror responses in particular. **Reader** outlines studies showing that associative learning allows both birds and insects to learn from conspecifics, while **Newman** discusses how experience modulates squirrel monkeys' vocal responses to other monkeys' calls. **Holt & Lotto** report data demonstrating that in infants, cortical responses to perceived speech sounds in motor areas show a developmental profile consistent with experience-dependent learning; and **Saygin & Dick** discuss a study showing effects of sensorimotor experience on responses to perceived sounds in premotor areas (Dick et al. 2011).

A number of commentators suggest ways in which the associative account could be extended to reward processing, speech processing, and high-level social interaction. **Brown & Brüne** (see also **Giese**) suggest the associative account may provide a useful framework for conceptualizing the role of reward in the development and function of the mirror mechanism. This line of enquiry is well worth pursuing, but interpreting the role of reward in the operation of a mature mirror mechanism is unlikely to be easy. Whereas Brown & Brüne suggest that putative examples of contextual modulation may in fact reflect differences in the processing or value of reward, an alternative interpretation is that instances of putative modulation by reward reflect stimulus-driven contextual control. Moreover, where participants attend closely to actions associated with reward or punishment, differential mirror responses may also reflect input modulation (Heyes 2011).

In their commentary, **de la Rosa & Bülthoff** highlight the value of contingency sensitivity and contextual modulation for understanding how humans behave in social interactions. We certainly echo this view. Contingency sensitivity offers an elegant account of the emergence of automatic imitation of some actions, but prepotent complementary responses for others (Tiedens & Fragale 2003). Moreover, interactive behavior is frequently ambiguous: The appropriate response to an observed action may be imitative in one situation, but complementary in another. Contextual modulation by physical features of the context (e.g., visual, auditory cues) or internal states (e.g., level of arousal, presence of hormones) may serve to resolve this ambiguity and thereby enable flexibly adaptive behavior (Cook et al. 2012a).

Another commentary that addresses behavior in social interactions is that of **Duran, Dale, & Richardson** (**Duran et al.**). These authors endorse the associative account, but we disagree with their characterization of our account as "negative eliminativist": On the contrary, we believe our proposal for a new approach to investigation of MN function is a positive message, and it has been viewed as such by most commentators (see R7.2). However, we applaud the ambition of Duran et al.'s thesis, which seeks to use domain-general processes, including associative learning, to explain social interaction in naturalistic settings.

R7. Looking ahead

The final section of O2F called for a new approach to research on MNs, with a keen eye on participants' developmental history, and using system-level theory to define putative functions of MNs and rigorous experimental methods to test the system-level hypotheses. In this section we respond to comments on the theoretical (R7.1) and empirical (R7.2) components of these proposals.

R7.1. Understanding "action understanding"

In O2F we pointed out that there is "no consensus about exactly what is meant by 'action understanding,' or how it differs from cognate functions such as 'action perception,' 'action recognition,' and 'action selection' " (sect. 3.1, para. 2). This is a conceptual problem that has generated a major empirical problem. When it is not clear what a mechanism is supposed to be doing, it is all but impossible to design experiments finding out whether the supposition is correct. We also suggested that the best way to solve this problem would be to focus on the development of system-level theories (sect. 9.1.2), in which MNs feature as one component of a system defined by its outcome or typical effect and in which the role of MNs is clearly distinguished from, and related to, the roles of other components (Heyes, in press).

In the commentaries, no one denies that understanding "action understanding" is a problem, and many endorse the need for system-level theory, explicitly or by discussing particular system-level theories with enthusiasm (**Behme**; **Heil et al.**; **Holt & Lotto**; **Kilner & Friston**; **Lingnau & Caramazza**; **Saygin & Dick**). (We particularly like Kilner & Friston's slogan, "no neuron is an island.") However, confirming that we have not constructed a straw man (cf. the claim by **Oberman et al.**), members of the Parma group eschew the system-level approach. Instead, these commentators seek to elucidate the "action understanding" function of MNs by (1) repeating the claim that they encode or interpret action "goals" (**Fogassi**; **Gallese & Sinigaglia**), and are therefore "bearers of intentionality" (Gallese & Sinigaglia); (2) noting that MNs transform "sensory information into a motor format" (**Rizzolatti**); and (3) describing MN-mediated action understanding as "action understanding 'from inside' (Rizzolatti & Sinigaglia 2010): 'a *first person process*, where the self feels like an *actor*, rather than a *spectator*' " (Rizzolatti).

The first of these strategies is not promising because, as we argued in O2F (sect. 4), the term "goal" is at least as ambiguous as "action understanding," and on at least two natural interpretations of "goal" – as an object of action and as a high-level intention – the evidence suggests that goals are not selectively encoded by MNs. The second strategy is more straightforward, but it is clearly insufficient because it does not refer to the cardinal, matching properties of MNs. They can certainly be said to transform sensory information into a motor format, but that is also true of, for example, canonical neurons. The third strategy is phenomenological; it distinguishes MN-mediated action understanding from other sorts of action understanding with reference to the actor's conscious experience – whether he or she "feels" like an actor or a spectator. This suggestion is coherent and intuitively appealing, but it is unlikely to be helpful as a guide for experimental research. Without a return to the methods of introspectionism, researchers in psychology and neuroscience are "spectators"; we are "on the outside," trying to work out the function of MNs, not by examination of our own conscious experience, but by studying the brains and behavior of other people. Therefore, to use the phenomenological strategy we would need to be told how, from the outside, to distinguish "inside" and "outside" action understanding; how these types of action understanding differ in terms of the observable behavior they produce.

Rizzolatti also explains with helpful clarity that he now believes that mirror neurons contribute to social cognitive functions such as imitation, empathy, and song recognition, as well as action understanding, and regards "the problem of how MNs originate [as] utterly irrelevant as far as their *function* is concerned." We have no quarrel whatever with these views; they are wholly in accord with the "functionally permissive" character of the associative hypothesis (O2F, sect. 9) and the way in which it splits questions about the origin of MNs from questions about their function. However, it is important to note that these views do not make the genetic hypothesis a straw man – **Fogassi**'s commentary and the quotations in O2F (sect. 3.1), attest to its reality – or obviate the need for system-level theory. Indeed, they increase that need. There are just two widely recognized methods of defining the function of a trait in a biological system: one does it with reference to the trait's history, typically its evolutionary history, and the other, "functional analysis," does it in the context of what we have described as system-level theory (Cummins 1975; Godfrey-Smith 1994). Given that these are the two paths available, rejection of the history route – denial that the function of MNs relates to their origins – makes pursuit of the alternative, system-level theory, absolutely essential; and multiplying the putative functions of MNs means that we need system-level theories defining the role of MNs, not only in action understanding, but also in imitation, empathy, and song recognition.

Gallese & Sinigaglia are absolutely right: the mere fact that "action understanding" is a new term is not a reason to reject it. All we are saying, here and in O2F, is that those who use the term need to tell us what it means, and to do so in the context of system-level theory.

R7.2. Experimental approaches

Few commentators (except perhaps **Fogassi**) disagree with our proposal that MN research should report participants' developmental history: that is, their sensory, motor, and sensorimotor experience with the actions for which MNs are being tested. Indeed, **Gervais** comments on the "value of the enterprise" of documenting the effects that variation in developmental environment may have on the ontogeny and function of MNs. In this vein, the developmental data described by **Krogh-Jespersen, Filippi, & Woodward** (**Krogh-Jespersen et al.**) are a promising start. These data demonstrate how infants' motor experience (specifically, in this case, their tendency to produce goal-directed actions) relates to their neural responses to observation of others' actions; to their ability to understand others' actions; and to their ability to imitate. These findings are consistent with the predictions of the associative account; however, they serve to highlight the importance of assessing participants' previous sensorimotor (not just motor; cf. **Gallese & Sinigaglia; Rizzolatti**) experience with specific actions when investigating neural responses to, understanding of, or imitation of those actions (see earlier response to **Bertenthal** for further explication of this point).

Several other commentators appear to embrace our suggestion that MN research pay closer attention to developmental history: **Simpson et al.** propose examining the effects of early sensorimotor experience on imitation, while **Ho et al.** note that it would be informative to consider the development of MNs in infants who have atypical experience, for example, those who cannot walk themselves or whose parents suffer from depression. We wholeheartedly concur that research with these populations could prove highly informative in dissociating the relative roles played by sensory, motor, and correlated sensorimotor experience in the development of MNs, and perhaps also shed some light on their function.

We are pleased that most commentators have endorsed our call for a more rigorous, experimental approach to the investigation of MN function (**Behme**; **Gervais**; **Holt & Lotto**; **Krogh-Jespersen et al.**; **Lingnau & Caramazza**; **Newman**; **Oosterhof et al.**; **Reader**; **de la Rosa & Bülthoff**). Here we address some criticisms of our proposals and discuss the commentators' additional suggestions for future research.

Orban's commentary illustrates the constraints that have been placed on MN research to date by the genetic account. It suggests that MNs have only, and will only, be found for grasping actions; that MNs can only be considered such when found in classical areas; and that only a primate model holds any value for understanding the human brain. Such suggestions are in accord with an account that considers MNs to be a genetic adaptation for representing others' grasping actions in one's own motor system (see also **Fogassi**). They illustrate the risk that the genetic account will confine future research to certain actions, brain areas, and species. However, as we indicated in the target article, the associative account predicts (and data support these predictions) that mirror neurons will be found for a range of actions (e.g., Ferrari et al. 2003), in a range of brain areas (e.g., Dushanova & Donoghue 2010; Mukamel et al. 2010; Tkach et al. 2007), and across a range of species (e.g., Prather et al. 2008). We therefore see no reason to reject the possibility that MNs could be induced in other species through sensorimotor training of species-appropriate actions.

We are not aware of any research that has investigated whether MNs are present in rodents. However, those commentators who deny that MNs are (**Gervais**), or could be (**Orban**), present in rodents (or in other species; **Oberman et al.**) seem to have misunderstood our point. The associative account suggests that whether MNs are likely to exist in laboratory (or indeed free-living) rats will depend on their prior learning history; but it makes the strong prediction that regardless of whether they are present or not, appropriate experience in which the sight or sound of an action is paired contingently with execution of that action should produce visuo- or auditory-motor MNs for that action, in rodents and indeed in any other species. This approach is also endorsed by **Reader**'s commentary, in which he proposes the use of insect or fish models to investigate MNs. Building on the previous point, **Newman**'s commentary provides an interesting description of behaviors consistent with the existence of audio-vocal mirror-like circuits in a variety of species. We agree with Newman that it would be interesting to test for MNs in these species – indeed the presence of audio-vocal MNs in swamp sparrows has already been demonstrated (Prather et al. 2008).

The preceding commentators have focused on experimentation into MN properties. Other commentators propose investigation of the possible role of MNs in contagious behavior (**Provine**) and in higher-level social cognition tasks: **Martin & Santos** advocate carrying out single-unit recording while macaques undergo tests assessing their awareness of others' knowledge. We believe that such an endeavor would benefit from the kind of system-level analysis we have outlined in the target article (see also **Holt & Lotto**). Such an analysis would specify, for example, the role that MNs are predicted to play in these tests and whether or not this role must be carried out by MNs.

Several commentaries touch on the methodological challenges facing future MN research. **Lingnau & Caramazza** understood us to be suggesting that research into the modulation of MN responses by associative learning is sufficient to provide evidence of the role of MNs in social cognition. This is certainly not the case. Instead, the associative account implies that the function of MNs cannot be discovered solely by research on their field properties; tests of the kind described in O2F (sect. 9.1.3), and promoted by Lingnau & Caramazza, are also needed. We agree, therefore, that temporary and permanent lesion studies are an important component of research on MN function; indeed, we presented some evidence from such studies in the target article. However, such studies are vulnerable to what we termed the "localization problem": not all neurons in "classical" MN areas are mirror neurons and thus lesion studies may overestimate the involvement of MNs in the cognitive function of interest.

Oosterhof et al. point out that MVPA, although not a causal technique, can help to overcome the localization problem. This method, unlike standard fMRI approaches, allows measurement of spatially distributed responses to *specific* observed and executed actions. Oosterhof et al. provide an interesting description of how this technique could be used to test further the predictions of the associative account, and we agree that MVPA may also prove a promising additional tool to investigate the functional properties of MNs.

Bonaiuto argues that computational models can provide a convincing demonstration of the concepts underlying the associative account. We agree and have therefore previously presented such a model (Cooper et al. 2013a; 2013b). As Bonaiuto suggests, this model requires appropriate input representations of actions. It demonstrates how sensorimotor associative learning can modulate the development of mirror properties (Cooper et al. 2013b) and how mirror networks operate, once developed, to produce imitative behavior (Cooper et al. 2013a). Other computational models which use domain-general learning processes and demonstrate the development of MN-like properties in the domain of speech processing are described by **Holt & Lotto** and **Saygin & Dick. Giese** also summarizes how insights from visual pattern recognition may be applied to computational modeling of MNs. Thus, we consider computational modeling to be important not only for testing accounts of how MNs develop, but also for providing novel predictions regarding the functional properties of mature mirror systems.

R8. Conclusion

We are grateful to all of our commentators, combatants and supporters alike, for studying O2F and contributing their insights and opinions to the debate. Given our focus on tests and testability – both in comparing the associative account with genetic and hybrid models of the origin of MNs, and in future research on the function of MNs – we have found the methodological and empirically grounded commentaries especially valuable, but they are all both thoughtful and provocative. The contributions from **Rizzolatti** and other members of the Parma group were especially welcome. We disagree with the Parma group on a number of points, but we have no doubt that their shining discovery, mirror neurons, will intrigue scientists and philosophers for many years to come.

NOTES

1. Contrary to what some commentators suggest, we have demonstrated this not only behaviorally, but also with all of the neurophysiological measures commonly used to detect MNs in humans (**Bertenthal**) and with measures that demonstrate action-specificity (**Oosterhof et al.**).

2. We are very grateful to Nick Shea for suggesting that we lay out the argument in this way.

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[The letters "a" and "r" before authors' initials stand for target article and response references, respectively]

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