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**The ontogenetic origins of mirror neurons:**

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**Evidence from ‘tool-use’ and ‘audiovisual’ mirror neurons**

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Mirror neurons, associative learning, audiovisual mirror neurons, tool-use mirror neurons

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30 **ABSTRACT**

31 Since their discovery, mirror neurons - units in the macaque brain which discharge both  
32 during action observation and execution - have attracted considerable interest. Whether mirror  
33 neurons are an innate endowment or acquire their sensorimotor matching properties  
34 ontogenetically has been the subject of intense debate. It is still widely believed that these  
35 units are an innate trait; that we are born with a set of mature mirror neurons because their  
36 matching properties conveyed upon our ancestors an evolutionary advantage. However, an  
37 alternative view is that mirror neurons acquire their matching properties during ontogeny,  
38 through correlated experience of observing and performing actions. The present article re-  
39 examines frequently overlooked neurophysiological reports of 'tool-use' and 'audiovisual'  
40 mirror neurons within the context of this debate. It is argued that these findings represent  
41 compelling evidence that mirror neurons are a product of sensorimotor experience, and not an  
42 innate endowment.

43

44

45 **1. INTRODUCTION**

46 Mirror neurons (MNs) are single units identified in the ventral premotor [1-3] and inferior  
47 parietal [4, 5] cortices of the macaque brain, which respond to both the sight and execution of  
48 transitive and communicative actions. Approximately 25-30% of the MNs reported are  
49 strictly congruent; that is they respond to the observation and execution of the same action.  
50 The remaining MNs (so-called ‘broadly congruent’, ‘logically related’ and ‘non-congruent’  
51 MNs) respond to similar, related, or different actions in observe and execute conditions. Since  
52 their discovery in monkeys, considerable indirect evidence has accumulated suggesting that  
53 humans also have a MN system [6-8].

54

55 Whether MNs are an innate endowment or acquire their properties ontogenetically has been  
56 the subject of intense debate [9]. Crucially, while few now doubt that independent sensory  
57 and motor experience can fine-tune the response profiles of MNs [9, 10], there continues to be  
58 considerable disagreement as to the how these units acquire their fundamental sensorimotor  
59 matching properties [11]. The present article contributes to this debate by considering the  
60 insights afforded by ‘tool-use’ and ‘audiovisual’ MNs. It is argued that despite being  
61 frequently overlooked, the existence and properties of these units provide compelling  
62 evidence that MNs acquire their matching properties during ontogeny, as a consequence of  
63 correlated sensorimotor experience.

64

65 **2. THE ORIGINS OF MIRROR NEURONS**

66 Where do MNs come from? One possibility is that MNs are an innate endowment; that we are  
67 born with a set of mature MNs because their matching properties conveyed upon our  
68 ancestors an evolutionary advantage [3, 12-14]. Several authors have argued that early  
69 selection pressure favoured MNs because they afforded ‘action understanding’ [3, 12].  
70 According to this view, congruent MNs mediate the covert simulation of observed actions; a  
71 process which yields first person insights into the intentions and goals of conspecifics [15]. At  
72 subsequent stages in primate evolution, MNs may have conveyed further adaptive benefits,  
73 including theory of mind [14], imitation learning [12], and language development [13]. Innate  
74 MN theory appears to receive some support from reports that neonates ‘imitate’ certain mouth  
75 gestures [16-18] (but see [19] for an alternative interpretation).

76

77 A different view is that MNs acquire their sensorimotor properties ontogenetically, through  
78 the same domain-general associative mechanisms that mediate conditioning [11, 19, 20].  
79 Where visual and motor representations of actions are predictive of one another, the two may  
80 become associated. Thereafter action observation may excite associated motor programs.  
81 Sources of correlated sensorimotor experience likely to promote the emergence of congruent  
82 MNs include visual monitoring of one's own actions either directly or in mirrors; being  
83 imitated by others; and synchronous activity in response to a common stimulus (e.g. a crowd  
84 cheering victory in a sporting arena [19]). Sources of non-matching sensorimotor experience  
85 likely to cause the emergence of non-congruent or logically-related MNs include co-ordinated  
86 instrumental action (e.g. when an object is passed between interactants, the sight of object-  
87 releasing predicts the performance of object-grasping [21]) and control behaviours (the  
88 observation of dominant expansive gestures predicts the execution of submissive contractive  
89 movements [22]). The associative account is consistent with evidence that neuroimaging,  
90 electrophysiological and behavioural markers of the human MN system may be readily  
91 modified through correlated sensorimotor experience [23-25].

92

### 93 **3. TOOL-USE & AUDIOVISUAL MIRROR NEURONS**

94 Despite this ongoing debate, direct evidence that macaque MNs acquire their properties  
95 through correlated sensorimotor experience exists within the neurophysiological literature, but  
96 continues to be frequently overlooked. MNs have been reported in the ventral premotor area  
97 F5 of the macaque which discharge both during observation of actions performed by an  
98 experimenter with tools (pliers or a stick) and during manual execution (i.e. performed with  
99 the hands) of the same actions by the macaque [26]. Testing was conducted after a two month  
100 training period during which the tools were used to pass food items to the monkeys.  
101 According to an associative account, this sort of sensorimotor experience is likely to cause  
102 motor representations for grasping food items to become associated with the visual  
103 representations of actions made with sticks and pliers, because the former was reliably  
104 predicted by the latter. Reports of tool-use MNs therefore accord well with the associative  
105 account of MN origins, and appear to challenge the view that the sensorimotor matching  
106 properties of MN's are an innate endowment [11].

107

108 So-called ‘audiovisual’ MNs have also been identified in the F5 region of the macaque  
109 premotor cortex [27, 28]. In addition to the sight and execution of actions, these neurons also  
110 respond to the sounds associated with actions. A range of ripping and tearing sounds cause F5  
111 MNs to discharge including the sound of a peanut breaking; paper ripping; plastic crumpling;  
112 metal striking metal; and paper shaking. This finding is again entirely consistent with an  
113 associative view. Action execution is frequently predictive of both action observation and  
114 characteristic ‘action sounds’. Repeated exposure to these sensorimotor contingencies will  
115 cause the motor representations for ripping and tearing to become associated with both the  
116 auditory and visual sensory consequences. Consistent with reports of tool-use MNs,  
117 audiovisual MNs also suggest that the linkage between sensory and motor representations  
118 appears to be determined by the correlated sensorimotor experience that individuals are  
119 exposed to.

120

121 Reports of tool-use and audiovisual MNs appear to argue against the nativist account:  
122 Evidently MNs may emerge which respond to seemingly arbitrary stimuli provided they have  
123 been paired contingently with the execution of an action. However, ‘mediated activation’  
124 accounts may be advanced to sustain the innate MN hypothesis, if it is assumed that the sight  
125 of tool actions, or action sounds, become associated, not with motor programs directly, but  
126 rather with hardwired visual descriptions of hand actions [18, 26] or hardwired  
127 representations of “action goals” (*cf.* [29]). The observation of grasping with pliers or the  
128 sound of paper tearing might thereby excite motor representations indirectly, via innate  
129 representations of grasping or tearing (Figure 1), rather than via direct sensorimotor  
130 associations. According to mediated activation accounts, sensory-sensory associations are  
131 acquired through experience, rather than sensorimotor associations.

132

133 Nevertheless, while logically plausible, mediated activation accounts cannot explain all of the  
134 neuronal responses observed. Crucially, tool-use MNs discharged significantly less often, if at  
135 all, to the sight of actions performed with biological effectors, despite robust responses to the  
136 sight of the same actions performed with tools [26, p214]. Similarly, several audiovisual MNs  
137 showed no response to the sight of their effective action alone [28, p847], or responded more

138 strongly to the sound of actions than to the combined sight and sound of actions [27, p633].  
139 These observations are inconsistent with mediated activation accounts, as they imply that the  
140 receptive fields of tool-use and audiovisual MNs are tuned to the sensory inputs of tool  
141 actions and action sounds, rather than to i) the sight of actions executed with biological  
142 effectors or ii) to the ‘goals’ of actions. Mediated activation accounts predict the opposite  
143 pattern; that MNs ought to respond maximally to the sight of hand actions executed with  
144 biological effectors, indicative of tuning, and weaker responses to any associated sensory  
145 inputs. These observations suggest that the sight of tool actions and sensory representations of  
146 action sounds excite motor representations directly and not via intermediate hardwired  
147 representations.

148

#### 149 **4. CONCLUSION**

150 Despite being frequently overlooked within the literature, the existence and properties of tool-  
151 use and audiovisual MNs argue against the view that the sensorimotor matching properties of  
152 MNs are an innate endowment; a product of natural selection [3, 12-14]. These reports  
153 indicate that the receptive fields of MNs may be tuned to sensory inputs to which the  
154 subjects’ ancestors could not possibly have been exposed; e.g. the sight of actions performed  
155 with pliers or to the sound of a plastic crumpling. Instead, such findings accord well with the  
156 view that all MNs acquire their sensorimotor matching properties ontogenetically, through  
157 correlated sensorimotor experience [11, 19, 20].

158

159 To account for the evidence provided by tool-use and audiovisual MNs, nativist MN theory  
160 needs to posit these units are somehow qualitatively distinct from the MNs that could become  
161 hardwired through natural selection [18, 30]. However, delineating different classes of MNs  
162 on the basis of which units accord with a nativist account, and which do not, may be  
163 construed as fitting data to theory and not theory to data. Attempts to distinguish audiovisual  
164 and tool-use MNs from those units which respond the observation and execution of actions  
165 made with biological effectors appear redundant when an associative framework [11, 19, 20]  
166 offers a single comprehensive account of the existence and properties of all of these  
167 sensorimotor units.

168

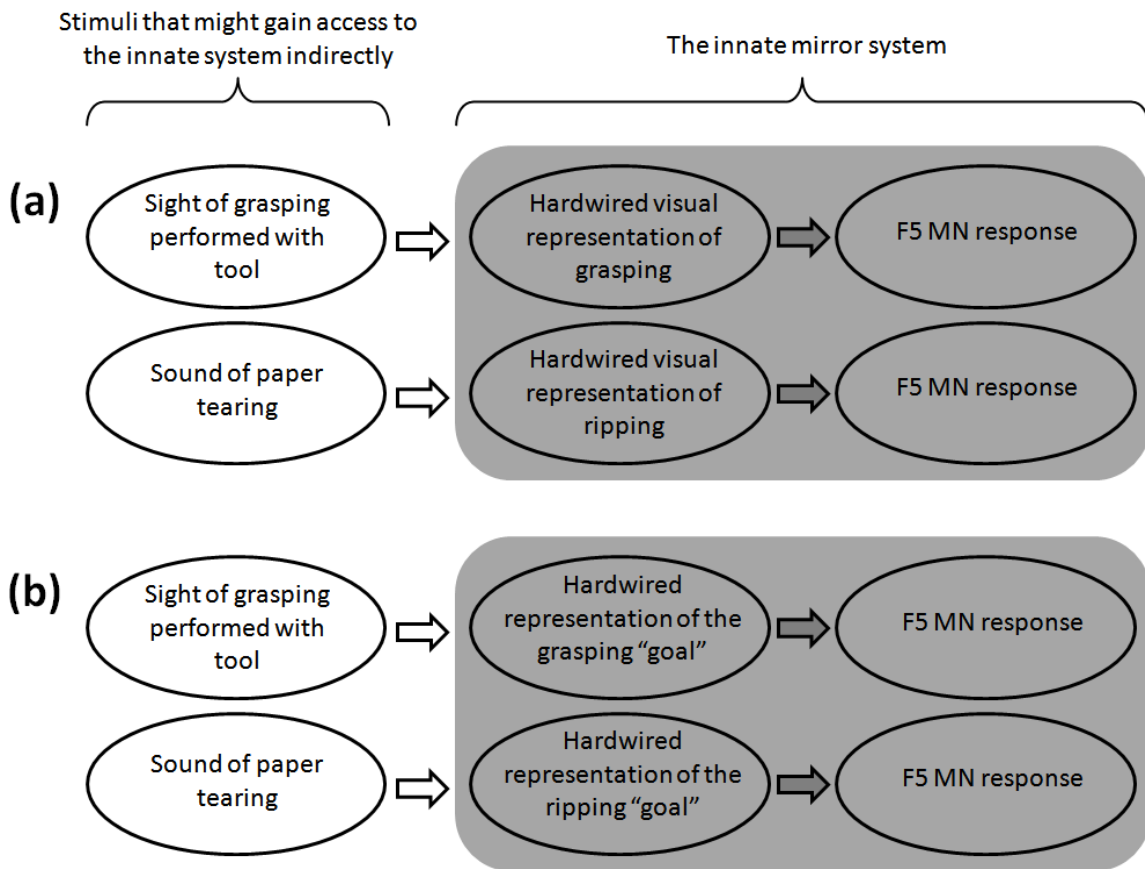


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172

173 **FIGURE:**



174

175 Figure 1: Mediated activation accounts may be proposed to explain MN responses to tool-use  
176 and action sounds if it is assumed that sensory inputs gain access to an innate MN system via  
177 (a) hardwired visual descriptions of action executed with biological effectors, or (b)  
178 hardwired representations of abstract action goals. However, while these interpretations are  
179 logically plausible, findings that MNs show stronger responses to the sight of actions  
180 performed with tools, and to action sounds, than to the sight of grasping or ripping alone,  
181 argue against mediated activation. Instead, some MNs appear to have receptive fields tuned to  
182 sensory inputs other than the sight of gripping or tearing executed with biological effectors.

183

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