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The ontogenetic origins of mirror neurons:

Evidence from 'tool-use' and 'audiovisual' mirror neurons

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12   **Richard Cook**

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14   Department of Psychology,

15   City University London, UK.

16   Richard.Cook.1@city.ac.uk

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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.

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1. INTRODUCTION

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

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

2. THE ORIGINS OF MIRROR NEURONS

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

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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.

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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.

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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].

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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
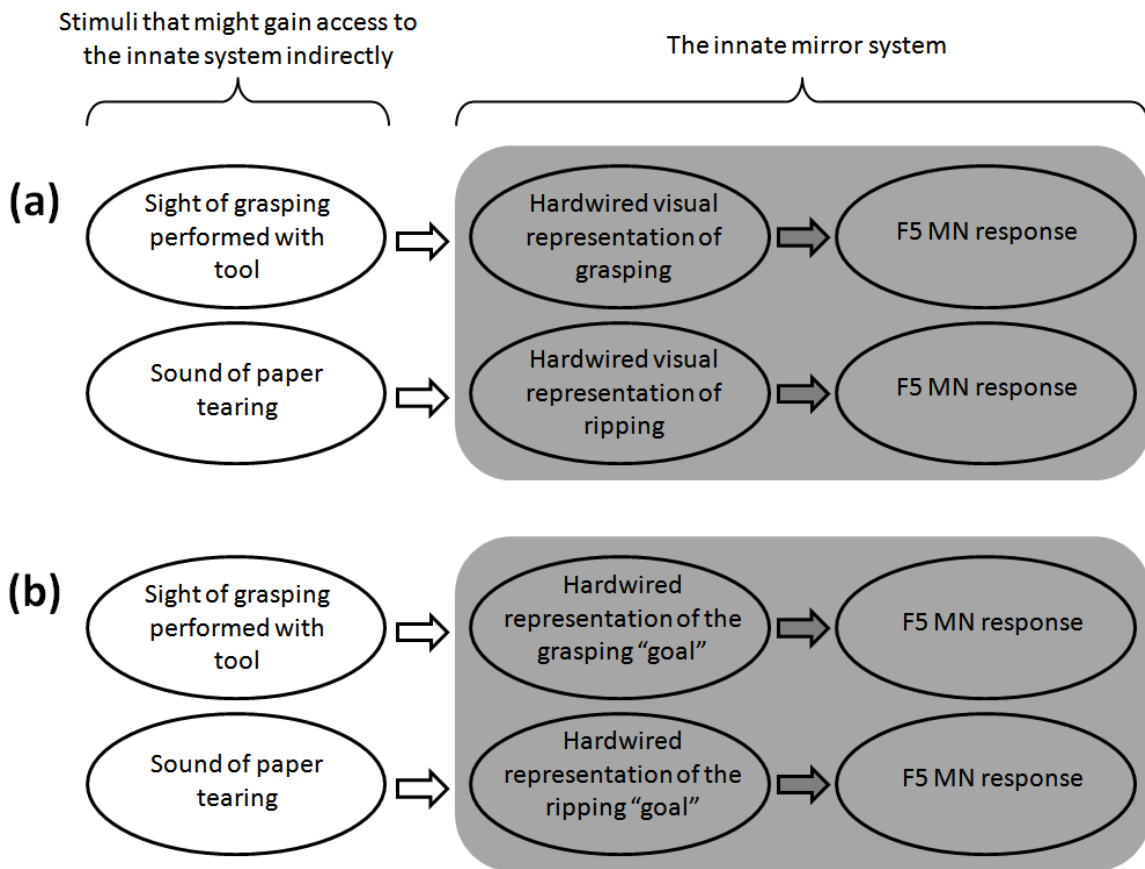167 sensorimotor units.

168

FIGURE:

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

184   **REFERENCES:**

185   1.   di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. & Rizzolatti, G. 1992 Understanding
186   motor events: a neurophysiological study. *Experimental Brain Research* **91**, 176-180.

187   2.   Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. 1996 Action recognition in the premotor
188   cortex. *Brain* **119 (Pt 2)**, 593-609.

189   3.   Rizzolatti, G., Fadiga, L., Gallese, V. & Fogassi, L. 1996 Premotor cortex and the recognition
190   of motor actions. *Cognitive Brain Research* **3**, 131-141.

191   4.   Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F. & Rizzolatti, G. 2005 Parietal
192   lobe: from action organization to intention understanding. *Science* **308**, 662-667.

193   5.   Rozzi, S., Ferrari, P.F., Bonini, L., Rizzolatti, G. & Fogassi, L. 2008 Functional organization
194   of inferior parietal lobule convexity in the macaque monkey: electrophysiological characterization of
195   motor, sensory and mirror responses and their correlation with cytoarchitectonic areas. *European*
196   *Journal of Neuroscience* **28**, 1569-1588.

197   6.   Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles,
198   K., Rizzolatti, G. & Freund, H.J. 2001 Action observation activates premotor and parietal areas in a
199   somatotopic manner: an fMRI study. *European Journal of Neuroscience* **13**, 400-404.

200   7.   Kilner, J.M., Neal, A., Weiskopf, N., Friston, K.J. & Frith, C.D. 2009 Evidence of mirror
201   neurons in human inferior frontal gyrus. *Journal of Neuroscience* **29**, 10153-10159.

202   8.   Mukamel, R., Ekstrom, A.D., Kaplan, J., Iacoboni, M. & Fried, I. 2010 Single-neuron
203   responses in humans during execution and observation of actions. *Current Biology* **20**, 750-756.

204   9.   Gallese, V., Gernsbacher, M., Hickok, G., Heyes, C. & Iacoboni, M. 2011 Mirror neuron
205   forum *Perspectives on Psychological Science* **6**, 369-407.

206   10.   Rizzolatti, G. & Fabbri-Destro, M. 2010 Mirror neurons: from discovery to autism.
207   *Experimental Brain Research* **200**, 223-237.

208   11.   Heyes, C. 2010 Where do mirror neurons come from? *Neuroscience and Biobehavioral*
209   *Reviews* **34**, 575-583.

210   12.   Rizzolatti, G. & Craighero, L. 2004 The mirror-neuron system. *Annual Review of*
211   *Neuroscience* **27**, 169-192.

212   13.   Rizzolatti, G. & Arbib, M.A. 1998 Language within our grasp. *Trends in Neurosciences* **21**,
213   188-194.

214   14.   Gallese, V. & Goldman, A. 1998 Mirror neurons and the simulation theory of mind-reading.
215   *Trends in Cognitive Sciences* **2**, 493-501.

216   15.   Gallese, V. & Sinigaglia, C. 2011 What is so special about embodied simulation? *Trends in*
217   *Cognitive Sciences* **15**, 512-519.

218   16.   Ferrari, P.F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A. & Suomi, S.J. 2006
219   Neonatal imitation in rhesus macaques. *PloS Biology* **4**, 1501-1508.

220   17.   Meltzoff, A.N. & Moore, M.K. 1977 Imitation of facial and manual gestures by human
221   neonates. *Science* **198**, 74-78.

222   18.   Ferrari, P.F., Bonini, L. & Fogassi, L. 2009 From monkey mirror neurons to primate
223   behaviours: possible 'direct' and 'indirect' pathways. *Philosophical Transactions of the Royal Society*
224   *B-Biological Sciences* **364**, 2311-2323.

225   19.   Ray, E. & Heyes, C. 2011 Imitation in infancy: the wealth of the stimulus. *Developmental*
226   *Science* **14**, 92-105.

227   20.   Heyes, C. 2001 Causes and consequences of imitation. *Trends in Cognitive Sciences* **5**, 253-
228   261.

229   21.   van Schie, H.T., van Waterschoot, B.M. & Bekkering, H. 2008 Understanding action beyond
230   imitation: reversed compatibility effects of action observation in imitation and joint action. *Journal of*
231   *Experimental Psychology: Human Perception and Performance* **34**, 1493-1500.

232   22.   Tiedens, L.Z. & Fragale, A.R. 2003 Power moves: Complementarity in dominant and

233   submissive nonverbal behavior. *Journal of Personality and Social Psychology* **84**, 558-568.

234   23.   Calvo-Merino, B., Grezes, J., Glaser, D.E., Passingham, R.E. & Haggard, P. 2006 Seeing or

235   doing? Influence of visual and motor familiarity in action observation. *Current Biology* **16**, 1905-

236   1910.

237   24.   Catmur, C., Walsh, V. & Heyes, C. 2007 Sensorimotor learning configures the human mirror

238   system. *Current Biology* **17**, 1527-1531.

239   25.   Heyes, C., Bird, G., Johnson, H. & Haggard, P. 2005 Experience modulates automatic

240   imitation. *Cognitive Brain Research* **22**, 233-240.

241   26.   Ferrari, P.F., Rozzi, S. & Fogassi, L. 2005 Mirror neurons responding to observation of

242   actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience* **17**,

243   212-226.

244   27.   Keysers, C., Kohler, E., Umilta, M.A., Nanetti, L., Fogassi, L. & Gallese, V. 2003

245   Audiovisual mirror neurons and action recognition. *Experimental Brain Research* **153**, 628-636.

246   28.   Kohler, E., Keysers, C., Umilta, M.A., Fogassi, L., Gallese, V. & Rizzolatti, G. 2002 Hearing

247   sounds, understanding actions: action representation in mirror neurons. *Science* **297**, 846-848.

248   29.   Csibra, G. 2007 Action mirroring and action understanding: an alternative account. In

249   *Sensorimotor Foundations of Higher Cognition Attention and Performance XXII* (eds. Haggard P.,

250   Rosetti Y., Kawato M.). Oxford, Oxford University Press.

251   30.   Rochat, M.J., Caruana, F., Jezzini, A., Escola, L., Intskirveli, I., Grammont, F., Gallese, V.,

252   Rizzolatti, G. & Umilta, M.A. 2010 Responses of mirror neurons in area F5 to hand and tool grasping

253   observation. *Experimental Brain Research* **204**, 605-616.

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