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Brain  
and  
Cognition

Brain and Cognition xxx (2003) xxx-xxx

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# New insights on sensorimotor integration: From hand action to speech perception

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Accepted 14 April 2003

## 8 Abstract

9 In the last two decades the integrative role of the frontal premotor cortex (a mosaic of agranular/disgranular areas lying in front  
10 of the primary motor cortex) have been more and more elucidated. Among its various functions, sensorimotor transformation, and  
11 action representation storage, also for nonstrictly motor purposes, are the most intriguing properties of this region, as shown by  
12 several researches. In this article we will mainly focus on the ventro-rostral part of the monkey premotor cortex (area F5) in which  
13 visual information describing objects and others' acting hands are associated with goal-directed motor representations of hand  
14 movements. We will describe the main characteristics of F5 premotor neurons and we will provide evidence in favor of a parallelism  
15 between monkeys and humans on the basis of new experimental observations. Finally, we will present some data indicating that,  
16 both in humans and in monkeys, action-related sensorimotor transformations are not restricted to visual information but concern  
17 also acoustic information.  
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## 20 1. Introduction

21 The capacity to use the hand for grasping objects  
22 represents an evolutionary new ability that characterizes  
23 the behavior of higher primates. The "precision grip,"  
24 characterized by the opposition of the index finger and  
25 the thumb in order to grasp and manipulate small ob-  
26 jects, represents the zenith of such an ability. The ki-  
27 nematic analysis of grasping movements shows that the  
28 finger configuration present when the hand makes con-  
29 tact with an object, is the final outcome of a complex  
30 motor sequence starting at the beginning of the reach-  
31 ing-grasping movement (Jeannerod, 1988). As soon as  
32 the arm begins to move toward the object, the fingers  
33 start assuming the configuration necessary for grasping  
34 it (preshaping). The maximal aperture of the hand, al-  
35 though larger than that necessary for grasping the ob-  
36 ject, has a fixed relation with the size of the object. It is  
37 evident from this description that there are two funda-  
38 mental requisites which are necessary for an effective

execution of grasping movements: (i) the capacity to 39  
transform the intrinsic visual properties of the object 40  
(shape and size) into finger movements and (ii) the ca- 41  
pacity to fractionate and independently control finger 42  
movements. 43

Lesion experiments in monkeys and clinical data in 44  
humans show that a correct execution of grasping 45  
movements requires the integrity of area F1 (primary 46  
motor cortex or Brodmann area 4). Lesions of this area 47  
cause a profound deficit in what is a fundamental 48  
property of F1—the control of individual finger move- 49  
ments. As a consequence, individuals with F1 lesions are 50  
almost totally unable to grasp objects. The anatomical 51  
correlate of finger control is represented by the direct 52  
connections that F1 has with individual spinal moto- 53  
neurons. As a result of this arrangement, F1 is able to 54  
overcome the reflex synergies and to recruit spinal cord 55  
motoneurons in variable combinations according to the 56  
size and shape of the object to be grasped. By injecting 57  
neural tracers into the hand field of F1, connections 58  
have been found with several frontal premotor areas. 59  
Among these areas, area F5 receives the largest amount 60  
of object-related visual information from the parietal 61

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62 lobe. Physiological studies confirmed that F5 plays a  
63 crucial role in the organization of grasping movements  
64 (see Jeannerod, Arbib, Rizzolatti, & Sakata, 1995).

65 Area F5 forms the rostral part of inferior area 6  
66 (Fig. 1).

67 Microstimulation and single neuron studies show  
68 that in area F5 are represented hand and mouth  
69 movements. The two representations tend to be spatially  
70 segregated with hand movements mostly represented in  
71 the dorsal part of F5, whereas mouth movements are  
72 mostly located in its ventral part. Although not much is  
73 known about the functional properties of “mouth”  
74 neurons, the properties of “hand” neurons have been  
75 extensively investigated. Rizzolatti et al. (1988) recorded  
76 single neuron activity in monkeys trained to grasp ob-  
77 jects of different size and shape. They found that most of  
78 the hand neurons discharge in association with goal-  
79 directed actions such as grasping, manipulating, tearing,  
80 and holding. F5 neurons do not discharge during finger  
81 and hand movements similar to those effective in trig-  
82 gering them when made with other purposes (e.g.,  
83 scratching, pushing away). Furthermore, many F5  
84 neurons become active during movements that have an  
85 identical goal regardless of the effectors used for at-  
86 taining it. For example, many grasping neurons dis-  
87 charge when the monkey grasps an object with its right  
88 hand, with its left hand or with its mouth.

89 The class of neurons most represented in F5 is that of  
90 grasping neurons. Typically, these neurons begin to  
91 discharge before the contact between the hand and the  
92 object: Some of them stop firing immediately after  
93 contact, whereas others keep firing for a while after it.  
94 The temporal relation between grasping movement and  
95 neuron discharge varies from neuron to neuron. Some  
96 neurons become active during the initial phase of the  
97 movement (opening of the hand), some discharge during

98 hand closure, and others discharge during the entire  
99 grasping movement from the beginning of fingers  
100 opening until their contact with the object. In addition  
101 to temporal specificity, many grasping neurons dis-  
102 charge in association with a particular type of grip.  
103 Most of them are selective for one of the three most  
104 common monkey’s grip types: precision grip, finger  
105 prehension, and whole hand grasping. Sometimes there  
106 is also specificity within the same general type of grip.  
107 For instance, within the whole hand grasping, the pre-  
108 hension of a sphere, which requires the opposition of all  
109 fingers, is codified by different neurons from those  
110 codifying the prehension of a cylinder. A typical exam-  
111 ple of a grasping neuron is shown in Fig. 2. This neuron  
112 fires during precision grip (Fig. 2, top) but not during  
113 whole grasping (Fig. 2, bottom). Note that the neuron  
114 discharges both when the animal grasps with its right  
115 hand and when the animal grasps with its left hand.

116 Taken together, these data show that in area F5 there  
117 is a storage—a “vocabulary”—of motor actions related to  
118 the hand use. The “words” of the vocabulary are rep-  
119 resented by populations of neurons. Each indicates a  
120 particular motor action or an aspect of it. Some indicate  
121 a complete action in general terms (e.g., take, hold, and  
122 tear). Others specify how objects must be grasped, held  
123 or torn (e.g., precision grip, finger prehension, and whole  
124 hand prehension). Finally, some subdivide the action in  
125 smaller segments (e.g., fingers flexion or extension).

## 2. Canonical and mirror “visuomotor responses” in 126 monkeys 127

128 One of the most fascinating neurophysiological dis-  
129 coveries of the last two decades is that some *premotor*  
130 neurons *in addition to their motor discharge, respond also*  
131 *to the presentation of visual stimuli*. Neurons with this  
132 property mainly pertain to Frontal Eye Fields (FEF,  
133 Bruce & Golberg, 1985), to area F4 and to area F5  
134 (Gentilucci, Scandolaro, Pigarev, & Rizzolatti, 1983,  
135 1988; Rizzolatti, Scandolaro, Matelli, & Gentilucci,  
136 1981, 1988) that, taken together, represent the main  
137 target for the inferior parietal lobule projections carry-  
138 ing out visual information. Note that visual responses  
139 are related to the effectors that are somatotopically  
140 represented in these areas.

141 Let us examine the visuomotor responses of area F5.  
142 The motor properties of F5 described in Section 1 are  
143 common to all F5 neurons. If one examines, however,  
144 F5 neurons that respond also to visual stimuli, it be-  
145 comes clear that in this area there are two completely  
146 different categories of visuomotor neurons. Neurons of  
147 the first category discharge when the monkey observes  
148 graspable objects (“canonical” F5 neurons, Rizzolatti et  
149 al., 1988; Rizzolatti & Fadiga, 1998). Neurons of the  
150 second category discharge when the monkey observes

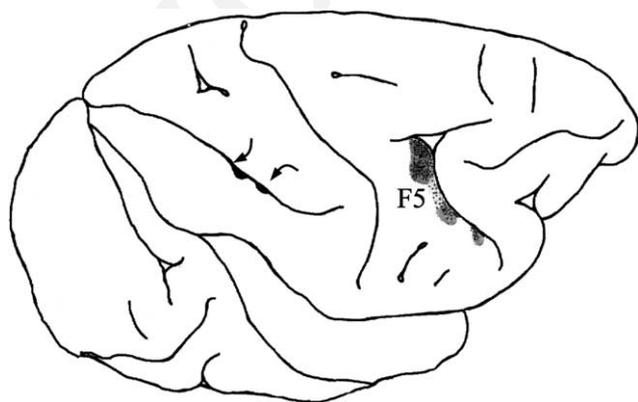


Fig. 1. Lateral view of monkey right hemisphere. Area F5 is buried inside the arcuate sulcus (posterior bank) and emerges on the convexity immediately posterior to it. Area F5 is bidirectionally connected with the inferior parietal lobule. Here, the F5 neurons labeled after two tracer injections (see arrows) in the anterior intraparietal area, are shown.

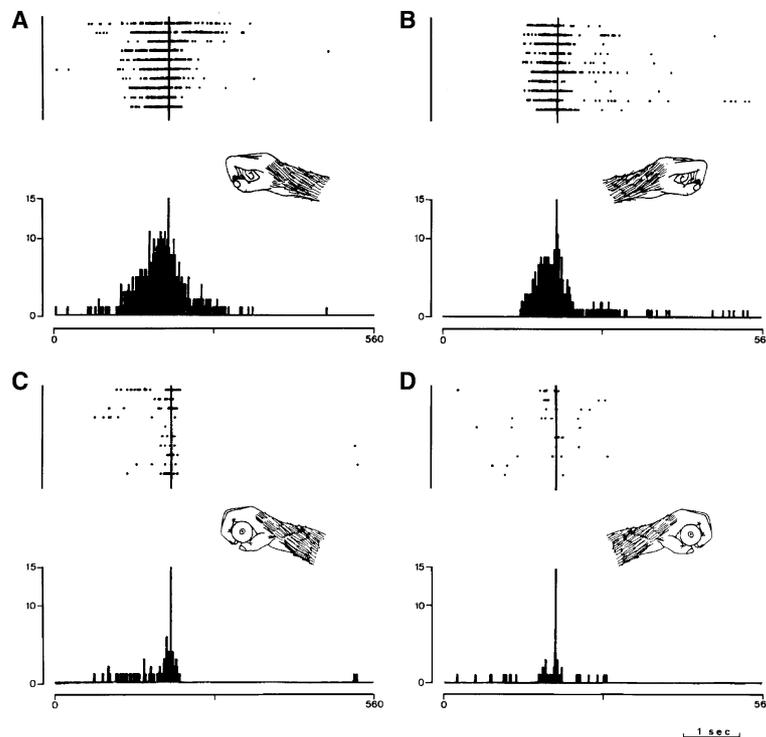


Fig. 2. A typical F5 grasping motor neuron. In the uppermost part of each panel eight successive trials are represented (rasters). Each dot represent an action potential. In the lowermost part the sum histogram is drawn. Trials are aligned with the moment at which the monkey touches the target (vertical lines across rasters and histograms). Ordinates: spikes/second; abscissae: 20 ms bins.

151 another individual making an action in front of it (Di  
152 Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992;  
153 Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti,  
154 Fadiga, Gallese, & Fogassi, 1996a). For this peculiar  
155 “resonant” properties, neurons belonging to the second  
156 category have been named “mirror” neurons (Gallese et  
157 al., 1996). The two categories of F5 neurons are located  
158 in two different sub-regions of area F5: “canonical”  
159 neurons are mainly found in that sector of area F5  
160 buried inside the arcuate sulcus, whereas “mirror”  
161 neurons are almost exclusively located in the cortical  
162 convexity of F5.

163 Recently, the visual responses of F5 “canonical”  
164 neurons have been re-examined using a formal behav-  
165 ioral paradigm, which allowed to separately test the  
166 response related to object observation, during the  
167 waiting phase between object presentation and move-  
168 ments onset, and during movement execution (Murata  
169 et al., 1997). The results showed that a high percentage  
170 of the tested neurons, in addition to the “traditional”  
171 motor response, responded also to visual presentation of  
172 3D graspable object. Among these visuomotor neurons,  
173 two thirds were selective to one or few specific objects.

174 Fig. 3A (grasping in light) shows the responses of a  
175 F5 visually selective neuron. While observation and  
176 grasping of a ring produced strong responses, responses  
177 to the other objects were modest (sphere) or virtually  
178 absent. Fig. 3B (object fixation) shows the behavior of

the same neuron during the mere fixation of the same 179  
objects. In this condition the objects were presented in 180  
the same way as during the task represented in A, but 181  
grasping was not allowed and, at the go-signal, the 182  
monkey had simply to release a key. Note that in this 183  
condition the object is totally irrelevant for task execu- 184  
tion, which only requires the detection of the go-signal. 185  
Nevertheless, the neuron strongly discharged at the 186  
presentation of the preferred object. When visual and 187  
motor properties of F5 neurons are compared, it be- 188  
comes clear that there is a strict congruence between the 189  
two types of responses. Neurons that become active 190  
when the monkey observes small size objects, discharge 191  
also during precision grip. On the contrary, neurons 192  
selectively active when the monkey looks at a large ob- 193  
ject, discharge also during actions directed towards large 194  
objects (e.g., whole hand prehension). 195

“Mirror” neurons constitute a class of F5 visuomotor 196  
neurons that become active when the monkey acts on an 197  
object and when it observes another monkey or the experi- 198  
menter making a similar goal-directed action (Di 199  
Pellegrino et al., 1992; Gallese et al., 1996). “Mirror” 200  
neurons appear, therefore, to be identical to “canonical” 201  
neurons in terms of motor properties, but they radically 202  
differ from them as far as visual properties are con- 203  
cerned (Rizzolatti & Fadiga, 1998). 204

The visual stimuli most effective in triggering mirror 205  
neurons discharge are actions in which the experi- 206

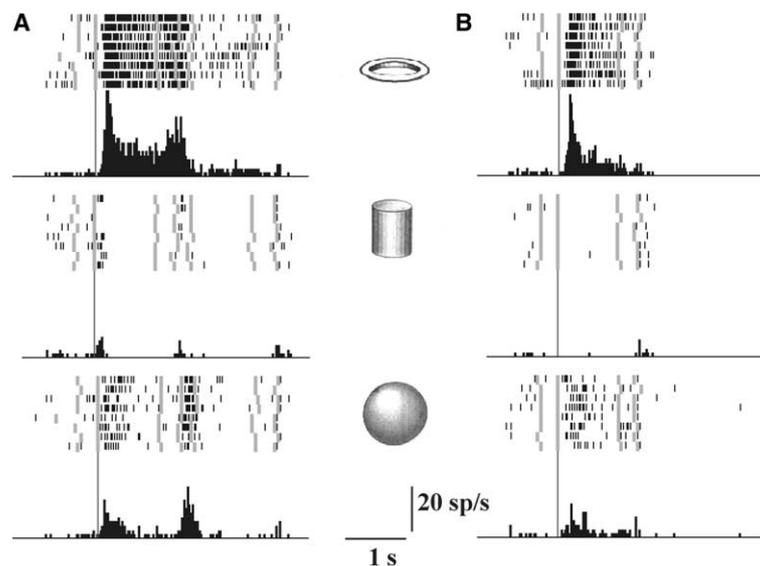


Fig. 3. Responses of a visuomotor neuron of the F5 area. Each panel shows the neuronal activity recorded during the observation and grasping (A) or the mere observation (B) of different 3D objects. The alignment of the single trials coincides with the moment in which the object becomes visible (line through rasters and histogram). In A, the first gray bar following the alignment represents the appearance of the signal which commands the beginning of grasping movement. The conventions used in the visualization of the responses are the same as those used in Fig. 2. Modified from Murata et al. (1997).

207 menter's hand or mouth interacts with objects. The mere  
 208 presentation of 3D objects or food is ineffective in  
 209 evoking mirror neurons discharge. Similarly, actions  
 210 made by tools, even when conceptually identical to those  
 211 made by hands (e.g., grasping with a pliers), do not  
 212 activate the neurons or activate them very weakly. The  
 213 observed actions which most commonly activate mirror  
 214 neurons are grasping, placing, manipulating, and hold-  
 215 ing. Most mirror neurons respond selectively to only one  
 216 type of action (e.g., grasping). Some are highly specific,  
 217 coding not only the type of action, but also how that  
 218 action is executed. They fire, for example, during ob-  
 219 servation of grasping movements, but only when the  
 220 object is grasped with the index finger and the thumb.

221 Typically, mirror neurons show congruence between  
 222 the observed and executed action. This congruence can  
 223 be extremely strict, that is the effective motor action  
 224 (e.g., precision grip) coincides with the action that, when  
 225 seen, triggers the neurons (e.g., precision grip). For  
 226 other neurons the congruence is broader. For them the  
 227 motor requirements (e.g., precision grip) are usually  
 228 stricter than the visual ones (any type of hand grasping).  
 229 One representative highly congruent mirror neuron is  
 230 shown in Fig. 4.

231 It is interesting to note that both canonical and  
 232 mirror neurons are characterized by congruence be-  
 233 tween the action they motorically code and the ob-  
 234 served-object/observed-action that evokes the visual  
 235 discharge.

236 The interpretation we favor for visual discharge in  
 237 canonical neurons is that, at least in adult individuals,  
 238 there is a close link between the most common 3D

stimuli and the actions necessary to interact with them. 239  
 Thus, every time a graspable object is visually presented, 240  
 the related F5 neurons are addressed and the action is 241  
 "automatically" evoked. Under certain circumstances, it 242  
 guides the execution of the movement, under others, it 243  
 remains an unexecuted representation of it that might be 244  
 used also for semantic knowledge. 245

246 The most likely interpretation of mirror neurons is  
 247 that their discharge evokes an internal representation of  
 248 the observed action. In other terms, the observed action  
 249 selects, in the F5 motor vocabulary, a congruent "motor  
 250 word," a potential action.

251 It seems plausible that the visual response of both  
 252 canonical and mirror neurons address the same motor  
 253 vocabulary the words of which constitute the monkey  
 254 motor repertoire. What is different is the way in which  
 255 "motor words" are selected: in the case of canonical  
 256 neurons they are selected by object observation, in the  
 257 case of mirror neurons by the sight of an action. Thus,  
 258 the visuomotor coupling shown by canonical neurons  
 259 could be at the basis of the sensorimotor transformation  
 260 that adapt the hand to a given object. The visuomotor  
 261 discharge that characterizes mirror neurons could be at  
 262 the basis of action imitation and action understanding  
 263 (see Fadiga & Gallese, 1997; Rizzolatti et al., 1996b).

### 3. Canonical and mirror "visuomotor responses" in humans 264 265

266 Recently, a series of studies have addressed the  
 267 question if visuomotor responses, similar to those ob-

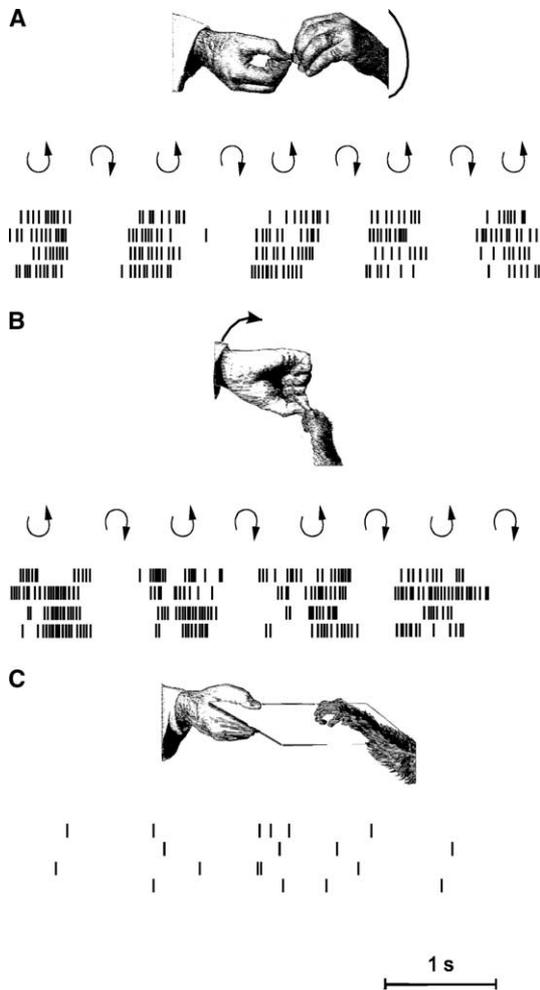


Fig. 4. Example of a highly congruent mirror neuron. The behavioral situations are schematically represented in the upper part of each panel. In the lower part are shown a series of consecutive rasters and the relative peristimulus response histograms. (A) The monkey observes the experimenter who rotates his hands around a raisin in opposite directions alternating clockwise and counterclockwise movements. The response is present only in one rotation direction. (B) The experimenter rotates a piece of food held by the monkey who opposes the experimenter movement making a wrist rotation movement in the opposite direction. (C) Monkey grasps food using a precision grip. Four continuous recordings are shown in each panel. Small arrows above the records indicate the direction of rotations. From Rizzolatti et al. (1996).

268 served in the monkey, are present also in humans. Thus,  
269 by approaching the theme with different techniques,  
270 these studies were aiming to establish the existence of a  
271 link between motor representation and both object-  
272 observation and action-observation.

273 3.1. Object-observation related responses

274 Evidence that an automatic link between objects and  
275 motor programs exists also in humans was recently  
276 provided by reaction time experiments carried out in  
277 normal subjects (Craighero, Fadiga, Umiltà, & Rizzol-

278 atti, 1996, 1998). In these experiments, drawings of dif-  
279 ferently oriented rectangles were presented on a  
280 computer screen around a fixation point before  
281 (-100 ms), simultaneously with (0 ms) or after (+100 ms)  
282 a go-signal, which consisted in a change in color of the  
283 fixation point (see Fig. 5A). At the appearance of the go-  
284 signal, the subject had to respond, as fast as possible, by  
285 grasping an object whose orientation was either the  
286 same or different from that of the presented drawing.  
287 The results showed a difference in reaction times when  
288 the drawings were presented before the go-signal. Re-  
289 action times decreased when the orientation of the  
290 drawing was the same of the orientation of the object to  
291 be grasped (congruent trials) (See Fig. 5B).

292 This facilitatory effect of congruent stimuli was  
293 present only when the drawing was presented before the  
294 go-signal. Note that, being the response exclusively deter-  
295 mined by the go-signal, the analysis of the drawing  
296 has no utility for task solution. The effect of the con-  
297 gruent stimulus indicates, therefore, that the mere ob-  
298 servation of a task-irrelevant visual stimulus  
299 automatically facilitates the grasping of a real object  
300 when the intrinsic properties of the latter are congruent  
301 with those of the drawing.

302 Another evidence that the presentation of an object  
303 may automatically facilitate actions directed to it, is  
304 given by a study of Tucker and Ellis (1998). These au-  
305 thors presented normal human subjects with photo-  
306 graphs of common graspable objects. The subjects had  
307 to decide by a key-pressing made either with the left or  
308 the right hand whether the presented object was upright  
309 or inverted. The results showed that the reaction times  
310 were faster when the key-press response was executed by  
311 the hand most suited to grasp the presented object,  
312 suggesting that visual objects potentiate actions that  
313 may be performed on them, even in the absence of ex-  
314 plicit intentions to act.

315 Direct evidence of an activation of premotor areas  
316 during observation of graspable objects was provided by  
317 a PET experiment (Grafton, Fadiga, Arbib, & Rizzol-  
318 atti, 1997). Normal right-handed subjects were scanned  
319 during observation of bidimensional colored pictures  
320 (meaningless fractals), during observation of 3D objects  
321 (real tools attached to a panel), and during silent naming  
322 of the presented tools and of their use. The most im-  
323 portant result was that the premotor cortex became  
324 active during the simple observation of the tools. This  
325 premotor activation was further augmented when the  
326 subjects named the tool use. This result show that, as in  
327 the case of canonical F5 monkey neurons, also in the  
328 absence of any overt motor response or instruction to  
329 use the observed stimuli, the presentation of graspable  
330 objects increases automatically the activity of premotor  
331 areas.

332 A very recent PET study made by Grèzes and Decety  
333 (2002) indicated that the perception of objects, irre-

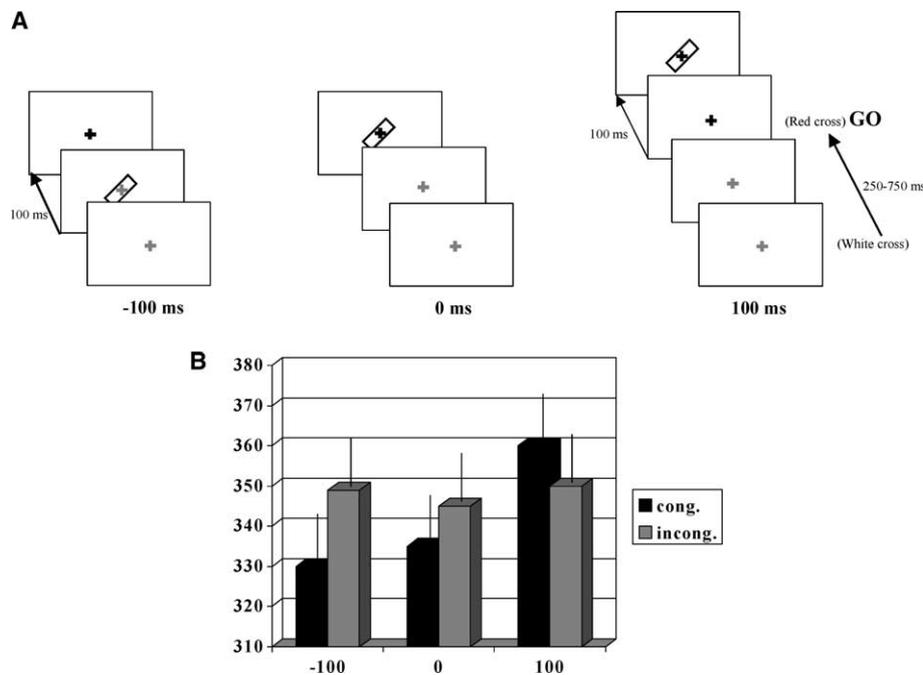


Fig. 5. (A) Schematic representation of the procedure used by Craighero et al. (1998). The beginning of the trial was marked by the appearance of the white (here gray) cross on the screen. After a variable interval (250–750 ms), the cross turned red (here black), giving the signal to execute the grasping response. Before (Stimulus Onset Asynchrony,  $SOA = -100$  ms), simultaneously with ( $SOA = 0$  ms) or after ( $SOA = 100$  ms) the go-signal, drawings representing differently oriented rectangles were presented around the cross. (B) Mean RTs for congruent (cong.) and incongruent (incong.) trials in the three experimental conditions. Standard errors are represented by solid lines above each bar.

334 spectively of the task required to the subject (judgement of  
 335 the vertical orientation, motor imagery, and silent gen-  
 336 eration of the noun or of the corresponding action verb),  
 337 versus perception of non-objects, was associated with  
 338 activation of a common set of cortical regions. The oc-  
 339 cipito-temporal junction, the inferior parietal lobule, the  
 340 SMA-proper, the pars triangularis in the inferior frontal  
 341 gyrus, the dorsal and ventral precentral gyrus were en-  
 342 gaged in the left hemisphere. The ipsilateral cerebellum  
 343 was also involved. These activations are congruent with  
 344 the idea of an involvement of motor representation al-  
 345 ready during the perception of objects, providing evi-  
 346 dence that the perception of objects automatically  
 347 affords actions that can be made toward them.

348 The monkey experiments reviewed above indicate that  
 349 the presentation of graspable objects determines the  
 350 automatic activation of the premotor area F5. From  
 351 monkey neurophysiological studies it is known that the  
 352 main origin of object-related visual information is a pa-  
 353 rietal area buried inside the intraparietal sulcus (area  
 354 AIP, Sakata, Taira, Murata, & Mine, 1995). Given the  
 355 fact that, in general, cortico-cortical connections are bi-  
 356 directional, it is possible that the preparation to act to-  
 357 ward an object facilitates the connected parietal areas  
 358 rendering them more sensitive to detect the object toward  
 359 which the action has been prepared. More in general, this  
 360 putative mechanism could represent a way through  
 361 which “intention to do” can influence perception.

362 The possibility of such a top-down activation was  
 363 recently investigated by Craighero, Fadiga, Rizzolatti,  
 364 and Umiltà (1999). The experiments were carried out in  
 365 normal subjects instructed to grasp a bar (placed out of  
 366 their sight) that could be oriented either clockwise or  
 367 counterclockwise. Before the beginning of each trial the  
 368 subjects were informed about the incoming bar orien-  
 369 tation. The instructions were to prepare the required  
 370 grasping movement and to execute it, as fast as possible,  
 371 at the presentation of a go-signal. The go-signal con-  
 372 sisted of a rectangle which was presented on the com-  
 373 puter screen, around a fixation point. The orientation of  
 374 the rectangle could be either the same or different as that  
 375 of the bar. The results showed that reaction times to  
 376 initiate grasping were faster in response to the rectangles  
 377 whose orientation was the same of the bar to be grasped  
 378 than to the rectangles having an opposite orientation.  
 379 These data indicated that preparation of a specifically  
 380 oriented grasping movement facilitates visual processing  
 381 of stimuli sharing the same intrinsic properties.

### 3.2. Action-observation related responses

382 The first evidence of the existence of mirror-like vis-  
 383 uomotor activation in humans has been provided by  
 384 Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) in a  
 385 transcranial magnetic stimulation (TMS) experiment.  
 386 The motor cortex of normal human participants was  
 387

388 magnetically stimulated and motor evoked potentials  
389 (MEPs) were recorded from intrinsic and extrinsic hand  
390 muscles. It was reasoned that, if the observation of a  
391 hand movement activates the premotor cortex, this  
392 should, in turn, induce an enhancement of MEPs elicited  
393 by the magnetic stimulation of the hand representation  
394 of the motor cortex. The results confirmed this hy-  
395 pothesis showing a pattern of muscle facilitation re-  
396 vealed by TMS during action observation strictly  
397 resembling that occurring during actual execution of the  
398 observed movements. In other terms, looking at a hand  
399 closing onto an object evokes a facilitation of the ob-  
400 server's flexors muscles. Further experiments demon-  
401 strated the cortical origin of this facilitation (Baldissera,  
402 Cavallari, Craighero, & Fadiga, 2001; Strafella & Paus,  
403 2000). Strafella and Paus (2000), by using the double  
404 stimulus TMS technique, showed that the interstimulus  
405 interval (It) between two close stimulations that evoked  
406 the larger motor facilitation during action viewing, was  
407 compatible with cortico-cortical facilitating connec-  
408 tions. Baldissera et al. (2001) investigated the spinal  
409 excitability of hand motoneurons in normal volunteers  
410 while observing a video-clip showing different kinds of  
411 goal directed hand actions. Their results showed that,  
412 during observation of hand actions, the spinal excit-

ability was modulated *reciprocally* with respect to the  
effect shown by Fadiga et al. (1995) during cortical  
stimulation: when subjects were observing finger closing  
onto an object, hand flexors were inhibited while when a  
hand opening movement was shown, hand flexors  
muscles were facilitated. The opposite behavior was  
demonstrated for extensor muscles.

These experiments, taken together, indicate that  
during action observation there is both an activation of  
cortical areas connected (directly and/or indirectly) with  
M1 and the generation, in the spinal cord, of a signal  
opposite in sign that determines the reciprocal behavior  
observed by Baldissera et al. (2001) (see Fig. 6 for a  
schematic view of the proposed mechanism).

Note that the presence of such a peripheral, *move-  
ment-specific* inhibition may favour the cortical pro-  
cessing of observed actions, leaving free the cortical  
motor system to "re-act" the observed actions without  
the risk of overt movements generation. This "motori-  
cally silent" mapping of observed actions on the ob-  
server's motor repertoire might be at the basis of the  
identification/recognition process of actions performed  
by other individuals.

Further evidence that cortical motor areas are acti-  
vated during movement observation comes from MEG

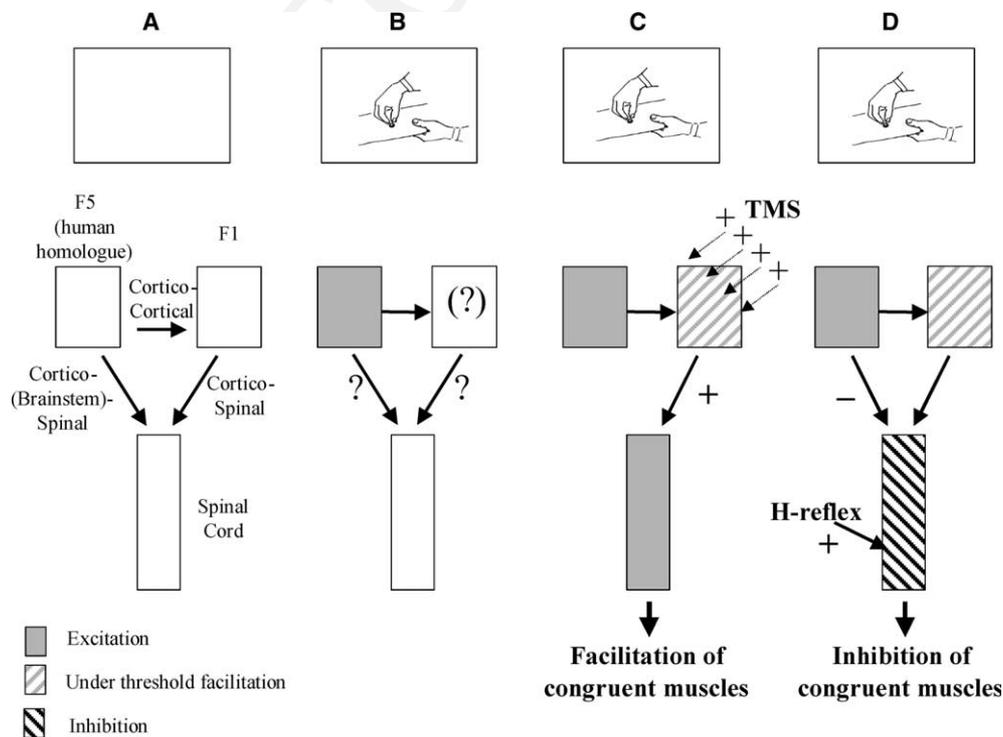


Fig. 6. Effects of action viewing at the cortical and spinal cord levels. (A) Schematic representation of the nervous centers and connections postulated to be involved during action observation. During hand action viewing (B), the human homologue of monkey's area F5 becomes active (mirror neurons, orange). Due to cortico-cortical connections linking F5 with primary motor cortex (F1), the excitation spreads to the primary motor cortex and facilitates it under threshold (diagonal orange bars) (C). We say 'under threshold' because: (1) normally, we do not move when we look at others' actions; (2) single neuron recordings performed in monkey's area F1 never showed activation related to action observation (L.F., personal observation). When TMS is applied on F1 it reveals the underlying facilitation by inducing in hand muscles motor evoked potentials larger than those evoked during control conditions (C). When spinal excitability is tested with H-reflex technique, the reciprocal behavior is shown (D).

438 experiments. Hari et al. (1998) recorded neuromagnetic  
439 oscillatory activity of the human precentral cortex elic-  
440 ited by median nerve stimulation in healthy volunteers  
441 during rest (i), manipulation of a small object kept in  
442 their right hand (ii), and observation of another indi-  
443 vidual performing the same task (iii). The cortical 15–  
444 25 Hz rhythmical activity was measured. In agreement  
445 with previous data (Salmelin & Hari, 1994), this activity  
446 was suppressed during movement execution. Most inter-  
447 estingly, the rhythm was also significantly diminished  
448 during movement observation. Control experiments  
449 confirmed the specificity of the suppression effect. Be-  
450 cause the recorded 15–25 Hz activity originates mostly in  
451 the anterior bank of the central sulcus, it appears that  
452 the human primary motor cortex desynchronizes (and  
453 therefore becomes more active) during movement ob-  
454 servation in the absence of any active movement. Similar  
455 results were obtained also by Cochin, Barthelemy, Le-  
456 jeune, Roux, and Martineau (1998), who recorded EEG  
457 from subjects observing video movies in which human  
458 movements were displayed. As a control, moving ob-  
459 jects, moving animals, and still objects were presented.  
460 The data showed that the observation of human  
461 movements, but not that of objects or animals, desyn-  
462 chronizes the EEG pattern of the precentral cortex.

463 Recently, a series of reaction time experiments in-  
464 vestigated the possibility that the activation of the pre-  
465 motor cortex induced by hand action preparation  
466 facilitates the discrimination of hand poses visually  
467 presented (Craighero, Bello, Fadiga, & Rizzolatti, 2002).  
468 Normal participants were instructed to prepare a hand  
469 grasping movement towards one of two bars that dif-  
470 fered in orientation (clockwise or counterclockwise).  
471 They then had to execute the prepared grasping move-  
472 ment at the presentation of a picture representing a gi-  
473 ven hand pose (go-signal) on the computer screen. Two  
474 were the possible picture presented to subjects and both  
475 of them were images of the right hand as seen in a  
476 mirror. One represented the posture of the hand when it  
477 reached the bar clockwise oriented, the other repre-  
478 sented the posture of the hand when it reached the bar  
479 counterclockwise oriented. At the presentation of the  
480 go-signal the subject had to respond by grasping the bar.  
481 The combination of picture and actual grasping gave  
482 origin to congruent and incongruent conditions. Results  
483 showed that the reaction times were faster when there  
484 was congruency between the hand depicted in the visual  
485 stimulus and the subsequent grip. A possible interpre-  
486 tation of this finding is the presence of a specific visuo-  
487 motor link between the visual stimulus and the sub-  
488 sequent action.

489 Which are the brain areas involved in the action-  
490 observation/execution resonant system? A series of brain  
491 imaging experiments were made in order to assess which  
492 cortical area could be the homologue of the monkey F5  
493 mirror system. Hand grasping movements (Grafton,

Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 494  
1996b) as well as, more recently, more complex hand/ 495  
arm movements were used as visual stimuli (Decety et 496  
al., 1997; Grèzes, Costes, & Decety, 1998). The results of 497  
the first experiments showed that during the observation 498  
of hand grasping there was an activation of the left in- 499  
ferior frontal cortex, in correspondence of the Broca's 500  
region. In addition activations were found in the left 501  
superior temporal sulcus (STS), the rostral part of the 502  
left inferior parietal lobule (area 40), the left opercular 503  
parietal region and the rostral part of the supplementary 504  
motor area (SMA-proper) (Grafton et al., 1996; Riz- 505  
zolatti et al., 1996b). The first three regions most likely 506  
correspond to the monkey cortical areas where there are 507  
neurons that discharge when the monkey observes bio- 508  
logical actions, namely: area F5 (Gallese et al., 1996), 509  
the STS region (Carey, Perrett, & Oram, 1997; Perrett et 510  
al., 1989), and the rostral part of the inferior parietal 511  
lobule (Fogassi, Gallese, Fadiga, & Rizzolatti, 1998). In 512  
studies carried out by the Lyon group (Decety et al., 513  
1997; Grèzes et al., 1998) the involvement of Broca's 514  
area during observation of hand/arm actions was further 515  
confirmed. The authors instructed subjects to observe 516  
meaningful (with a goal) and meaningless movements. 517  
The main results of the condition in which subjects 518  
observed meaningless arm movements were an activa- 519  
tion of the parietal lobe bilaterally, in the left precentral 520  
gyrus and the cerebellum on the right side (Grèzes et al., 521  
1998). On the contrary, the observation of meaningful 522  
hand actions, in addition to the already mentioned 523  
frontal and parietal areas, activates the left inferior 524  
frontal gyrus (Broca's region). Note that the activation 525  
of Broca's region during observation of action, suggests 526  
for this area the putative role of human homologue of 527  
area F5. In this direction point also some comparative 528  
cytoarchitectonical data (see Petrides & Pandya, 1994) 529  
and recent fMRI data from (Binkofski et al. (1999)) 530  
demonstrating that Broca's region become active also 531  
during manipulation of complex objects. In a very recent 532  
fMRI study (Buccino et al., 2001) the authors were 533  
aiming to assess whether the observation of actions 534  
made with different effectors would activate specific 535  
parts of the premotor cortex in accord with the soma- 536  
totoxic organization of the region. While being scanned, 537  
normal participants were asked to carefully observe 538  
different videotaped object- and non-object-related ac- 539  
tions, performed by another individual with different 540  
effectors (mouth, arm/hand, and foot). Results showed 541  
that observation of both object- and non-object-related 542  
actions determined a somatotopically organized activa- 543  
tion of premotor cortex. The somatotopic pattern was 544  
similar to that of the classical motor cortex homunculus. 545  
In addition, during the observation of object-related 546  
actions, an activation, also somatotopically organized, 547  
was found in the posterior parietal lobe. Thus, when 548  
individuals observe an action, an internal replica of that 549

550 action is automatically generated in their premotor  
551 cortex. In the case of object-related actions, a further  
552 object-related analysis is performed in the parietal lobe,  
553 as if the subjects were indeed using those objects. These  
554 results bring the previous concept of an action obser-  
555 vation/execution matching system (mirror system) into a  
556 broader perspective: this system is not restricted to the  
557 ventral premotor cortex, but involves several somato-  
558 topically organized motor circuits.

#### 559 4. Is the visually evoked motor resonance the only 560 example of motor activation induced in the brain by a 561 sensory percept?

562 Both canonical and mirror F5 neurons discharge in  
563 response to visual stimuli. They address a common  
564 reservoir of action representation, that, in our view,  
565 could be used to categorize action-related visual per-  
566 cepts for imitation and identification purposes. Thus, in  
567 the case of canonical neurons, vision of graspable ob-  
568 jects activates the motor representations more appro-  
569 priate to interact with those objects; in the case of mirror  
570 neurons, objects alone are no more sufficient to evoke a  
571 premotor discharge: what is necessary is a visual stim-  
572 ulus describing a goal directed hand action in which  
573 both, an acting hand and a target must be present.  
574 Others' actions, however, do not generate only visually  
575 perceivable signals. Action-generated sounds and noises  
576 are also very common in nature. One could expect,  
577 therefore, that also these sensory information, related to  
578 a particular action, can determine a motor activation  
579 specific for that same action.

580 A very recent neurophysiological experiment ad-  
581 dressed this point. Kohler et al. (2002) investigated  
582 whether there are neurons in area F5 that discharge  
583 when the monkey makes a specific hand action and also  
584 when it *hears* the corresponding action-related sounds,  
585 starting from the observation that a large number of  
586 object-related actions (e.g., breaking a peanut) can be  
587 recognized by a particular sound. The authors found  
588 that 13% of the investigated neurons discharge both  
589 when the monkey performed a hand action and when it  
590 heard the action-related sound. Moreover, most of these  
591 neurons discharge also when the monkey observed the  
592 same action demonstrating that these 'audio-visual  
593 mirror neurons' represent actions independently of  
594 whether they are *performed, heard or seen*.

595 These results have been very recently extended to  
596 humans by a TMS experiment (Fadiga, Craighero,  
597 Buccino, & Rizzolatti, 2002) during speech listening. In  
598 agreement with the idea originally proposed by Liberman  
599 (Liberman, Cooper, Shankweiler, & Studdert-  
600 Kennedy, 1967; Liberman & Mattingly, 1985; Liberman  
601 & Wahlen, 2000), the authors started from the per-  
602 spective that sounds conveying verbal communication

could be a vehicle of motor representations (articulatory 603  
gestures) shared by both the speaker and the listener, on 604  
which speech perception could be based upon. In other 605  
terms, the listener understands the speaker when his/her 606  
articulatory gestures representations are activated by 607  
verbal sounds (motor theory of speech perception). To 608  
test this hypothesis, normal subjects were requested to 609  
attend to an acoustically presented randomized se- 610  
quence of disyllabic words, disyllabic pseudo-words and 611  
bitonal sounds of equivalent intensity and duration. 612  
Words and pseudo-words were selected according to a 613  
consonant-vowel-consonant-consonant-vowel (cvccv) 614  
scheme. The embedded consonants in the middle of 615  
words and of pseudo-words were either a double 'f' 616  
(labiodental fricative consonant that, when pronounced, 617  
requires slight tongue tip mobilization) or a double 'r' 618  
(lingua-palatal fricative consonant that, when pro- 619  
nounced, requires strong tongue tip mobilization). Bi- 620  
tonal sounds, lasting about the same time as verbal 621  
stimuli and replicating their intonation pattern, were 622  
used as a control. The excitability of motor cortex in 623  
correspondence of tongue movements representation 624  
was assessed by using single pulse transcranial magnetic 625  
stimulation (TMS) and by recording motor evoked po- 626  
tentials (MEPs) from the anterior tongue muscles. The 627  
TMS stimuli were applied synchronously with the dou- 628  
ble consonant of presented verbal stimuli (words and 629  
pseudo-words) and in the middle of the bitonal sounds. 630  
Results (see Fig. 7) showed that during speech listening 631  
there is an increase of motor evoked potentials recorded 632  
from the listeners' tongue muscles when the listened 633  
word strongly involves tongue movements, indicating 634  
that when an individual listens to verbal stimuli his/her 635  
speech related motor centers are specifically activated. 636  
Moreover, words-related facilitation was significantly 637  
larger than pseudo-words related one. 638

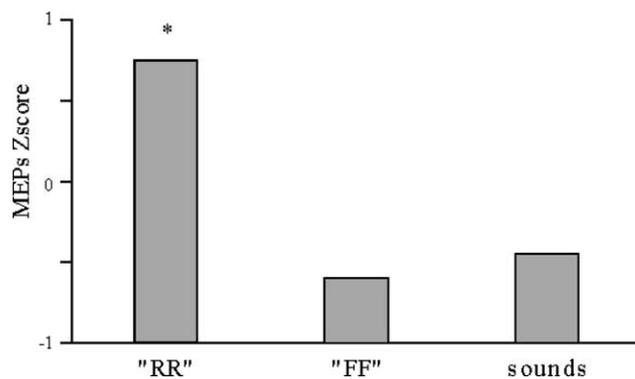


Fig. 7. Average value of intrasubject normalized MEPs total areas. "RR" and "FF" refer to verbal stimuli containing a double lingua-palatal fricative consonant "r," and containing a double labio-dental fricative consonant "f," respectively. The asterisk indicates that the MEPs z-score relative to the experimental condition "RR" is significantly higher than both those relative to the "FF" or the bitonal sounds presentation experimental conditions.

639 The presence of 'audio-visual mirror neurons' in the  
 640 monkey and the presence of speech-related acoustic  
 641 motor "resonance" in humans, indicate that indepen-  
 642 dently from the sensory nature of the perceived stimulus,  
 643 the mirror resonant system retrieves from action vo-  
 644 cabulary (stored in the frontal cortex) the stimulus-re-  
 645 lated motor representations. The immediate translation  
 646 of different sensory information into motor representa-  
 647 tions could be the key to have a congruent, unique  
 648 representation of the environment, always crowded of  
 649 acting individuals, allowing an automatic understanding  
 650 of others' different occupations.

## 651 5. Conclusions

652 The data reviewed in this paper altogether indicate  
 653 that in both monkeys and humans there is a region of  
 654 the premotor cortex that responds to actions-related  
 655 sensory information. Experimental data suggest that in  
 656 this premotor region action representations could be  
 657 evoked by different types of sensory information: the  
 658 mere vision of a sphere on a table, the vision of another  
 659 individual's hand reaching a cup, the sound of the  
 660 breaking of a peanut and, in humans, also the sound of  
 661 the voice of a friend calling us. When an action is evoked  
 662 by visual or acoustic information this region "reso-  
 663 nates" determining in the subject an internal, under-  
 664 threshold for overt movement, activation mimicking the  
 665 grasping of the sphere or of the cup, the breaking of the  
 666 peanut, the articulation of the listened word. There are  
 667 not yet enough experimental data to demonstrate the  
 668 precise function of such a "mirror" system, even if its  
 669 functional characteristics strongly suggest that it could  
 670 be relevant for interindividual relationships (and imita-  
 671 tion). What we know is that there is a brain region  
 672 acting as a comparator between own and others' motor  
 673 representations that could allow individuals to "auto-  
 674 matically understand" the perceived action just because  
 675 they are able to reproduce, when necessary, that same  
 676 action or, in other terms, the same sensory consequences  
 677 of that action.

## 678 Uncited reference

679 Rizzolatti and Gentilucci (1988).

## 680 Acknowledgments

681 This work was supported by EC Contract IST-2000-  
 682 28159, by European Science Foundation and CNR  
 683 (Eurocore OMLL) and University of Ferrara local  
 684 funds. We thank Mrs. C. Clemente for her continuous  
 685 support and collaboration.

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