

Research report

The observation and hearing of eating actions activates motor programs related to eating in macaque monkeys

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Received 19 October 2004; received in revised form 11 January 2005; accepted 19 January 2005

Available online 17 February 2005

Abstract

The observation of actions can lead, in some cases, to the repetition of those same actions. In other words, motor programs similar to those observed can be recruited. Since this phenomenon is expressed when in the presence of another individual, it has been named social facilitation. In the present study we investigated whether the observation and/or hearing of eating actions facilitate eating behaviors in observing/listening pig-tailed macaques. In experiment 1, the observation of an eating room mate significantly enhanced eating behavior in the observer. Similar results were obtained (experiment 2) in response to the sound of eating actions but not to control sounds (experiment 3). We propose that eating facilitation triggered by observation or listening of eating actions can rely on the mirror neuron system of ventral premotor cortex that provides a matching between the observed/listened action and the executed action. This matching system can subsequently trigger the motor programs necessary for repeating the observed/heard actions.

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Keywords: Mirror neurons; Response facilitation; Eating; Behavioral coordination; Imitation; Action observation

1. Introduction

In the macaque's ventral premotor area (F5) there is a class of visuomotor neurons, named mirror neurons [13], that become active both when the monkey makes a specific action with its hand (or mouth) and when the monkey observes similar hand (or mouth) actions performed by another individual [11,13,31]. According to these authors, mirror neurons are implicated in the processes of action recognition, in that the visual description of an action is mapped onto the motor representation of the same action (see [33]). Recently, Kohler et al. [22] described a new class of mirror neurons that become active when monkeys not only observe but also hear the sound of an action (audio-visual mirror neurons). The response of these neurons is specific for the type of action seen and heard. For example, they respond to peanut breaking when the ac-

tion is only observed, only heard or both heard and observed. Conversely, these neurons do not respond to the vision and sound of another action, or to unspecific sounds. In other words, the motor system of the observer is activated whenever appropriate visual and/or acoustic input related to actions are presented, although this does not necessarily imply the production of an overt movement.

Rizzolatti and coworkers [29,30,33] proposed that the internal motor representation of the observed action can be used for response facilitation, i.e. for triggering the repetition of an observed action that is already in the observer's motor repertoire. According to this view, response facilitation is achieved by means of a "resonance" mechanism [29] in which the motor system of the observer (or of the listener) is activated specifically by observing (or listening) actions.

At behavioural level the observation of actions can actually lead, in some cases, to the repetition of those same actions. This phenomenon has been named social facilitation.

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Social facilitation is marked by an increase in the frequency or intensity of behaviors already present in an animal's repertoire, or in the initiation of particular behaviors, when in the presence of others engaged in the same behavior [6,12]. A behavior particularly sensitive to social input is eating. In fact, social facilitation of eating behavior has been reported for a variety of animals [2,8,9,18,19,21,23,34].

Recent studies in capuchin monkeys showed that watching group members eating food increases eating behavior in the observer [14,35,37,38]. These results could be attributed to the observation of food and/or of eating behavior by group members. However, since social facilitation of eating occurs regardless of whether the food eaten by group members matches that available to the observer [37] and since the increase in number of eating group members increases the eating behavior of the observer [35] it is likely that action observation per se plays a primary role in triggering eating behavior.

Although the previously cited studies demonstrated social facilitation of eating behavior in monkeys [37,38,14], clear-cut evidence that the effect is due to action observation or, even less, to action hearing is lacking. The aim of our experiments was to test the hypothesis, based on the mirror system function, that the observation and hearing of eating actions activate the motor programs underlying similar actions, thus facilitating their execution. The study consisted of three experiments labeled according to the stimulus provided by the demonstrator(s) to the experimental subject: (1) observation and hearing of eating actions; (2) hearing of eating actions; (3) hearing of paper-ripping actions.

In order to control for the effect of the observation alone, the use of videoimages would have been theoretically more appropriate. However, we did not employ this methodology for two main reasons: monkey's attention to videoimages tends to drop very rapidly if the monkey has not been highly trained. Second, it has been demonstrated (see [11]) that 2D and 3D video clips of behaving monkeys or humans elicit a weaker response in the observer's mirror neurons than true-acting individuals. This could prevent the motor system of the observing monkey to be facilitated. For these reasons we decided to use a more naturalistic approach.

2. Experiment 1: observation and hearing of eating

Many years ago, Harlow and Yudin [17] reported that rhesus macaques (*Macaca mulatta*) ate more food when in the presence of a feeding conspecific than when alone. More recent and better controlled studies on captive capuchin monkeys (*Cebus apella*) indicated that social facilitation of eating occurs regardless of the monkey familiarity with the food, even when observers are satiated during stimulus presentation [14,36].

However, the studies on social facilitation of eating behavior in capuchin monkeys [14] did not allow to clarify whether

the observation of eating actions per se is sufficient to trigger eating behaviors in the observer.

In order to isolate the effects of action observation on the observer's motor behaviors related to eating, we compared the observer's eating behavior during two periods: (a) baseline period, during which the demonstrator is present but not eating because the food is visible but not available and (b) testing period, in which the demonstrator is eating. Both during testing and baseline the observer was satiated and had plenty of food in its cage.

2.1. Methods

2.1.1. Subjects and housing

Subjects were eight captive-born pig-tailed macaques (*Macaca nemestrina*), aged from 4 to 15 years. Each subject participated in all experiments. All subjects lived at the Primate Section of the Department of Neuroscience in Parma. They were singly housed (cage measuring 100 cm × 160 cm × 100 cm) or pair housed (cage measuring 200 cm × 160 cm × 100 cm). Cages were located indoor (7.02 m × 3.51 m × 2.33 m). Subjects were assigned to two experimental groups (groups 1 and 2) consisting of four animals each. The cages belonging to the monkeys of groups 1 and 2 were at 4–5 m distance from each other and positioned in order to avoid visual contact between groups. Within each experimental group, monkeys had visual and some physical access to each other. All monkeys were accustomed to interacting with the experimenters. Cages were provided with toys and foraging boards.

Monkeys were fed once a day, in the morning (between 8:00 a.m. and 9:30 a.m.), with standard Purina® chow, bread, fruit, carrots, eggs (once a week) and seeds. All experiments complied with the ASAB guidelines and the European law on the humane care and use of laboratory animals.

The experiment consisted of three sessions per subject. Sessions were carried out on three different days. Each session consisted of a 3-min baseline period followed by a 3-min testing period. In each session, there was one demonstrator and one observer (experimental subject), both belonging to the same experimental group. Their cages were positioned in front of each other at a distance of about 1.5 m, to allow visual and auditory contact. All subjects served as observers and the order in which they were tested was randomly balanced. The demonstrator had a light morning meal so that during the test period it was eager to eat. In contrast, the observer was given abundant familiar preferred food (fruit, bread, carrots, and peanuts) in order to satiate it and to have left-over food on the cage floor when, about 2 h after the morning meal, the session started. Before beginning the session the left-over food present in the cages of all monkeys housed in the room was removed with the only exception of the observer's food. This procedure was adopted so that during the experiment only the demonstrator could eat and provide the required input. Moreover, the experimenter started the test only after having checked that the observer did not have food stored in its cheeks, and after having observed it not eating for 5 min.

In the baseline period the experimenter sat at about 2 m from both the demonstrator and the observer and scored the behavior of the latter. Then he gave a large amount of familiar food (pieces of apple) to the demonstrator (this procedure lasted about 15–20 s). During the baseline this food was kept in view of both monkeys in a box near the experimenter. Immediately after the food was

provisioned, the test period began during which the experimenter scored the observer's behavior.

Before the beginning of each session, the experimenter habituated the monkey to his presence. Data were collected by P.F. and C.M. Instantaneous sampling was used to score live eating behavior (bringing food into the mouth and chewing it) at 30-s intervals. This interval was chosen on the basis of observations on the duration of eating bursts. These may last 15–25 s when the monkey eats small pieces of left-over food (i.e. peanuts, pieces of apples, etc.). Since both the baseline and the test period lasted 3 min, there were six scans for each period. At each scan we recorded the occurrence of eating behavior (event). Moreover, latency to eat in the baseline and in the test period was scored by means of a stopwatch. Each session was also videotaped with a VHS videocamera (Sony) positioned so that both the demonstrator and the observer were filmed. This allowed to double check the live scoring made by the experimenters.

2.2. Statistical analysis

The median values of eating events and of eating latencies scored for each subject during baseline and test periods were compared using a Wilcoxon test (two-tailed). Differences in the median numbers of eating scans during baseline and test periods were analysed by Friedman analysis of variance.

2.3. Results

During testing all demonstrators provided the input required by the experimental design, i.e. they continuously ate the provided food. As shown in Fig. 1(A), the observer's eating behavior was by far more frequent during testing than during the baseline ($Z=2.38$, $p<0.02$, Wilcoxon test). Median latencies to eating were 155.3 s (38.3 interquartile interval) during baseline and 66.2 s (33.0 interquartile interval) during testing period, the difference between the two periods being significant ($Z=2.53$, $p<0.02$, Wilcoxon test). Finally, the increase in the eating behavior of the observer occurred already in the first scan of the test period and was evident during the whole test period. As illustrated in Fig. 2(A), the average number of eating events did not differ across the six baseline sampling points, whereas it did differ across the test sample points ($X^2=12.6$, $p<0.02$, Friedman test); in particular, the median value of the last scan of the baseline and that of the fourth scan of the test were significantly different ($Z=2.20$, $p<0.03$, Wilcoxon test).

2.4. Discussion

Our results demonstrate that the observation of eating actions by one demonstrator elicits eating behavior in the observer. The phenomenon of social facilitation of eating is indeed robust; it is triggered very soon by the social input and it lasts as long as the stimulus (i.e. demonstrator eating food) is present. The fact that during baseline as well as during testing the observer was satiated, that the food given to the demonstrator was always in view of the

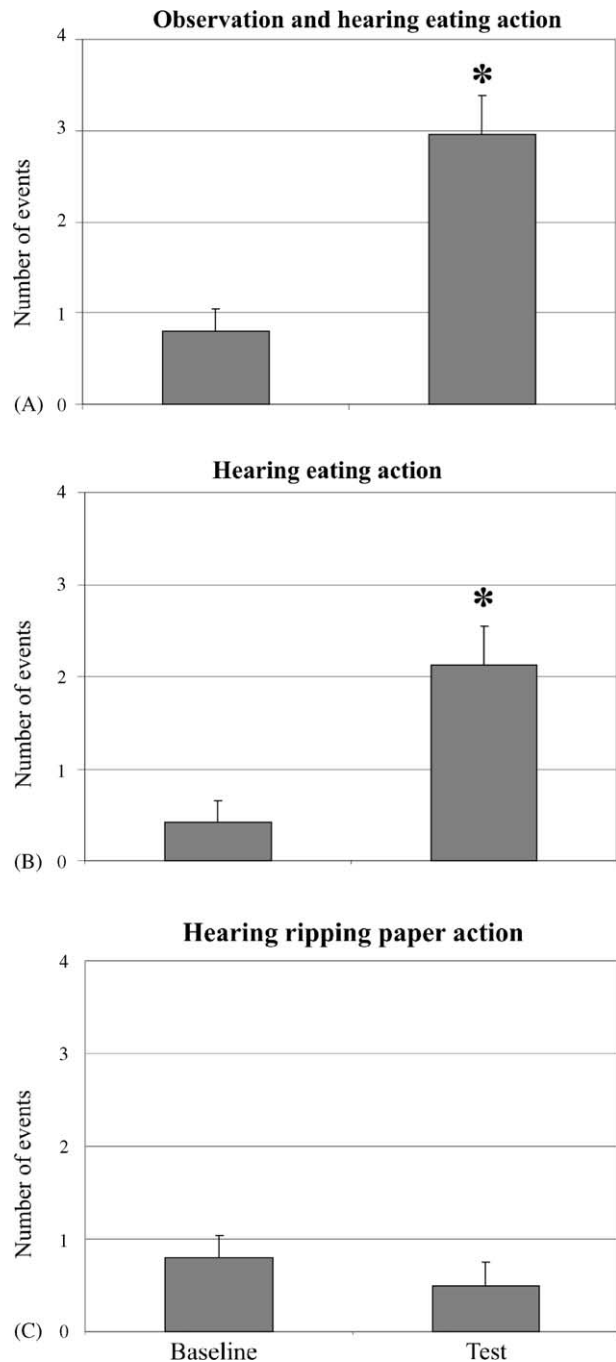


Fig. 1. Mean number of instantaneous eating sample points scored during baseline and test period. Each individual contributed with the averaged value of its three sessions. (A) Experiment 1, (B) experiment 2, and (C) experiment 3. * Indicate significant differences between test and baseline period scan samples ($p<0.05$, Wilcoxon test). Medians difference of eating events between baseline and test period: experiment 1 = 2.0; experiment 2 = 2.5; experiment 3 = 0.5.

observer, and that the observer had food available in its cage during baseline as well as during testing, rule out alternative interpretations of the results (such as stimulus enhancement) other than response facilitation triggered by the observation of eating actions performed by the demonstrator.

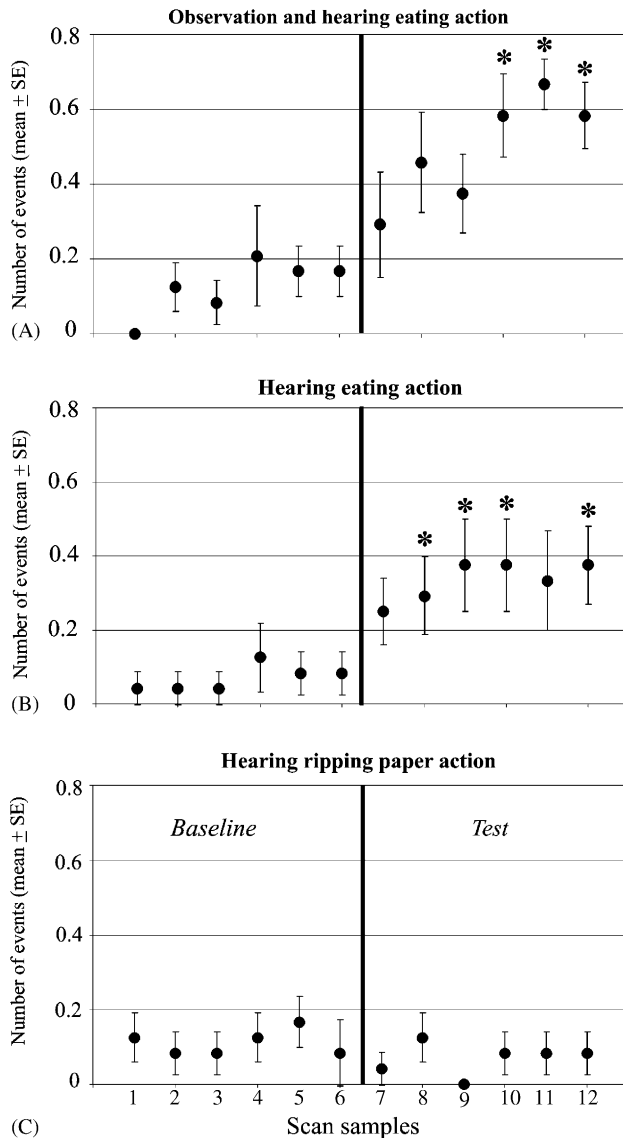


Fig. 2. Mean number of instantaneous eating sample points scored at each scan during baseline and test period. Each individual contributed with the averaged value of its three sessions. (A) Experiment 1, (B) experiment 2, and (C) experiment 3. *Indicate significant differences between the last scan sample during the baseline and the scans samples during the test period ($p < 0.05$, Wilcoxon test).

3. Experiment 2: hearing of eating actions

In experiment 1 the demonstrator was eating apples that, when masticated, produce a specific sound. Therefore, both observing the demonstrator eating and/or hearing the sound produced by eating could account for the results. In experiment 2, we assessed whether the acoustic stimulus related to eating actions alone could trigger motor behaviors related to eating in a listener.

3.1. Methods

Subjects, procedure and data analysis were as in experiment 1. To be sure that the sounds of eating were as much

continuous and salient as possible, we used four demonstrators and peanuts as consumed food. In fact eating peanuts is acoustically more salient than eating apples since breaking of the shell produces a distinctive sound. During baseline the experimenter sat at about 2 m from the listener and scored its behavior. Since the stimulus provided to the experimental subject was the sound of eating, the demonstrators were in the same room but out of view of the observer.

When testing a subject belonging to group 1, the acoustic stimulus was provided by the monkeys of group 2, and vice versa. When the baseline period had elapsed, the experimenter gave peanuts to the monkeys of the other group. This procedure took about 20 s. Then, the test period began. The demonstrators had a light morning meal to make sure that they actually would eat peanuts during the entire test period.

3.2. Results

Since the demonstrators continuously ate the peanuts, they provided the required input during the entire test period. As shown in Fig. 1(B), listeners' eating behavior was by far more frequent during testing than during baseline ($Z = 2.36$, $p < 0.02$, Wilcoxon test). Median latencies to eating were 172.5 s (21.3 interquartile-interval) during baseline and 81.0 s (77.2 interquartile interval) during test period; these values were significantly shorter during testing than during baseline ($Z = 2.52$, $p < 0.02$, Wilcoxon test). Finally, the increase in eating behavior of the listener occurred already in the first scan of the test and was evident during test period. As illustrated in Fig. 2(B), the average number of eating scans did not differ across the six baseline sampling points ($X^2 = 5.55$, NS, Friedman test) nor did it differ across the six test sampling points ($X^2 = 2.40$, NS, Friedman test). In particular, there was a significant difference between the last scan of the baseline and the second scan of the test ($Z = 2.02$, $p < 0.05$, Wilcoxon test).

The noise produced in experiment 1 (one demonstrator eating apples) was different from that of experiment 2 (4 demonstrators eating peanuts). Nevertheless, results show that the observers did not eat more in experiment 2 than in experiment 1 ($Z = 1.06$, NS, Wilcoxon test), nor did their latencies to eat differ significantly ($Z = 0.98$, NS, Wilcoxon test).

3.3. Discussion

Our results demonstrate that sounds produced by eating activities elicit eating behavior in the listener. The phenomenon is indeed robust: it was triggered very soon by the social input and it lasted for the entire test period. Given the different food and procedure (number of demonstrators, distance from the observer, etc.) used in experiments 1 and 2, we can argue that the facilitatory effect produced by hearing eating peanuts is at least as powerful as that produced by observing and hearing eating apples. Further ad hoc designed experiments should investigate the issue of the

respective roles of visual and acoustic stimuli on response facilitation.

4. Experiment 3: hearing of paper-ripping actions

This experiment was carried out to (1) control for the specificity of the acoustic stimulus in activating motor behaviors related to eating and to (2) rule out the possibility that the timing of the test period per se (i.e. the fact that it occurred always after baseline) elicited eating behavior. In fact, it is possible that the probability that a satiated monkey eats increases through time as the motivation to feed increases.

4.1. Methods

Subjects, procedure and data analysis were as in experiment 2 with the only exception that the stimulus was the sound of ripping paper performed by a second experimenter out of view of the listener for the whole duration of the test. To reproduce the experimental procedure of experiments 2, at the end of the baseline period, the experimenter stood up and moved shortly out of view from the listener, as he did in experiment 2 for giving peanuts to the demonstrator monkeys.

4.2. Results

Listeners' eating behavior during baseline and test periods were not significantly different ($Z=0.94$, NS, Wilcoxon test). As shown in Fig. 2(C), average number of eating scans did not differ across the six baseline ($X^2=2.50$, NS, Friedman test) and test ($X^2=5.71$, NS, Friedman test) sampling points. Median latencies to eating were 156.7 s (78.5 interquartile interval) in the baseline and 166.5 s (38.1 interquartile interval) during test; these values were not significantly different ($Z=0.98$, NS, Wilcoxon test).

4.3. Discussion

The results of this experiment rule out the possibility that the sound of an action not related to feeding behavior, (i.e. ripping paper) increases eating. The finding that during the test period of experiment 3 the frequency of eating did not increase rules out the possibility that in experiment 1 and 2 the macaques ate during the test simply because they were more motivated to eat as time went on.

5. General discussion

Our results confirm the view that eating behavior is socially facilitated in monkeys and extend this finding by showing that macaques' eating increases both when they observe or hear eating activities performed by conspecifics [14,17,36]. In other words, motor behaviors related to eating

are triggered by seeing their occurrence in another individual as well as by hearing their occurrence. In addition, our findings show that the observation (and hearing) of the action per se is the key factor in activating similar motor programs in the observer/listener. The increase of eating activities cannot be accounted for by the mere presence of food, since the observer could see the food during both baseline and testing, nor by a generic sound or by an increase of motivation to feed (experiment 3).

Generally speaking, spontaneous repetition of an observed familiar action is not a common phenomenon in monkeys. Why then did we find social facilitation for eating behavior in macaques? A possible explanation might be that this behavior is essential for survival. Feeding in primates is characterised by being primarily social and we can speculate that primates' feeding activities necessitate social sensitiveness aimed at tuning their own behavior with that of group members. Behavioral coordination, i.e. doing the same things at the same time [7] has undoubted advantages; for example, group cohesiveness (that is an effective anti-predator behavioral strategy) is promoted by timing similar activities with others. Accordingly, the discovery and the acceptance of novel food sources are fostered by eating in the vicinity of others eating at the same time. Therefore, eating appears as a behavior for which the motor response triggered by action observation is advantageous for individual survival. In this perspective, it is reasonable to believe that not all behavioral social systems, for example sexual or aggressive behavior, necessitate similar requirements in term of social coordination.

5.1. Social facilitation of eating behavior and neurophysiological mechanisms

Eating behavior requires a complex sequence of motor acts: orienting the body toward food, reaching and grasping it, and finally eating it. It has all the characteristics of a voluntary behavior directed to a goal. Social facilitation of eating behaviors implies the recognition of the observed and heard motor acts and their reproduction. We propose that the mirror neuron system can likely represent the neural basis for social facilitation of eating behavior through a mechanism of resonance of the observed/heard motor acts onto the motor system of the observer/listener representing the same motor acts.

If this hypothesis is correct, the question is which type of mirror neurons could be involved in this social facilitation response. Two recently discovered subcategories of mirror neurons could play a crucial role. The first is constituted by mouth mirror neurons that are activated by the observation and execution of eating actions [11]. The actions coded by these neurons are biting, chewing, sucking, holding, tearing and breaking food; in other words, the motor repertoire involved in eating behavior. The second subcategory is constituted by audio-visual mirror neurons [22]. These neurons respond to the sound of a specific action, for example peanut breaking, and during the execution of the same action. The

activity of these two subcategories of mirror neurons could account for two recognition processes: (a) the recognition of the crucial parts of the observed actions (experiment 1), such as biting the food, introducing it into the mouth and chewing it; (b) the recognition of the same actions from their sound when the demonstrator is out of view (experiment 2).

The view that the visual and acoustic modalities can access the motor cortex by influencing its excitability and that specific actions (either observed or heard) can activate a resonance mechanism probably involving mirror neurons is supported by recent studies in humans. Using transcranial magnetic stimulation (TMS), it has been shown that the observation or hearing of actions increases the motor corticospinal excitability of specific hand muscles [1,10,15]. Furthermore, brain imaging studies showed that ventral premotor/inferior cortical areas (area BA 44) are specifically activated when subjects merely observed hand actions [3,16,32]. It has also been demonstrated that the areas involved during the observation of hand actions are the same that are active during the execution of those same actions [20,25,4] thus confirming the presence of a mirror system also in humans.

Summing up, observing or hearing actions related to eating behavior activate the motor representation of those same actions. This basic mechanism allows individuals to recognise other's actions. In addition, once the motor system related to eating actions 'resonates', this motor information can be used, subsequently, to reproduce the observed/listened actions.

Since it was out of the aims of this study, we did not explore the possibility that the type of food eaten by the demonstrator would elicit a food-specific motor facilitation. However, we should note that what is important for eliciting a discharge in mirror neurons is not the type of object to be grasped but the grasping action performed on it. Thus, if the monkey observes a grasping action on a piece of apple or on a peanut, the same mirror neuron will fire independently from the type of food and hence a facilitation of the motor system would be present in both cases.

One interesting issue is how the mirror system could interact with motivational and decisional systems to facilitate eating behavior by action observation and action hearing. One possibility is that the activation of mirror neurons with action observation/hearing may directly facilitate the motor programs of premotor cortex related to actions similar to the observed/listened ones. In turn, this facilitation process would be extended on one hand, in the motor cortex, to neurons related to ingestive behavior and, on the other, to those brain structures responsible for the motivation of feeding behavior. Once the "motivational" system for eating behavior is activated it may provide information to the premotor cortex in order to select and keep active the appropriate motor programs for eating. Alternatively, the mirror system can be activated by action observation/hearing without directly leading to an overt motor output. In this case, the mirror system activation would trigger the motivational centers for feeding behavior that, in turn, would activate, in the premotor cortex,

the appropriate motor programs involved in eating behavior. Both hypotheses require also an activation of the decisional process that starts the appropriate sequence of eating actions. This process may probably involve prefrontal cortical areas.

The involvement of motivational systems in conjunction with the mirror system in facilitating eating behavior can be supported by neuroanatomical data in monkeys which show that ventral premotor cortex have substantial connections with orbital, medial prefrontal [5,28] and cingulate cortex [24,28]. In addition, it is worth noting that orbitofrontal cortex contains cells responding to gustatory stimuli [26]. According to Carmichael and Price [5], the orbitofrontal connections with premotor areas are important for providing the motivational input that triggers the initiation of feeding. Thus, in premotor areas there is a convergent information of sensory input related to feeding, and of inputs conveying motivational and affective information. However, it is not known, at present, which brain area involved in motivation plays a major role in facilitating motor programs for eating behavior.

5.2. Conclusions

Our findings can be considered the first clear-cut evidence in monkeys of a response facilitation phenomenon that is simply triggered by action observation and action hearing. Moreover, our data provide further information on the possibility that the monkey mirror system can be involved not only in action understanding but also in facilitating behaviors that have important social meaning (i.e. eating). However, a direct evidence of the role of the mirror system in the phenomenon we investigated is required, for example by using reversible inactivation or lesions.

Up to now the only evidence of the mirror system involvement in processes other than action recognition was provided by brain imaging studies in humans. These studies [3,4,20] showed that the mirror system in humans, involving the inferior frontal gyrus (area BA 44) which is the human homologue of monkey area F5 [27], is activated not only during action observation but also during the imitation of observed actions.

In an evolutionary perspective the intrinsic properties of mirror neurons, in particular their activation during action observation/hearing, seem to be suitable for being recruited for social purposes (i.e. response facilitation and imitation). This would not be the first time in which emerging properties of a brain area (i.e. F5) would favour the evolution of new functions.

Acknowledgements

We acknowledge financial support to by the grant RBNE01SZB4 from the FIRB/MIUR and by the CNR that provided E. Addressi with a fellowship.

We would like to thank G. Rizzolatti for his valuable comments on an early draft of the manuscript and A. Paukner for her careful reading and corrections made on the paper.

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