

Selective reaching in macaques: evidence for action-centred attention

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Abstract When a monkey selects a piece of food lying on the ground from among other viable objects in the near vicinity, only the desired item governs the particular pattern and direction of the animal's reaching action. It would seem then that selection is an important component controlling the animal's action. But, we may ask, is the selection process in such cases impervious to the presence of other objects that could constitute potential obstacles to or constraints on movement execution? And if it is, in fact, pervious to other objects, do they have a direct influence on the organization of the response? The kinematics of macaques' reaching movements were examined by the current study that analysed some exemplars as they selectively reached to grasp a food item in the absence as well as in the presence of potential obstacles (i.e., stones) that could affect the arm trajectory. Changes in movement parameterization were noted in temporal measures, such as movement time, as well as in spatial ones, such as paths of trajectory. Generally speaking, the presence of stones in the vicinity of the acting hand stalled the reaching movement and affected the arm trajectory as the hand veered away from the stone even when it was not a physical obstacle.

We concluded that nearby objects evoke a motor response in macaques, and the attentional mechanisms that allow for a successful action selection are revealed in the reaching path. The data outlined here concur with human studies indicating that potential obstacles are internally represented, a finding implying basic cognitive operations allowing for action selection in macaques.

Keywords Reach to grasp · Kinematics · Selective attention · Macaque · Action representation · Motor control

Introduction

Selectivity is one of the most striking features characterizing the behaviour of mammals. Many different objects may be present in a visual field, yet information specific to just one of these objects appears to uniquely determine the spatiotemporal coordinates of the end-point of the reaching and the orientation and opening of the hand. Such selective behaviour is achieved because the many actions that are evoked by visual inputs are not released. Consider the apparently trivial task of selecting a glass from a table containing several other glasses. How does the hand consistently reach that particular glass, given that each of the other glasses represents a potential obstacle? Extremely efficient mechanisms to achieve goals such as these have no doubt evolved linking action/s with targeted object/s (Allport et al. 1985; Allport 1987; Neumann 1990). By necessity, these systems must, nevertheless, represent more than just the object targeted for action. As the hand is clearly able to move around as well as above the irrelevant objects (in this case, other glasses), these too must be internally represented (Tipper et al. 1997). These selection mechanisms have been associated with the subjective

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phenomenon of attention by which the mind selects a single input from a multitude of available ones for deeper contemplation and action (James 1890). In short, the environmental context within which a movement will take place is assessed for potential obstructions or disturbances as it must be planned in such a way that the trajectories of contributing body parts are unobstructed.

A number of studies examining the properties of selective reach-to-grasp actions in humans have shown that in some situations motor systems have to process information about the surroundings that are located near to a target. Selection-for-action paradigms (Tipper et al. 1997; Chieffi et al. 1993; Jackson et al. 1995; Castiello 1996, 1998; Howard and Tipper 1997; Bonfiglioli and Castiello 1998; Tresilian 1998; Deubel et al. 1996, 1998; Schiegg et al. 2003; Kritikos et al. 2000; Tresilian 1998) have revealed that the location of the objects surrounding a target determines changes in the motor execution level. More specifically, the kinematic properties of reaching movements have been found to be evoked by nearby objects contaminating those evoked by the target (Tipper et al. 1998; Castiello 1999). In a classic selection-for-action paradigm (Tipper et al. 1997), participants were instructed to initiate reaching after two stimuli (a target and a nearby object) were presented. When the investigators compared a condition in which the target was presented alone with that in which there was a nearby object acting as a potential obstacle, they found that the reaching path was affected in the latter case as the arm trajectory deviated away from the nearby object. This was observed even with regard to nearby objects *that were unlikely obstacles to the reaching action*. As those objects are also included in the initial processing of the whole context where the action will be carried out, the motor program appropriate to avoid them is also produced in parallel, thus producing trajectory changes (Tipper et al. 1992, 1997). Any veering, therefore, could be considered the obstructing effect of the nearby object (Tresilian 1998). This would suggest that the brain considers multiple, simultaneous motor signals before it executes the correct program for a particular target stimulus (Goldberg and Segraves 1987). This effect has been explained in terms of selective attention mechanisms mediating the selection of objects for action, with a specific mechanism acting to inhibit competing internal representations of surrounding objects (Tipper 1985; Tipper et al. 1992; Meegan and Tipper 1998). Put simply, the effects caused by the presence of nearby objects seem to reflect inhibitory mechanisms. Importantly, Tipper and co-workers (e.g., Tipper et al. 1992, 1997) suggested that during selective reaching for a target when there are objects nearby, attention accesses an action-centred internal representation, implying that the frame of reference was the responding hand.

In contrast with a wealth of psychophysical data concerning action selection in humans (Tipper et al. 1998;

Castiello 1999), it is unclear whether this process also applies to motor programming in non-human primates such as macaques. The current study was undertaken with the intent of ascertaining whether the selection principles applied by macaques are similar to those found in humans. The arena of prehensile actions was considered the most favourable condition in comparative terms to investigate action selection mechanisms in macaques given their similarities to humans with regard to their kinematic patterns of reaching and grasping (Fogassi et al. 1991; Christel and Billard 2002; Roy et al. 2000, 2002, 2006; Sartori et al. 2013a, b; Sacrey et al. 2009) and the possibility of capitalizing on a paradigm already successfully utilized to study those mechanisms in humans (Tipper et al. 1997).

The current study was designed to systematically investigate reach-to-grasp movement kinematics in free-ranging macaques as they reached out to grasp pieces of food in the presence or absence of nearby objects that could act as potential obstacles (i.e., stones). We filmed Old World monkeys (*Macaca sylvanus*) from a distance as they reached and grasped objects naturally found in their habitat during their normal activities. We then selected film segments registering those movements performed to grasp one of those food objects in the presence or absence of stones located in close proximity of the hand. Kinematic analysis of some aspects of those movements (movement duration and spatial trajectories) was performed using an in-house software. Other investigators have shown that those parameters efficaciously measure the effects of nearby objects during reaching movements in humans (Tipper et al. 1998; Castiello 1999).

We hypothesized that just as in humans, if monkeys employ action selection principles during reaching movements, the duration of the movement and the path of the arm trajectory should vary depending on nearby viable objects. Evidence, instead, indicated that within a similar timeframe, reaching to grasp movements of the exemplars produced steeper, wider excursions of the elbow and of the wrist, smaller abduction of the shoulder joint and larger displacement of the torso than they do in humans (Christel and Billard 2002), thus suggesting that different control mechanisms are involved. We also hypothesized that different morphological constraints, with specific reference to the wrist, could be linked to diverse strategies utilized for cluttered environments.

Methods

Species studied

Six adult monkeys (*Macaca sylvanus*; common name: *Barbary Macaque*) with an estimated age of no more than

12 years [their age was estimated according to Fa (1984)] all belonging to a fission and fusion troop of about 25 individuals, part of a *Macaca sylvanus* population that has been studied by Camperio Ciani et al. (1999, 2005) since 1983, were included in the study. The troop lives in the Azrou cedar forest located in an area called La Carriere Toumliline, Morocco (Middle atlas—Mixed Cedar and Oak forest near the town of Azrou, 33.15°N; 5.15°W). Eighteen exemplars were visible during the video sequences selected.

Data collection

Video footage was filmed using a digital camcorder (GoPro camera Hero3; sampling rate 100 Hz) exclusively between 10 a.m. and 1 p.m. between the 2 and the 12 September 2013. The hidden camera was located at a distance of 10 m from the monkeys and commanded via a remote control application. In view of the difficulty of filming any particular monkey grasping an object for any length of time before it moved away or turned its back, continuous sampling was considered the more appropriate method to film the exemplars being observed (Altmann 1974). As the study aimed to capture the animals in their natural habitat, a zoom lens was utilized in order to film them from a distance as they sat on the ground or moved from place to place going about their normal activities.

Experimental stimuli

Our attention was focused on analysing movements directed towards those objects/food items leading to precision grips.

Grip classification

The precision grips appearing in the video sequences were classified depending on the areas of skin surface making contact with the objects being grasped. Two operators who were unaware of the study hypothesis and blinded to the experimental conditions were instructed to classify the grips as pinched (precision) when the distal pad of the thumb was opposed to the radial side of the index finger. Cohen's kappa value of 0.78 confirmed inter-rater reliability. It is nevertheless important to remember that in natural situations/environments, spontaneous movements do not necessarily fit into classical precision grip categories: at times three fingers may be involved, and at others, various finger combinations which often flow fluidly from one configuration to another can be observed. For the sake of comparison with previous studies (Roy et al. 2000, 2002, 2006; Fogassi et al. 1991; Sartori et al. 2013a, b, 2014a, b), only precision grip movements in

which the monkey exclusively used the thumb and index fingers were analysed. The current study was exclusively concerned with right-hand reaching movements. The laterality quotient (LQ) was 66 (± 12) with a LQ of 100 reflecting a full right-hand preference (Hopkins 1995).

Test conditions

Segments of grasping movements by the six macaques considered here (200 for each animal) in contexts that were suitable for our experimental hypotheses were extracted. Sixty of these, 15 for each experimental condition being studied, were randomly chosen. Conditions that were analogous to those previously adopted to investigate similar mechanisms in humans (Tipper et al. 1997) were chosen for analysis. These were:

1. Reaching towards a left target situated alone (LTA; Fig. 1a). In this condition, the monkey reached for a stimulus located to the left at a ≈ 17 cm (± 0.5 cm) distance; there were no other objects either to the left or the right near to the reaching hand;
2. Reaching towards a right target situated alone (RTA; Fig. 1b). In this condition, the monkey reached for a stimulus located to the right at a ≈ 17 cm (± 0.5 cm) distance; there were no other objects either to the left or the right near to the reaching hand;
3. Reaching towards the left with a nearby object acting as a potential obstacle in a near-right location (LTO; Fig. 1c). In this condition, the monkey was reaching for a stimulus located to the left at a ≈ 17 cm distance (± 0.5 cm); nearby there was a stone (height: ≈ 7 cm; diameter: ≈ 8 cm) that was *not* impeding a movement to reach the target nor requiring a change in trajectory.
4. Reaching towards the right with a nearby object acting as an obstacle in the near-right location (RTO; Fig. 1d). In this condition, the monkey was reaching for a stimulus located to the right at a ≈ 17 cm distance (± 0.5 cm); nearby there was a stone (height: ≈ 7 cm; diameter: ≈ 8 cm) that could impede reaching the target or that could make a change in trajectory necessary.

Data analysis

The video samples were analysed frame-by-frame using a software developed to perform two-dimensional (2D) post hoc kinematic analysis (AB-ACUS Technologies, Milan, Italy). Markers were inserted manually post hoc via software on the anatomical landmarks of interest on the videos (Fig. 2) and were tracked throughout the time course of the movement sequence. As shown in Fig. 2, markers were positioned on the wrist of each individual so

Fig. 1 Schematic drawing depicting the three experimental conditions and mean wrist trajectories. **a, b** The conditions in which the *left* and the *right* target is reached in isolation, respectively. **c** The *left* target along with the distractor (*solid line*). For the sake of comparison, the *dashed line* represents the mean trajectory path for the *left* target alone condition. **d** The *right* target with the distractor (*solid line*). For the sake of comparison, the *dashed line* represents the mean trajectory path for the *right* target alone condition

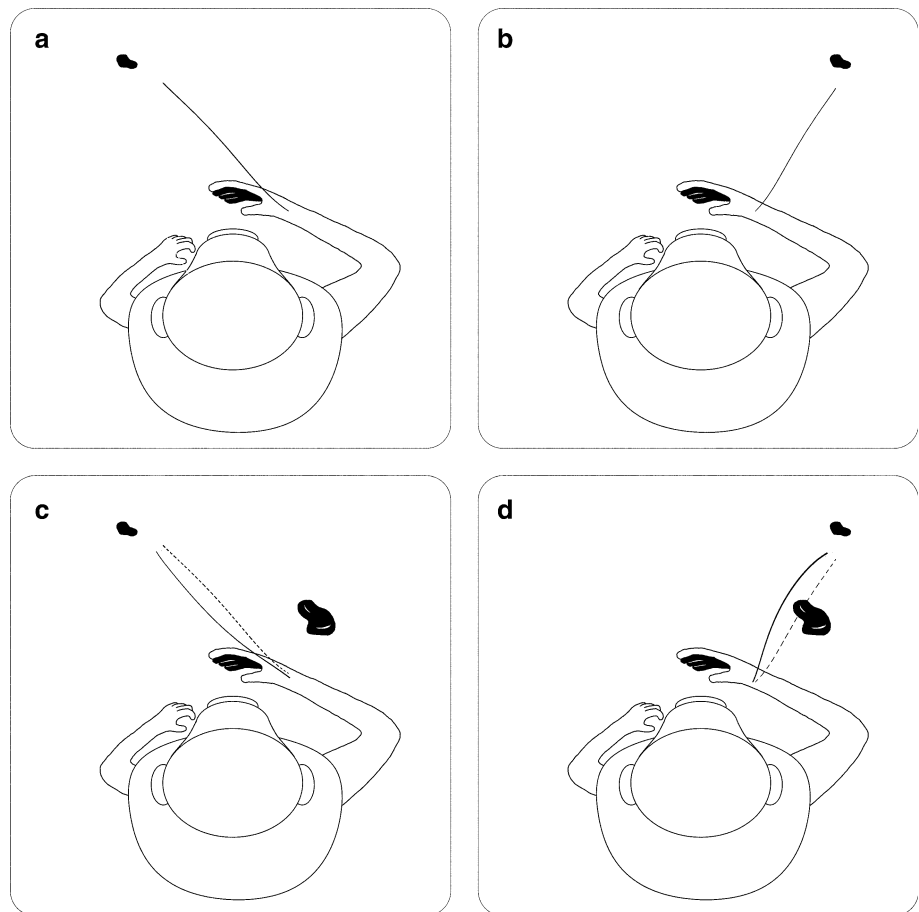
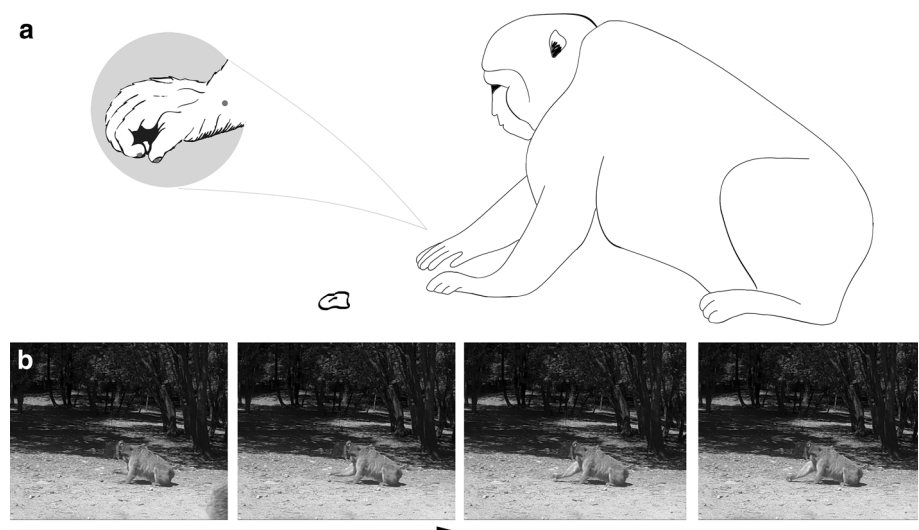


Fig. 2 a Schematic drawing showing the grip posture adopted by an animal. A precision grip (involving the tip of the forefinger and the thumb) used to grasp small objects is represented in the *upper* close up together with the positioning of the markers for the purpose of digitalization. Markers were located (post hoc) on the wrist and on the distal phalanx of the thumb and index finger. **b** A sequence of frames from a representative example



we could calculate the reaching component and on the nails of its index fingers and thumb so we could calculate the grip aperture (i.e., the distance in mm between the marker positioned on the index finger and the marker positioned on the thumb) as a function of time (Roy et al. 2000, 2002, 2006; Sartori et al. 2013a, b, 2014a, b). The

onset of movement was defined as the time the tangential velocity of the wrist marker crossed a threshold (5 mm/s) and remained above it for at least two frames. The end of the movement was defined as the time the fingers closed around the object, and there were no further changes in the distance between the index finger and the thumb (Roy

et al. 2000, 2002, 2006; Fogassi et al. 1991; Sartori et al. 2013a, b, 2014a, b). To avoid any skewing effect, only time frames in which reaching movements were performed along a plane that was perpendicular to the camera axis and in which the animal was located in the central part of the image were selected and analysed. The positioning of the video camera axis and the plane of motion was verified by measuring the length of selected bone elements (e.g., forearm). This procedure was utilized to guarantee a constant point of reference during movements taking place on the plane perpendicular to the camera axis. A frame of reference identifying, respectively, X and Y axes as horizontal (ground) and vertical directions was manually set by the operator. An item within the camera's field of view whose length was known and positioned in the same plane as the movement being observed was used as the reference measurement unit. Movement tracking procedures were performed to extract a number of kinematic parameters. In accordance with previous human studies exploring similar processes (Tipper et al. 1997), the following dependent measures were considered: (1) the movement time (i.e., the time between movement onset and when the monkey's hand grasped the object); (2) the lateral deviation wrist trajectory path; and (3) the maximum trajectory height. Wrist trajectories were calculated for each subject and then normalized over time (100 time steps) to produce mean trajectories of equivalent length for each trial type. The amount of the maximum curvature of the trajectory path from an ideal line linking the starting position and the object location was considered. A positive sign was given to this measure for right-sided deviations, and a negative sign was given to left-sided deviations. The maximum trajectory height was calculated as the maximum height reached by the wrist trajectory along a sagittal plane. The mean values of each dependent measure were calculated for each condition for each subject. The accuracy of the measurement depended on the size of the field of view of the camera and the resolution of the sensor in terms of pixels. In the specific case, accuracy is 3 mm. Mean values were entered into a separate analysis of variance (ANOVA) with the type of trial (LTA, RTA, LTO, RTO) and the target location (right, left) as within subject factors. All the main assumptions behind this statistical model (i.e., normality and sphericity) were checked before running the ANOVAs. The Kolmogorov–Smirnov test revealed that the normality assumption was satisfied (α -level 0.05), and the Mauchly test showed that the sphericity assumption was not violated (α -level 0.05). The post hoc pairwise comparisons of the SD analysis were carried out using t tests, and the Bonferroni adjustment for multiple comparisons was applied.

Results

Kinematics of the reach-to-grasp movement: general description

These findings were found to be in accordance with classical kinematic descriptions of reach-to-grasp movements in both humans and macaques (Castiello 1996; Fogassi et al. 1991; Christel and Billard 2002; Roy et al. 2000; Sartori et al. 2013a, b; Gentilucci et al. 1991; Jakobson and Goodale 1991). The reaching component was characterized by a bell-shaped wrist velocity profile with a single peak occurring at about 52% of the total movement time. The grasping component was characterized by a maximum grip aperture, which occurred at about 73–75% of the total movement time followed by a gradual closure of the grip, which was scaled to object size.

The effects of the nearby object

The main factor type of trial was significant for movement time [$F(1,5) = 47.22$, $P = 0.001$, $\eta_p^2 = 0.71$], the lateral deviation of the trajectory of the wrist [$F(1,5) = 28.06$, $P = 0.001$, $\eta_p^2 = 0.63$] and the maximum trajectory height [$F(1,5) = 32.12$, $P = 0.0001$, $\eta_p^2 = 0.75$]. The main effect of target location was not significant for the dependent measures considered [movement duration: $F(1,5) = 2.11$, $P = 0.12$; lateral deviation of the wrist trajectory: $F(1,5) = 1.48$, $P = 0.15$; trajectory height: $F(1,5) = 1.86$, $P = 0.18$].

Temporal effects

The movement duration for the LTO condition was longer than it was for the LTA one ($P < 0.05$; Table 1). Movements for the RTO condition were longer than those for the RTA one ($P < 0.05$; Table 1). The presence of a nearby object was found to increase the movement time for both right and left targets.

Spatial effects

Trajectory deviation. For left reaches, reaching deviations to the left were greater for the LTO than for the LTA condition ($P < 0.05$; see Fig. 1; Table 1). For right reaches, movements in the RTO condition were characterized by greater path deviations away from the nearby objects than those in the RTA condition ($P < 0.05$; Table 1).

Trajectory height. For right reaches in which the nearby object was really an obstacle, movements in the RTO condition were characterized by a higher maximum

Table 1 Mean scores for the considered dependent variables in the four experimental conditions

	RTA	RTO	LTA	LTO
Movement duration (ms)	487 (± 54)	528 (± 58)	492 (± 51)	533 (± 60)
Lateral deviation trajectory path (mm)	-4.8 (± 0.4)	-8 (± 0.5)	-4.2 (± 0.3)	-9.0 (± 0.7)
Maximum trajectory height (mm)	55 (± 6)	81 (± 8)	57 (± 6)	79 (± 7)

RTA right target alone, RTO right target with potential obstacle, LTA left target alone, LTO left target with potential obstacle

trajectory than those in the RTA one ($P < 0.05$; Table 1). For left reaches in which a nearby object was present although it did not represent an obstacle, the maximum trajectory height was greater for the LTO than for the LTA condition ($P < 0.05$; see Fig. 3; Table 1).

The spatial path results indicated that the presence of a nearby object caused the reaching trajectory towards both right and left targets to be wider and higher (Figs. 1 and 3).

Discussion

The current study focused on some aspects of action selection mechanisms in monkeys living in totally unconstrained situations, although the paradigm utilized here took place in a real world situated in a verifiable geographic area. It was our intent to watch the exemplars reaching for an object in a place where other articles were also located and to verify whether and how a nearby object affected the action plan. Generally speaking, the monkeys' behaviour was comparable with what is classically observed when humans carry out similar tasks: there were interference effects in movement kinematics when the monkeys set out to grasp a target in a context in which other articles were also conveniently available (Castiello 1999; Tipper et al. 1998).

Our analysis demonstrated that a nearby object, which can be interpreted as a potential obstacle, can produce measurable interference effects in tasks requiring the monkeys to reach out and pick up an object. We specifically observed that the temporal and spatial aspects of

reaching movements were affected by the presence of nearby objects. Our data demonstrated that the hand deviated away from any nearby objects and that the wrist trajectory was higher whenever these were present. This was an obvious reaction when a stone was a *real* obstacle to the right hand reaching towards a target on the right. But a similar reaction was noted even when the stone was *unlikely* to be an obstacle, as in the cases when nearby stones were located to the right and the target was on the left. These findings reflect parallel processing of internal representations rather than peripheral biomechanical properties of the reaching action. Similar deviations away from nearby objects have also been observed in human studies (Tipper et al. 1997), suggesting that the same selection mechanisms may well apply to both humans and macaques. We hypothesize that in macaques, just as in humans, these deviations reflect inhibition of action elicited by a nearby object. The point that should be emphasized here is that the relevance of a nearby object is linked to its role as a potential obstacle to action.

It has been suggested that only a limited number of objects can be processed in a parallel way during the initial analysis of an action space. As these perceptual inputs automatically activate their associated responses, initial perception processing flows continuously into brain areas that represent and subsequently initiate action. In view of this highly efficient, automatic conversion of perceptual inputs into actions, different objects in a scene can evoke actions (Goldberg and Segraves 1987). In other words, the type of representation created for a nearby object contains information *about the action that the object prompts* in that

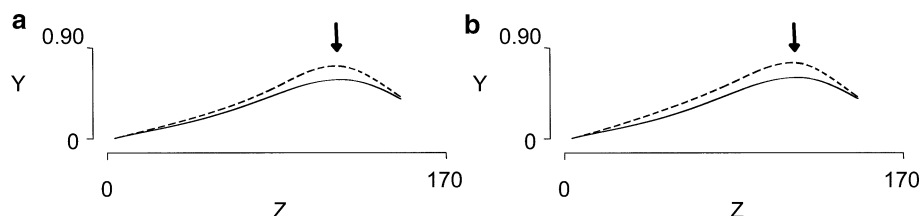


Fig. 3 Amplitude of maximum wrist height for the different experimental conditions. **a** Depicts a representative example of trajectories of the reaching component on the sagittal plane for the *right* target alone (*solid line*) and for the *right* target along with the distractor (*dashed line*) conditions. **b** Depicts a representative example of trajectories of the reaching component on the sagittal

plane for the *left* target alone (*solid line*) and for the *left* target along with the distractor (*dashed line*) conditions. Values on the axis are in millimetres (mm). Axis z = sagittal axis; axis y = vertical axis. The arrow indicates the point of maximum trajectory height. Please note that there is no contact with the target because the marker is placed on the wrist

particular context, and *that action is represented together with the one programmed for the target*. That hypothesis is in line with the theory that perceptions can flow directly into actions with little or no intention to act (Goldberg and Segraves 1987; Gibson 1979; Duncan-Johnson and Koppell 1981; Miller and Hackley 1992). Macaques, then, just as humans, are sensitive to the effects of nearby objects in view of their role, just as in the circumstances outlined here, as potential obstacles requiring a change in spatial path.

The similarity between the action pattern observed in macaques and that noted in human studies (e.g., Tipper et al. 1997; Tresilian 1998) focusing on visual processing of potential obstacles was evident not only at a spatial level but also at a temporal one. As previously reported, movement time increased when a potential obstacle was present (Tresilian 1998). The slower, in fact, that one moves, the easier it is to avoid something. In addition, if you need to approach something without touching or colliding with it, it is best to go as slowly as possible. Both humans and macaques seem to have adopted this strategy to ensure avoiding obstacles.

That is all very well for movement duration, but how can we explain the trajectory veering that was observed? When the nearby object is actually an obstacle, veering is a necessary manoeuvre to get around it. But veering needs to be explained in an entirely different way when the object is not in the path of a moving hand and therefore not directly an obstacle. It is possible that *path veering is the result of the macaque's inability to effectively ignore a nearby object (that could be a potential obstacle); the response then is an avoidance one that is activated by the object's presence, but that is then inhibited*. In order to plan a movement around something, you need to be aware of it. So basically veering is the result of noting something (activating) and then recognizing that the reaction is not appropriate and thus inhibiting it. Overall, the hypothesis that could be formulated is that due to ineffective inhibitory mechanisms that are active during attentional selection of a target as a movement is being planned, the nervous system inadvertently modifies movement execution in response to the presence of nearby objects. Attention itself, which seems to derive from the activity of sensorimotor circuits, calls for strong, direct coupling between visual attention and premotor activity.

The fact that these effects were noted in Old World monkeys provides further insight into our understanding of how action selection mechanisms have evolved in primates within perception action systems. Some have postulated that action selection processes may have evolved to mediate the selection of particular objects for action, and one of these could be a mechanism inhibiting internal representations of nearby objects (Tipper 1985).

The results presented here seem to favour the hypothesis that, as previously demonstrated, monkeys and humans share not only a number of kinematic features and neural responses with regard to grasping actions but also some selection mechanisms, such as inhibition, specifically linked to the control of action (Castiello 2005). When attention is focused on a target, inhibition acts on the motor representation of other objects present in the scene. Both the target and other objects evoke actions, and inhibitory mechanisms are utilized to avoid chaotic motor behaviour. This hypothesis is largely compatible with theories suggesting that attention plays a predominant role in shaping behaviour by affecting motor output (Allport 1987). To conclude, the main implication of these findings is that macaques seem to be able to link perception to action through internal representations, implying that *they not only possess the ability to form mental representations of objects (Maestriperi 2012), but they are also able to assign a motor representation to them*. While the actions an object prompts appear to be activated automatically, inhibitory attentional processes channel the action into meaningful goal-directed behaviour.

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Compliance with ethical standards

Ethical approval “All the procedures followed were in accordance with the ethical standards set by the University of Padova ethics committee for animal experimentation (C.E.A.S.A)”.

References

- Allport A (1987) Selection-for-action: some behavioural and physiological considerations of attention and action. In: Heuer H, Sanders AF (eds) Perspectives on perception and action. Lawrence Erlbaum Associates Inc, Hillsdale, pp 395–419
- Allport DA, Tipper SP, Chmiel NRJ (1985) Perceptual integration and post-categorical filtering. In: Posner MI, Marin OSM (eds) Attention and performance, XI. Lawrence Erlbaum Associates Inc, Hillsdale, pp 107–132
- Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267
- Bonfiglioli C, Castiello U (1998) Dissociation of covert and overt spatial attention during prehension movements: selective interference effects. Percept Psychophys 60:1426–1440. doi:10.3758/BF03208003
- Camperio Ciani A, Mouna M, Arhou M (1999) Macaca sylvanus as a biological indicator of the cedar forest quality. In: Proceedings of the first international conference on biodiversity and natural resources preservation, pp 91–98
- Camperio Ciani A, Palentini L, Arahou M, Martinoli L, Capiluppi C, Mouna M (2005) Population decline of Macaca sylvanus in the middle atlas of Morocco. Biol Conserv 121:635–641. doi:10.1016/j.biocon.2004.06.009

- Castiello U (1996) Grasping a fruit: selection for action. *J Exp Psychol Hum Percept Perform* 22:582–603. doi:[10.1037//0096-1523.22.3.582](https://doi.org/10.1037//0096-1523.22.3.582)
- Castiello U (1998) Attentional coding for three-dimensional objects and two-dimensional shapes: differential interference effects. *Exp Brain Res* 123:289–297. doi:[10.1007/s002210050571](https://doi.org/10.1007/s002210050571)
- Castiello U (1999) Mechanisms of selection for the control of hand action. *Trends Cogn Sci* 3:264–271. doi:[10.1016/S1364-6613\(99\)01346-7](https://doi.org/10.1016/S1364-6613(99)01346-7)
- Castiello U (2005) The neuroscience of grasping. *Nat Rev Neurosci* 6:726–736. doi:[10.1038/nrn1744](https://doi.org/10.1038/nrn1744)
- Chieffi S, Gentilucci M, Allport A, Sasso E, Rizzolatti G (1993) Study of selective reaching and grasping in a patient with unilateral parietal lesion: dissociated effects of residual spatial neglect. *Brain* 116:1119–1137. doi:[10.1093/brain/116.5.1119](https://doi.org/10.1093/brain/116.5.1119)
- Christel MI, Billard A (2002) Comparison between macaques' and humans' kinematics of prehension: the role of morphological differences and control mechanisms. *Behav Brain Res* 131:169–184. doi:[10.1016/S0166-4328\(01\)00372-2](https://doi.org/10.1016/S0166-4328(01)00372-2)
- Deubel H, Schneider WX, Paprotta I (1996) Visual attention and manual aiming: evidence for obligatory and selective spatial coupling. *Perception* 25:13–14. doi:[10.1068/v96i0312](https://doi.org/10.1068/v96i0312)
- Deubel H, Schneider WX, Paprotta I (1998) Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Vis Cogn* 5:81–107. doi:[10.1080/713756776](https://doi.org/10.1080/713756776)
- Duncan-Johnson CC, Koppell BS (1981) The Stroop effect: brain potentials localize the source of interference. *Science* 214:938–940. doi:[10.1126/science.7302571](https://doi.org/10.1126/science.7302571)
- Fa JE (1984) *The barbary macaque: a case study in conservation*. Plenum Press, New York
- Fogassi L, Gallese V, Gentilucci M, Chieffi S, Rizzolatti G (1991) Studio cinematico dei movimenti di raggiungimento e prensione nella scimmia. *Boll Soc It Biol Sper* 7:715–721
- Gentilucci M, Castiello U, Corradini ML, Scarpa M, Umiltà C, Rizzolatti G (1991) Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia* 29:361–378. doi:[10.1016/0028-3932\(91\)90025-4](https://doi.org/10.1016/0028-3932(91)90025-4)
- Gibson JJ (1979) *The ecological approach to visual perception*. Publisher Houghton Mifflin, Boston
- Goldberg ME, Segraves MA (1987) Visuospatial and motor attention in the monkey. *Neuropsychologia* 25:107–118. doi:[10.1016/0028-3932\(87\)90047-9](https://doi.org/10.1016/0028-3932(87)90047-9)
- Hopkins WD (1995) Hand preferences for a coordinated bimanual task in 110 chimpanzees (Pan troglodytes): cross-sectional analysis. *J Comp Psychol* 109:291–297. doi:[10.1037/0735-7036.109.3.291](https://doi.org/10.1037/0735-7036.109.3.291)
- Howard LA, Tipper SP (1997) Hand deviations away from visual cues: indirect evidence for inhibition. *Exp Brain Res* 113:144–152. doi:[10.1007/BF02454150](https://doi.org/10.1007/BF02454150)
- Jackson SR, Jackson GM, Rosicky J (1995) Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Exp Brain Res* 102:519–530. doi:[10.1007/BF00230656](https://doi.org/10.1007/BF00230656)
- Jakobson L, Goodale MA (1991) Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Exp Brain Res* 86:199–208. doi:[10.1007/BF00231054](https://doi.org/10.1007/BF00231054)
- James W (1890) *The principles of psychology*. Holt, New York
- Kritikos A, Bennett KMB, Dunai J, Castiello U (2000) Interference from distractors in reach-to-grasp movements. *Q J Exp Psychol A* 53:131–151. doi:[10.1080/713755874](https://doi.org/10.1080/713755874)
- Maestriperi (2012) Comparative Primate Psychology. In: Ramachandran VS (ed) *Encyclopedia of human behaviour*, 2nd edn. Elsevier, London, pp 550–555. doi:[10.1016/B978-0-12-375000-6.00101-4](https://doi.org/10.1016/B978-0-12-375000-6.00101-4)
- Meegan DV, Tipper SP (1998) Reaching into cluttered visual environments: spatial and temporal influences of distracting objects. *Q J Exp Psychol A* 51:225–249. doi:[10.1080/02724989843000004](https://doi.org/10.1080/02724989843000004)
- Miller J, Hackley SA (1992) Electrophysiological evidence for temporal overlap among contingent mental processes. *J Exp Psychol Gen* 121:195–209. doi:[10.1037/0096-3445.121.2.195](https://doi.org/10.1037/0096-3445.121.2.195)
- Neumann O (1990) Visual attention and action. In: Neumann O, Prinz W (eds) *Relationships between perception and action: current approaches*. Springer, Berlin, pp 227–267
- Roy AC, Paulignan Y, Farne' A, Joffrais C, Boussaoud D (2000) Hand kinematics during reaching and grasping in the macaque monkey. *Behav Brain Res* 117:75–78. doi:[10.1016/S0166-4328\(00\)00284-9](https://doi.org/10.1016/S0166-4328(00)00284-9)
- Roy AC, Paulignan Y, Meunier M, Boussaoud D (2002) Prehension movements in the macaque monkey: effects of object size and location. *J Neurophysiol* 88:1491–1499
- Roy AC, Paulignan Y, Meunier M, Boussaoud D (2006) Prehension movements in the macaque monkey: effects of perturbation of object size and location. *Exp Brain Res* 169:182–193. doi:[10.1007/s00221-005-0133-8](https://doi.org/10.1007/s00221-005-0133-8)
- Sacrey LA, Alavardshvili M, Wishaw IQ (2009) Similar hand shaping in reaching-for-food (skilled reaching) in rats and humans provides evidence of homology in release, collection, and manipulation movements. *Behav Brain Res* 204:153–161. doi:[10.1016/j.bbr.2009.05.035](https://doi.org/10.1016/j.bbr.2009.05.035)
- Sartori L, Camperio Ciani A, Bulgheroni M, Castiello U (2013a) Reaching and grasping behavior in *Macaca fascicularis*: a kinematic study. *Exp Brain Res* 224:119–124. doi:[10.1007/s00221-012-3294-2](https://doi.org/10.1007/s00221-012-3294-2)
- Sartori L, Camperio Ciani A, Bulgheroni M, Castiello U (2013b) Reach-to-grasp movements in *Macaca fascicularis* monkeys: the Isochrony Principle at work. *Front Psychol* 4:114. doi:[10.3389/fpsyg.2013.00114](https://doi.org/10.3389/fpsyg.2013.00114)
- Sartori L, Camperio Ciani A, Bulgheroni M, Castiello U (2014a) How posture affects macaques' reach-to-grasp movements. *Exp Brain Res* 232:919–925. doi:[10.1007/s00221-013-3804-x](https://doi.org/10.1007/s00221-013-3804-x)
- Sartori L, Camperio Ciani A, Bulgheroni M, Castiello U (2014b) Monkey see, Monkey reach: action selection of reaching movements in the macaque monkey. *Sci Rep* 4:4019. doi:[10.1038/srep04019](https://doi.org/10.1038/srep04019)
- Schiegg A, Deubel H, Schneider WX (2003) Attentional selection during preparation of prehension movements. *Vis Cogn* 10:409–431. doi:[10.1007/s00426-003-0166-1](https://doi.org/10.1007/s00426-003-0166-1)
- Tipper SP (1985) The negative priming effect: inhibitory priming by ignored objects. *Q J Exp Psychol A* 37:571–590. doi:[10.1080/14640748508400920](https://doi.org/10.1080/14640748508400920)
- Tipper SP, Lortie C, Baylis GC (1992) Selective reaching: evidence for action-centered attention. *J Exp Psychol Hum Percept Perform* 18:891–905
- Tipper SP, Howard LA, Jackson SR (1997) Selective reaching to grasp: evidence for distractor interference effects. *Vis Cogn* 4:1–38. doi:[10.1080/713756749](https://doi.org/10.1080/713756749)
- Tipper SP, Howard LA, Houghton G (1998) Action-based mechanisms of attention. *Phil Trans R Soc Lond B* 353:1385–1393. doi:[10.1098/rstb.1998.0292](https://doi.org/10.1098/rstb.1998.0292)
- Tresilian JR (1998) Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension. *Exp Brain Res* 120:352–368. doi:[10.1007/s002210050409](https://doi.org/10.1007/s002210050409)