

# Prehension Movements in the Macaque Monkey: Effects of Object Size and Location

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**Roy, Alice C., Yves Paulignan, Martine Meunier, and Driss Bous-saoud.** Prehension movements in the macaque monkey: effects of object size and location. *J Neurophysiol* 88: 1491–1499, 2002; 10.1152/jn.00779.2001. Prehension movements were examined in freely behaving monkeys and compared with the well-known characteristics of human movements. The degree of independence of the components of movements (i.e., reaching and grasping) was investigated in animals trained to reach for and grasp three-dimensional objects. To this aim, the kinematics of prehension movements was recorded using an Optotrak system in two tasks. In one task, monkeys grasped a small or a large object (size task), in the other, they grasped an object of constant size placed at three different spatial locations (location task). We found that object size and its location affected both reaching and grasping. In particular, in the size task, we found that the maximum grip aperture strongly depended on the selection of the grip and not only on the size of an object. Our results also revealed that, in monkeys as well as in humans, the reaching parameters are highly sensitive to task-related constraints such as accuracy demands. The results of the location task showed a difference between rightward and leftward movements, a pattern of grip aperture that varied across animals, and a large degree of coordination between the two components. These findings argue against a strict postulate of independence between the visuo-motor channels, favoring instead the idea of variable degrees of coordination between the reach and grasp components depending on the task demands. Finally, this work emphasizes the relevance of studying monkey's prehension movements as a useful step to the understanding of visuo-motor control in humans.

## INTRODUCTION

Among the different models proposed to account for the organization of prehensile movements in primates, one of the most influential is the theory developed by Jeannerod and his colleagues in the early 1980s (Jeannerod 1981; Jeannerod and Biguer 1982). This theory postulates that prehension movement is organized in at least two components each controlled by a distinct visuo-motor channel. One of the components is the hand transport to the vicinity of the object, experimentally assessed by the wrist movement. The other is the grip formed by the hand, assessed as the distance between the thumb and index finger. The transport channel extracts the extrinsic object properties, in particular its location in a body-centered reference frame, and produces a pattern of proximal muscle activity. The grasp channel transforms the object intrinsic properties, in particular its size and shape, into a pattern of distal muscle

activity that shapes the grip. These processing streams have been proposed to be independent (Jeannerod 1981; Jeannerod and Biguer 1982), a postulate that has motivated numerous kinematic studies of normal prehension in humans. Indeed, a strict interpretation of this postulate would predict that selectively varying the visual input of one channel should influence the motor output of this component without affecting the other motor component.

Human kinematic studies that have attempted to test this hypothesis have led to contrasting findings. On the one hand, they have repeatedly confirmed Jeannerod's original finding (Jeannerod 1981, 1984) that changing object size affects the grasping component (Gentilucci et al. 1991; Paulignan et al. 1991a). On the other hand, the effects of decreasing object size on the reaching component are unclear. Some authors reported no effect of object size (Jeannerod 1981, 1984, 1986; Jeannerod and Biguer 1982; Paulignan et al. 1991a, 1997), whereas others found lengthening of movement time and wrist deceleration phase (Castiello et al. 1992; Churchill et al., 2000; Gentilucci et al. 1991; Kudoh et al. 1997; Marteniuk et al. 1990; Pryde et al. 1998). It is unclear, however, whether these effects reflect a direct influence of the decrease in object size or whether they are an indirect consequence. Indeed, a small object provides less contact surface for the fingers, hence increasing accuracy demands that can be met by decreasing movement speed.

The issue of independence of visuo-motor channels has been reciprocally addressed by investigating the impact of changing the object extrinsic properties, namely its location. Although an increase of both movement time and the amplitude of the wrist velocity peak is a well-known consequence of augmenting the distance between the object and the hand (Gentilucci et al. 1991; Kudoh et al. 1997; Paulignan et al. 1991b), the effect of varying object location on the grasping component are inconsistent. For example, Jeannerod observed no effect, whereas other groups reported an increase of maximum grip aperture (Chieffi and Gentilucci 1993; Jakobson and Goodale 1991). Moreover, imposing a via point in movement trajectory has been reported to result in a delayed grasping component (Haggard and Wing 1998), and varying movement direction to produce a linear variation of the grip amplitude (Paulignan et al. 1991b, 1997).

Despite these important kinematic studies in humans, the degree of independence of the two components remains a

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matter of debate (Mon-Williams and McIntosh, 2000; Smeets and Brenner 1999). Paradoxically, although this hypothesis partly originated from and has been supported by monkey anatomic-physiological evidence (Jeannerod et al. 1995; Rizzolatti et al. 1997; Sakata and Taira 1994), very little is known about the behavioral characteristics of prehension movement in this species. The few psychophysical investigations that have been conducted to date were either restricted to the reaching component or were of poor temporal resolution (Fogassi et al. 2001; Gardner et al. 1999; Georgopoulos et al. 1981; Scott and Kalaska 1997). Hence we have initiated a series of studies applying in monkey the high-resolution techniques and behavioral paradigms used in human studies. In a recent report (Roy et al. 2000), we provided evidence for important similarities between the two species behavior, suggesting that macaque monkey can be a useful model for understanding human motor control. In particular, data on a prehension task indicated that in monkeys as in humans, the reaching component is characterized by a single wrist velocity peak and the grasping component by a grip size that increases up to a maximum and decreases toward the end of movement. The present study was designed to evaluate the effect on monkey prehension of changing either intrinsic or extrinsic object properties from trial to trial. To this aim, the reaching and grasping components of three monkeys were measured in two different tasks, one varying the size of the target object, the other varying its location.

## METHODS

### Behavioral tasks

Three cynomolgus monkeys (*Macaca fascicularis*), one female (MK1) and two males (MK2 and MK3), weighing 4.5–7.5 kg participated to the present study. Testing procedure as well as animal care was in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and with the European Community's Council Directive of 24 November 1986 (86/609/EEC). The monkeys were seated in a primate chair with the head and both arms free to move. They were trained to perform two tasks, in separate sessions: one where object size varied (termed hereafter *size task*) and one where object location changed (termed *location task*).

In the size task, the monkey was trained to reach for, grasp, and lift with its right hand one of two objects presented in pseudo-random order. The objects were two concentric white plastic cylinders (Fig. 1). The inner cylinder (height: 40 mm, diam: 15 mm) will be referred to as the small object. The outer cylinder (height: 40 mm, diameter: 25 mm) will be referred to as the large object. These cylinders were placed on concentric metal platforms hidden inside an opaque box fitted onto the primate chair. The platforms were elevated by an automated pneumatic system so that the objects appeared at the surface of the box. A permanent magnet was fitted into the base of each cylinder to keep it in contact with the platforms during their fast up and down displacements.

The experiments were controlled by Cortex software (NIMH, Bethesda, MD). A trial began when the monkey put its right hand on a home pad, located immediately in front of its chest along the sagittal axis. After a variable delay (250 ms to 1 s), one of the two cylinders appeared straight in front the animal's body axis, at a distance of 21 cm from the home pad. The monkey had 10 s to grasp and lift the object to receive a liquid reward. The two objects were presented in a pseudo-random order.

In the location task, three identical objects were positioned on a tray fitted on the primate chair (Fig. 1). The objects were gray plastic

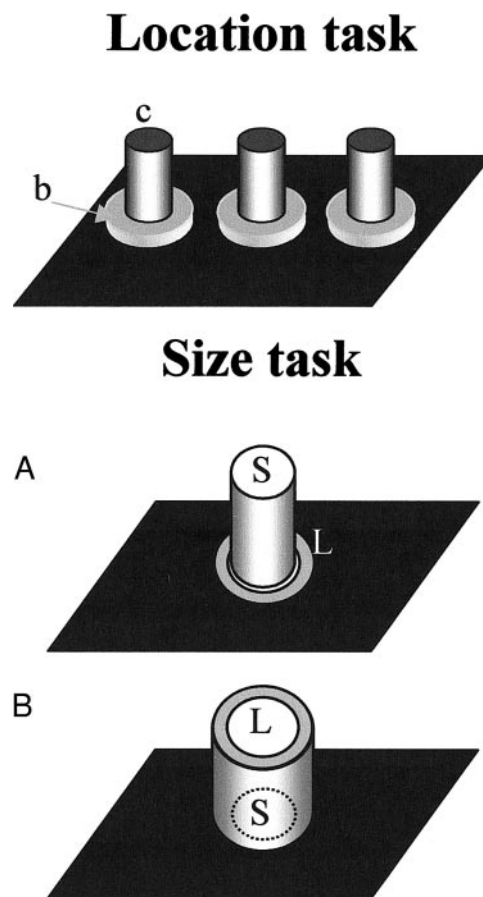


FIG. 1. Experimental design of size and location tasks. *Location task.* Three cylinders (c), each with a flat translucent base (b), are aligned perpendicularly to the monkey's sagittal axis. The monkey puts its hand on a starting position (home pad), and after a delay (see text), the base of 1 object is illuminated. The monkey has 5 s to reach for that object and lift it to receive a reward. *Size task.* Two concentric cylinders are used, one at a time. A: the small object (S) is up, while the large one (L) is down. B: opposite to A.

cylinders (height: 20 mm, diam: 15 mm), mounted on a flat base (height: 10 mm, diameter: 40 mm) that could be illuminated from underneath. As in the *size task*, a trial began when the monkey put its right hand on the home pad; after a variable delay (250 ms to 1 s), the base of one of the three objects was illuminated. The animal then had 5 s to grasp and lift the illuminated object to obtain a liquid reward. The objects were spaced 5 cm apart and aligned perpendicular to the monkey's sagittal axis so that the central and lateral (left and right) objects were at a distance of 20 and 21 cm from the home pad, respectively. Objects were illuminated in a pseudo-random order.

The animals underwent extensive training on both tasks before data acquisition was initiated, so that they reached a nearly perfect level of performance during recording sessions. All three animals were tested on both tasks, in variable order. However, for *monkey MK1*, data obtained in a size task were published previously (Roy et al. 2000) and will not be included in this paper.

### Movement recordings

An Optotrak 3020 (Northern Digital) was used to record the spatial positions of six to seven markers (infrared light-emitting diodes) at a frequency of 300 Hz and with a spatial resolution of 0.1 mm. One marker, taped on the wrist, characterized the reaching component. Two markers, one on the thumb nail, another on the nail of index finger, defined the grip aperture. For *MK2* and *MK3*, an additional marker was taped on the tip of the middle finger to assess a second

grip aperture, i.e., the distance between the thumb and the middle finger. The three remaining markers were fixed on the primate chair to define a space in which all recorded movements were systematically placed from session to session. For each trial, data acquisition started with object presentation (size task) or illumination (location task) and ended when the object was lifted.

### Data analysis

A second-order Butterworth dual pass filter (cutoff frequency, 10 Hz) was used for raw data processing. Individual movements were then visualized and analyzed using Optodisp software (Optodisp copyright UCBL-CNRS, Marc Thévenet et Yves Paulignan, 2001). For both tasks and all three animals, we measured several parameters such as: movement time, the latency and amplitude of the peaks of wrist acceleration and wrist velocity, and the latency and amplitude of the maximum grip aperture between the thumb and index finger (TI grip aperture). In addition, for *monkeys MK2* and *MK3*, we measured the latency and amplitude of the maximal distance between the thumb and middle finger (TM grip aperture). For the size task, the grip aperture at the end of movement (final grasp) and the length of the deceleration phase were also measured (i.e., the time elapsed between the time of the wrist velocity peak and the end of movement). All the preceding parameters were assessed for each individual movement. In a few cases, however, marker visibility was imperfect for a portion of movement (e.g., due to a light reflection), and the corresponding parameter was excluded from subsequent statistical analyses.

Figure 2 illustrates the approach used to measure the relevant

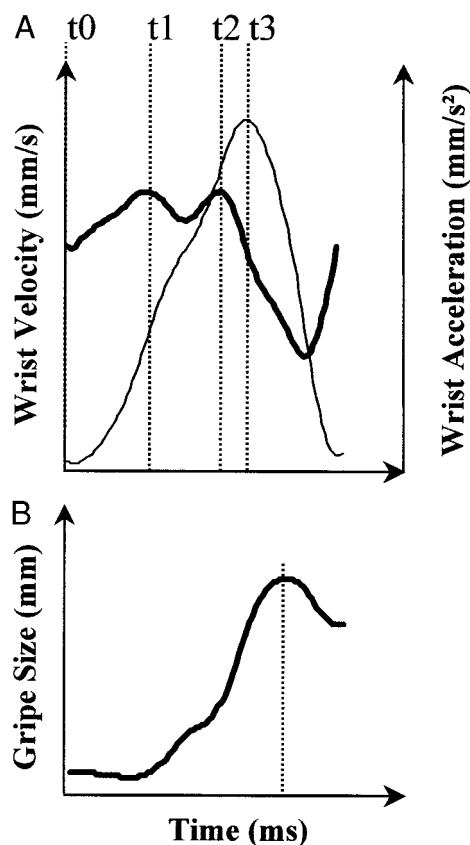


FIG. 2. Method of measurement of kinematic parameters. A: the transport component was characterized by the study of wrist kinematics: velocity (thin line) and acceleration (thick line). The dotted lines represent specific measures along the time axis:  $t_0$ , movement onset;  $t_1$  and  $t_2$ , 1st and 2nd acceleration peaks, respectively;  $t_3$ , velocity peak. B: the grasping component was described by the evolution of grip size as a function of time. The dotted line shows the time at which the maximum grip aperture occurs.

parameters. Movement onset was determined on the basis of the wrist, index, and thumb velocity profiles as the time of the first of seven consecutive measures of increasing amplitudes (Roy et al. 2000). The end of movement was determined as the time when there was no further change in the amplitude of the TI grip aperture (i.e., when a stable grasp was achieved, thereby enabling the subject to lift the object). Peak latencies were defined as the time elapsed between movement onset and each peak.

The values obtained for each kinematic parameter were analyzed, by experimental task and for each monkey, using one-way analyses of variance (ANOVA, significance level,  $P < 0.05$ ) to determine the influence of object size (small vs. large object) or object location (center, left, and right positions). For the location task, pairwise comparisons were performed using the Tukey test. Finally, for both tasks, the links between kinematic parameters were studied using Pearson correlation coefficients ( $r_s$ ). For these analyses, data from each monkey were averaged per daily session and then standardized to allow comparison across animals.

## RESULTS

The present study is based on a total of 2,142 movements in the size task and 2,910 movements in the location task. The results and their statistical analyses are summarized in Tables 1 and 2. Despite individual variations, the general pattern of prehension movements was the same for both tasks and all three animals. Figure 3 shows examples of movement trajectories in the two tasks; movement variability decreased as the fingers approached the object, indicating that the monkey always put his fingers at the same place on the object. The reaching component is characterized by a bell-shaped wrist velocity profile (Figs. 4A and 5A): the velocity peak is preceded by an acceleration phase presenting two peaks (Fig. 4B) and followed by a deceleration phase. The grasping component is characterized by the grip aperture(s), which increased up to a single peak and decreased as the hand approached the object (Figs. 4, C and D, and 5B). Maximum grip aperture(s) always occurred after the peak of wrist velocity.

### Effect of object size

We analyzed 1,029 movements in *MK2* and 1,113 movements in *MK3* (i.e., about 500 movements for each object size). Table 1 summarizes the means and statistics for each of the recorded kinematic parameters. Movement time and most of the parameters of the reaching component changed significantly with object size in both monkeys alike. By contrast, object size differentially affected the grasping parameters across monkeys. These differences may be related to the type of grip used by individual animals.

**Effect on movement time.** For both monkeys, total movement time was significantly longer for the small than for the large object. These differences in movement time are particularly appreciable on the wrist velocity and grip aperture profiles displayed in Fig. 4 (A, C, and D).

**Effect on reaching.** In both animals, wrist parameters presented longer latencies and smaller peaks for movements directed to the small, relative to the large object (Table 1). Specifically, size reduction led to: increased latency of either the first acceleration peak (*MK3*, Fig. 4B) or the subsequent velocity peak (*MK2*, Fig. 4A), lengthened deceleration phase (Fig. 4B), and smaller amplitude of the second acceleration and

TABLE 1. *Effect of object size on the transport and grasp components*

	Monkey	Object Size			Statistics
		Large	Small		
Movement time, ms	MK2	325 ± 1	362 ± 1	↗	$F_{1,1029} = 417, P < 0.001$
	MK3	353 ± 1	383 ± 1	↗	$F_{1,1113} = 171.9, P < 0.001$
Reach					
Time to the 1st acceleration peak, ms	MK2	102 ± 1	102 ± 1		$F_{1,1017} = 0.050, P : n.s.$
	MK3	82 ± 1	86 ± 1	↗	$F_{1,1110} = 5.351, P < 0.021$
Time to the 2nd acceleration peak, ms	MK2	139 ± 1	141 ± 1		$F_{1,436} = 0.722, P : n.s.$
	MK3	161 ± 1	162 ± 1		$F_{1,1012} = 0.236, P : n.s.$
Time to the velocity peak, ms	MK2	203 ± 1	211 ± 1	↗	$F_{1,1023} = 33.56, P < 0.001$
	MK3	213 ± 1	215 ± 1		$F_{1,850} = 0.949, P : n.s.$
Deceleration phase, ms	MK2	122 ± 0.8	151 ± 0.7	↗	$F_{1,1024} = 602.3, P < 0.001$
	MK3	138 ± 1	168 ± 1	↗	$F_{1,1112} = 366.0, P < 0.001$
Amplitude of the 1st acceleration peak, mm/s <sup>2</sup>	MK2	9436 ± 78	8764 ± 73	↘	$F_{1,1017} = 39.49, P < 0.001$
	MK3	7019 ± 80	7003 ± 87		$F_{1,1110} = 0.019, P : n.s.$
Amplitude of the 2nd acceleration peak, mm/s <sup>2</sup>	MK2	8199 ± 120	7383 ± 112	↘	$F_{1,436} = 24.37, P < 0.001$
	MK3	9297 ± 83	8918 ± 92	↘	$F_{1,1012} = 9.29, P < 0.002$
Amplitude of the velocity peak, mm/s	MK2	1033 ± 3	957 ± 3	↘	$F_{1,1023} = 267.2, P < 0.001$
	MK3	1156 ± 5	1130 ± 5	↘	$F_{1,850} = 12.94, P < 0.001$
Grasp					
Time to the maximum thumb-index grip aperture, ms	MK2	250 ± 1	265 ± 1	↗	$F_{1,996} = 106.3, P < 0.001$
	MK3	270 ± 1	266 ± 1	↘	$F_{1,1020} = 6.09, P < 0.014$
Time to the maximum thumb-middle finger grip aperture, ms	MK2	256 ± 1	271 ± 1	↗	$F_{1,861} = 80.19, P < 0.001$
	MK3	271 ± 1	266 ± 1	↘	$F_{1,1031} = 6.29, P < 0.012$
Maximum thumb-index grip aperture, mm	MK2	35.28 ± 0.1	37.79 ± 0.1	↗	$F_{1,996} = 189.5, P < 0.001$
	MK3	41.79 ± 0.1	39.97 ± 0.1	↘	$F_{1,1020} = 123.4, P < 0.001$
Maximum thumb-middle finger grip aperture, mm	MK2	44.5 ± 0.1	45.3 ± 0.1	↗	$F_{1,861} = 24.76, P < 0.001$
	MK3	50.9 ± 0.1	48.8 ± 0.1	↘	$F_{1,1031} = 169.7, P < 0.001$
Final thumb-index grip aperture, mm	MK2	26.8 ± 0.1	20.7 ± 0.1	↘	$F_{1,1018} = 1023, P < 0.001$
	MK3	36.1 ± 0.1	23.7 ± 0.1	↘	$F_{1,1075} = 4752, P < 0.001$

Values are means ± SE. Each kinematic parameter (left column) was measured for the small and the large object in each monkey. When the difference is significant (right column), an arrow indicates the direction of variation: a decrease (↘) or increase (↗) for the small object, relative to the large one; n.s., difference is not statistically significant.

velocity peaks (this effect was also noticeable on the first acceleration peak on MK2; Fig. 4B).

**Effect on grasping.** Object size differentially affected the grasping parameters in the two animals. Both the latency and amplitude of maximum TI and TM grip apertures decreased for the small object in MK3, whereas they unexpectedly increased in MK2 (Fig. 4, C and D). These inter-subject differences are further materialized by the differences in the final grip. As Table 1 shows, the final grip is smaller in MK2 (20.7 and 26.8 mm for the small and the large object, respectively) than in MK3 (23.7 and 36.1). Note that in general the final grasp is larger than the real object size, as the markers were placed on the external surface of the fingers (therefore adding the thickness of the fingers to the object diameter). Thus for a 10-mm change in object size, the final grip varied with only 6.1 mm in MK2 as opposed to 12.4 mm in MK3. These data suggest that the two animals used different types of grip (see DISCUSSION).

#### Effects of object location

Analyses were performed on 440 movements for MK1 (140 per condition), 990 movements for MK2 (330 per condition), and 1,480 movements for MK3 (500 movements for each direction). As summarized in Table 2, object location affected movement time and reaching parameters in all three animals in a comparable manner. Grasping parameters were also affected

by object location although in somewhat different ways across individuals.

**Effect on movement time.** Movement time tended to decrease progressively from the left (contralateral to the hand used) to the right (ipsilateral) position. The most prominent difference in all subjects was that movements to the contralateral object took significantly longer than movements directed to either the right or the central object. Differences between movements directed to the right and central objects were minor and reached statistical significance only in MK2.

**Effect on reaching.** In line with increased movement time for leftward movements, reaching to the left object was characterized by longer latencies and smaller peaks compared with movements to the right or the center. The increase in latencies for leftward movements was detectable on the first acceleration peak in MK1 and on the second acceleration peak in MK2 and MK3. This latency increase was, however, most salient on the velocity peak, which, like movement time, diminished gradually from the left to the right position in all monkeys (Fig. 5A). The decrease in amplitude for leftward movements (or conversely the increase for rightward movements) was obvious on the first acceleration peak for all monkeys, as well as on the velocity peak for MK1 and the second acceleration and velocity peaks for MK3.

**Effect on grasping.** The effect of object location on the time to maximum grip aperture was homogeneous across monkeys (Table 2): it was longer for movements to the left position than for movements to the other two positions (Fig. 5B). By contrast, the effect of object location on the maximum grip aper-

TABLE 2. Effect of object location on the transport grasp components

	Monkey	Object Location			Statistics
		Left	Center	Right	
Movement time, ms	<i>MK1</i>	489 ± 3.9 ●○	455 ± 3.6	447 ± 3.4	$F_{2,440} = 37.84, P < 0.001$
	<i>MK2</i>	382 ± 2.2 ●○	373 ± 2.2	363 ± 2.5 ●	$F_{2,989} = 17.25, P < 0.001$
	<i>MK3</i>	423 ± 2.1 ●○	410 ± 2.0	406 ± 2.0	$F_{2,1482} = 18.4, P < 0.001$
Reach					
Time to 1st acceleration peak, ms	<i>MK1</i>	125 ± 2 ●○	117 ± 2	117 ± 2	$F_{2,432} = 4.36, P < 0.013$
	<i>MK2</i>	110 ± 2	104 ± 2	106 ± 2	$F_{2,650} = 2.30, P : n.s.$
	<i>MK3</i>	88 ± 1	86 ± 1	88 ± 1	$F_{2,1416} = 1.3, P : n.s.$
Time to 2nd acceleration peak, ms	<i>MK2</i>	144 ± 3 ●	133 ± 2	143 ± 1 ●	$F_{2,245} = 7.34, P < 0.001$
	<i>MK3</i>	171 ± 2 ○	167 ± 2	165 ± 2	$F_{2,1326} = 3.05, P < 0.047$
Time to velocity peak, ms	<i>MK1</i>	238 ± 2 ●○	213 ± 2	198 ± 2 ●	$F_{2,440} = 69.68, P < 0.001$
	<i>MK2</i>	227 ± 2 ●○	214 ± 1	210 ± 2	$F_{2,685} = 28.94, P < 0.001$
	<i>MK3</i>	254 ± 2 ●○	243 ± 1	235 ± 2 ●	$F_{2,1425} = 38.8, P < 0.001$
1st acceleration peak, amplitude, mm/s <sup>2</sup>	<i>MK1</i>	7558 ± 130 ●○	8903 ± 151	9042 ± 160	$F_{2,432} = 31.76, P < 0.001$
	<i>MK2</i>	8462 ± 151 ●	9006 ± 159	8958 ± 181	$F_{2,650} = 3.58, P < 0.028$
	<i>MK3</i>	6092 ± 98 ●○	6701 ± 94	7115 ± 96 ●	$F_{2,1416} = 27.7, P < 0.001$
2nd acceleration peak, amplitude, mm/s <sup>2</sup>	<i>MK2</i>	8521 ± 236	8581 ± 208	8504 ± 217	$F_{2,245} = 0.03, P : n.s.$
	<i>MK3</i>	6399 ± 76 ○	6632 ± 72	7041 ± 76 ●	$F_{2,1326} = 18.1, P < 0.001$
Velocity peak, amplitude mm/s	<i>MK1</i>	747 ± 6 ●○	799 ± 5	809 ± 7	$F_{2,440} = 26.46, P < 0.001$
	<i>MK2</i>	1039 ± 4 ●○	1000 ± 4	991 ± 6	$F_{2,685} = 24.08, P < 0.001$
	<i>MK3</i>	1044 ± 5 ○	1047 ± 5	1077 ± 5 ●	$F_{2,1425} = 13.4, P < 0.001$
Grasp					
Time to maximum thumb-index finger grip aperture, ms	<i>MK1</i>	367 ± 3 ●○	333 ± 3	326 ± 3	$F_{2,426} = 48.80, P < 0.001$
	<i>MK2</i>	278 ± 2 ●○	259 ± 2	258 ± 2	$F_{2,750} = 33.16, P < 0.001$
	<i>MK3</i>	337 ± 2 ●○	321 ± 2	318 ± 2	$F_{2,1311} = 23.8, P < 0.001$
Time to maximum thumb-middle finger grip aperture, ms	<i>MK2</i>	285 ± 2 ●○	268 ± 1	270 ± 2	$F_{2,917} = 34.6, P < 0.001$
	<i>MK3</i>	337 ± 2 ●○	320 ± 2	318 ± 2	$F_{2,1310} = 25.3, P < 0.001$
Maximum thumb-index finger grip aperture, mm	<i>MK1</i>	35.5 ± 0.1 ●○	34.2 ± 0.1	32.8 ± 0.2 ●	$F_{2,426} = 51.46, P < 0.001$
	<i>MK2</i>	35.3 ± 0.1 ○	35.4 ± 0.1	34.5 ± 0.09 ●	$F_{2,750} = 25.95, P < 0.001$
	<i>MK3</i>	31.6 ± 0.1	31.5 ± 0.1	31.5 ± 0.1	$F_{2,1311} = 18.1, P < 0.001$
Maximum thumb-middle finger grip aperture, mm	<i>MK2</i>	44.1 ± 0.2	44.1 ± 0.1	44.1 ± 0.1	$F_{2,917} = 0.05, P : n.s.$
	<i>MK3</i>	40.2 ± 0.1 ○	40.2 ± 0.1	41.1 ± 0.1 ●	$F_{2,1310} = 8.14, P < 0.001$

Values are means ± SE. ●, different from the center; ○, different from the right. n.s., no significant differences.

ture varied from one individual to the other (Fig. 6). *MK1* displayed a peak of TI grip aperture increasing in steps from the right to the left position. *MK2*, likewise, showed the smallest TI (though not TM) grip aperture for movements to the right. By contrast, *MK3* showed the largest TM (though not TI) grip aperture for movements to the right.

#### Correlation between the different kinematic parameters

**Size task.** Correlation analyses over the two subjects and two object sizes underlined the links existing between the different

wrist parameters, in particular between the second acceleration and velocity peaks ( $r = 0.87, P < 0.001$ , for latency;  $r = 0.62, P = 0.002$ , for amplitude). The amplitude of these two reaching parameters was also strongly correlated with movement time ( $r = -0.72, P < 0.001$ , for 2nd acceleration peak;  $r = -0.66, P = 0.001$ , for velocity peak). Separate analyses for each object size yielded similar findings. By contrast, grasping variables were reliably correlated neither with the reaching parameters, nor with movement time, regardless of whether the two conditions were considered separately or together. Grasp-

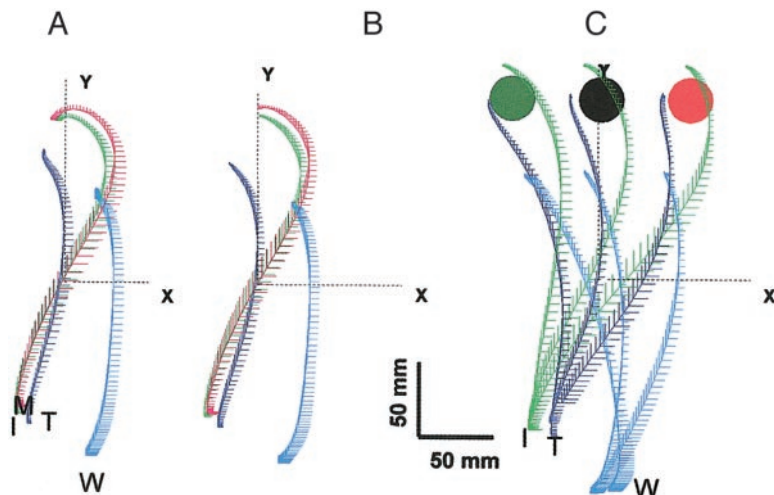


FIG. 3. Spatial path of movements in the size and location tasks. A and B: movements to the small and large objects, respectively. C: movements to the central (black), left (green), or right (red) objects in the location task. All examples are taken from *MK3* but are representative of the behavior of all the animals tested. Averaged XY spatial path of 10 movements of the wrist (W) and thumb (T) and index (I) and middle (M) fingers. Trajectories are viewed from above, thus the z axis is not shown. The horizontal and vertical lines attached to the trajectories represent the amplitude of one SD with respect to the mean spatial path in the X and Y dimensions. Note that the variability is very low at the end of the movement irrespective of object size or location.

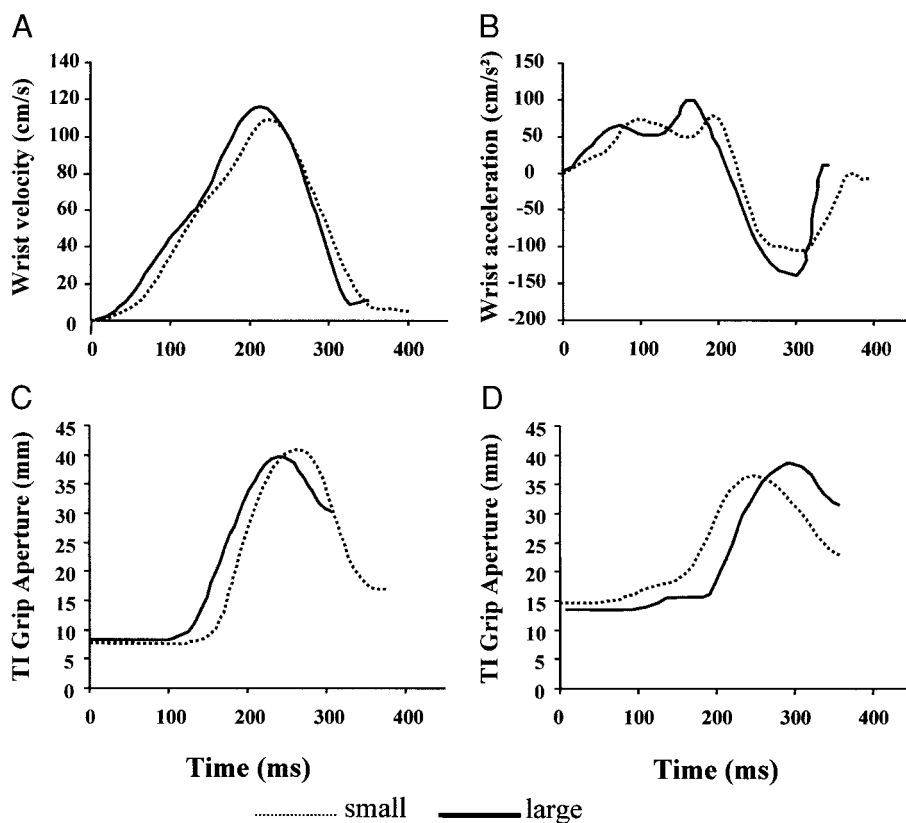


FIG. 4. Effect of object size on prehension movements. *A* and *B*: wrist velocity and acceleration profiles of 2 individual movements from *MK3* that are also representative of *MK2*'s behavior. *C* and *D*: thumb-index (TI) grip aperture for 2 individual movements made by *MK2* and *MK3*, respectively (for *MK3*, movements illustrated in *D* are different from those shown in *A* and *B*). Note that the effects of object size were similar across monkeys for the transport component (e.g., a longer movement time for a smaller object) but not for the grasp component.

ing analysis showed only a correlation between the latency and amplitude of the maximum TI grip aperture ( $r = 0.52$ ,  $P = 0.014$ ).

**Location task.** Analyses across the three subjects and three object positions unveiled links between grasping, on the one hand, and both reaching and movement time, on the other hand. Indeed, the latency of maximum TI aperture was correlated with the latency and amplitude of the wrist velocity peak ( $r = 0.73$ ,  $P < 0.001$  and  $r = -0.63$ ,  $P < 0.001$ , respectively), as well as with movement time ( $r = 0.89$ ,  $P < 0.001$ ). In addition, as for the size task, reaching (i.e., the velocity peak amplitude) was correlated with movement time ( $r = -0.67$ ,  $P < 0.001$ ). Finally, separate analyses of the maximum TI grip aperture for each condition revealed a contrast between the left and the other two positions that was present in all animals despite the grip inter-individual variability described above. Namely, for leftward movements, the amplitude and latency of TI maximum aperture were positively correlated ( $r = 0.49$ ,  $P = 0.049$ ); in addition, an increase in TI maximum aperture was associated with smaller velocity peaks and longer movement times ( $r = -0.66$ ,  $P = 0.004$  and  $r = 0.68$ ,  $P = 0.003$ , respectively). None of these relationships were observed for rightward and central movements.

## DISCUSSION

The present study examined the influence of object size and location on the kinematics of prehension movements in macaque monkeys. The results showed that the object's visual properties, whether intrinsic (size) or extrinsic (location), influenced both the reaching and the grasping components of the monkey's movements. More specifically, for both the size and

location tasks, we observed highly consistent changes of the reaching parameters, movements directed to the small, or to the left position being the longest and slowest in all monkeys. By contrast, modifications of the grasping parameters differed markedly across individuals. For the size task, these variations are likely to reflect the influence of the type of grip selected by the animal. Overall, the present findings converge with earlier data (Roy et al. 2000) to indicate that non human primates provide a highly relevant model to examine the kinematics but also the neural control of prehension.

### *Influence of the type of grip and not only of object size on grip scaling*

In monkey *MK3*, the larger object induced the latest and highest peak of maximum grip aperture (both TI and TM), thus confirming a well established phenomenon in humans (Churchill et al. 2000; Gentilucci et al. 1991; Jakobson and Goodale 1991; Jeannerod 1981, 1984; Kudoh et al. 1997; Marteniuk et al. 1990; Paulignan et al. 1991a, 1997; Pryde et al. 1998) and replicating data obtained in *MK1* for the same object diameters (Roy et al. 2000). Unexpectedly, monkey *MK2* showed the opposite pattern, i.e., the small object leading to a larger grip. Pilot data (200 movements) recorded when *MK2* was naive indicated, however, that this animal had a classical grip scaling (larger aperture for the larger object) at the beginning of the experiments. This suggested that this monkey has developed a particular grasping behavior, a hypothesis that is supported by the analysis of the final grasp. Analysis of the final grip size suggests that *MK2* used a power grip, whereas *MK3* used a precision grip. These types of grasping are characterized by different opposition axes, i.e., the axis along which the forces are applied to the object.

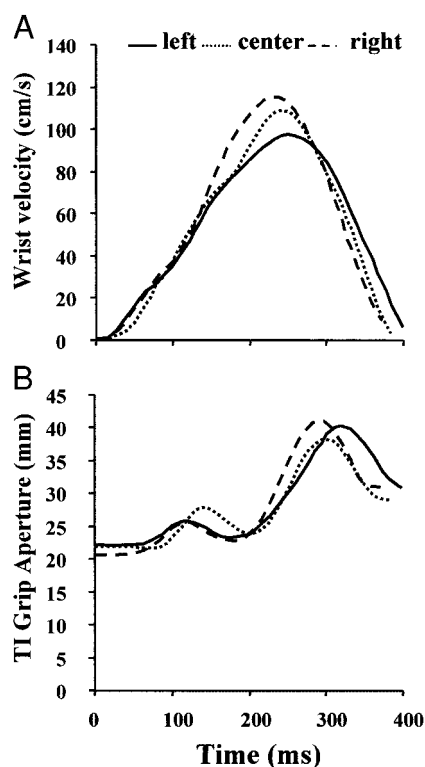


FIG. 5. Effect of object location on prehension movements. Representative examples taken from MK3: wrist velocity (A) and grip aperture (B) profiles of 3 individual movements directed to the 3 object locations. Note that leftward movements showed later wrist velocity and grip aperture peaks.

The opposition axis is between the thumb and fingers in the precision grip, the thumb and the palm in the power grip. Therefore in the case of a precision grip (i.e., without palmar contact with the object), the final aperture is roughly equal to object size, and it changes in close correlation with it. By contrast, a power grip does not require the final aperture to change in the same magnitude as the change in object size, as the fingers are wrapped around the object. In MK2, the 10-mm difference between the small and the large objects resulted in only a 6.1-mm difference in final grip amplitude, as opposed to 12.4 mm in MK3. Furthermore, the final grip size is smaller in MK2 than in MK3 (see Table 1), supporting our proposal that the former used a power grip, whereas the latter used a precision grip.

#### Effects of accuracy constraints and not only of object size on reaching

Contrasting with the results on the grasping component, the effect of object size on the reaching component was homogeneous for the two monkeys. Reducing object size induced later and lower wrist acceleration and velocity peaks, lengthened the deceleration phase, and, as a result, increased the total movement time. The same effect on movement time due to lengthening of the deceleration phase has been described in several studies in humans (Bootsma et al. 1994; Castiello et al. 1993; Gentilucci et al. 1991; Kudoh et al. 1997; Pryde et al. 1998; Zaal and Bootsma 1993). Although less frequently, previous studies in humans and monkeys have reported later latency and/or smaller amplitude of the wrist velocity peak following a decrease in object size. (Fogassi et al. 2001; Gentilucci et al.

1991; Jakobson and Goodale 1991). The effects of object size on the reaching component thus seem very similar in human and non human primates. Zaal and Bootsma (1993) have pointed out that reducing object size results in a decrease of the contact surface available for fingers. Their interpretation, however, remains controversial. These authors argue that this increase of spatial accuracy demands, rather than the decrease in object size, would be responsible for the changes observed in the reaching component. Indeed the same effect can be observed in pointing movements (where the grasping component is absent) following a reduction of target surfaces (Gentilucci et al. 1991). Also, by keeping constant accuracy demands for different object sizes, Bootsma et al. (1994) found no alteration in the reaching component. Does this mean that accuracy constraint selectively taxes reaching parameters? Probably not. The grasping component does not seem immune to accuracy demands. Namely changing the surface of contact without changing object size (Bootsma et al. 1994) or imposing variable movements speeds (Juengling et al. 2000) results in compensatory adjustments of the grasping parameters. In conclusion, accuracy demands stand out as another important factor modulating prehension in primates, but one that likely affects both visuo-motor channels.

#### Difference between contralateral and ipsilateral movements

Movements directed to the target contralateral to the hand used tended to be more difficult to control and execute as revealed by changes in wrist acceleration and velocity and global movement time. In humans, studies examining pointing movements revealed the same asymmetry: reaches that crossed the body axis showed longer latencies, weaker velocity, and longer movement time than reaches toward targets on the ipsilateral side of the body (Fisk and Goodale 1985; Prablanc et al. 1979). By contrast, prehension studies have mainly investigated the effect of movement amplitude (Berthier et al. 1996; Churchill et al. 2000; Gentilucci et al. 1991; Jakobson and Goodale 1991; Kudoh et al. 1997), and fewer studies have examined the effect of movement direction on prehension

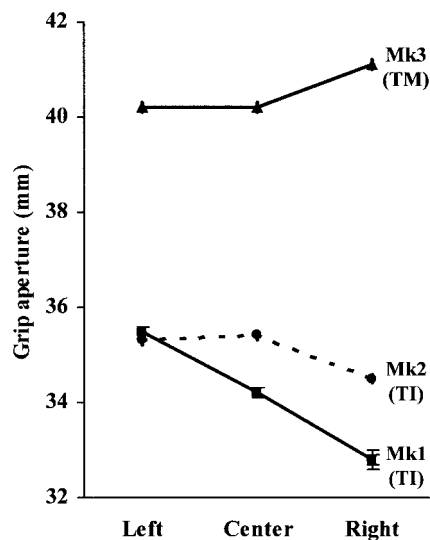


FIG. 6. Maximum grip aperture as a function of movement direction in the 3 monkeys. TM, thumb middle finger grip aperture; TI, thumb index finger aperture.

movements (Connolly and Goodale 1999; Paulignan et al. 1991b, 1997). Nevertheless, Paulignan and colleagues reported longer movement times and later and higher wrist velocity peaks for movement with the right hand to the left direction. It was unclear, however, whether these effects were truly due to object position or alternatively to the longer distance that existed between the wrist starting position and the leftmost object. Our results in monkeys clarify this issue. Indeed, in our experimental set-up, the distance between the starting position and the left and right objects was the same. The lengthened movements and later velocity observed are therefore clearly attributable to movement direction. Conversely, the higher wrist velocity peaks reported in humans might have been due to movement amplitude.

#### *Nonsystematic effects of object location on the grasping component*

Movement direction affected the grasping component in all three animals studied. However, the effects were either homogeneous or more variable across animals depending on the kinematic parameter examined. On the one hand, as already observed in humans (Connolly and Goodale 1999; Paulignan et al. 1997), the animals presented the same pattern of delayed time to maximum grip aperture for movements to the left object location. Later grip aperture for movements to the leftmost location, which presented the later wrist velocity peak, may be clearly understood as a temporal coordination between the reach and grasp channels. On the other hand, contrasting with the effects on the latencies, the alterations in the amplitude of the grip were variable. In *MK1* and *MK2*, we observed the smaller grip aperture for rightward movements, whereas *MK3* displayed the highest grip aperture for this movement direction (Fig. 6). The explanation of this inter-individual variability in the amplitude of the grip is unclear. First, it is unlikely due to a difference in the monkeys' behavior as examination of videotaped samples of movements indicated that all three animals used a similar type of grip. Second, Fitt's law (Fitt 1954) on the speed/accuracy trade-off, which predicts a larger grip aperture for a higher wrist velocity explains the data of *MK2* and *MK3* but not of *MK1*.

Another nonsystematic effect of object location on grip size concerns the differential evolution of TI and TM distances. A change in location significantly affected TI but not TM in *MK2*, whereas the reverse was true in *MK3*. One possible functional implication of this finding relates to the concept of *virtual finger*, introduced by Arbib and colleagues in 1985 (Arbib et al. 1985). Namely, grasping the handle of a cup or a mug requires one, two, or three fingers, depending on the size of the handle. In such a condition, all fingers have the same function, and move in conjunction as if they were a unique finger (hence the term *virtual finger*). This concept predicts that the kinematics of the components of a virtual finger should be identical. In line with this prediction, Castiello et al. (1993) observed a minor difference between TI and TM grip size (less than 3% of the maximal grip size) when subjects grasp big objects with a whole-hand prehension. In our case, however, the difference between TI and TM reached more than 12% of the maximal grip size, suggesting that the two fingers did not belong to a single virtual finger and might not have the same functional role.

#### *Implications for the visuo-motor channels model of primate prehension*

The present results demonstrate that changing one of the object's visual properties, whether intrinsic or extrinsic, affects both the grasping and the reaching kinematics of monkeys' prehension movements. They thus converge with earlier findings in man (Castiello et al. 1993; Jakobson and Goodale 1991) to refute the postulate of two strictly independent, parallel visuo-motor channels. Rather our data in monkeys are compatible with the idea of two partially independent, inter-related channels. First, the fact that grip amplitude modulation induced by varying object size or location differed across animals, despite identical reaching modifications, seems to us to plead for a relative autonomy of the grasping component. Second, the observation that reaching and grasping variables were correlated for the location, but not for the size task, is evidence for adaptive coordination between the two channels as a function of task constraints (Chieffi and Gentilucci 1993).

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