



Object motor representation and reaching–grasping control

Maurizio Gentilucci*

Istituto di Fisiologia Umana, Via Volturno 39, I-43100 Parma, Italy

Received 24 May 2001; received in revised form 12 December 2001; accepted 12 December 2001

Abstract

The following two competing hypotheses were tested in the present study. Is grasp guided by multiple representations of a single object, each of which codes a different grasp motor act according to the physical properties of that item? Conversely, is grasp guided by a single representation that codes all the possible affordances enabled by the object? Subjects reached different objects, but the object part used by subjects to grasp them was identical. In experiments 1 and 2, two familiar objects (fruits) which varied for size and shape were presented. Subjects grasped their stalks whose size and shape were equal. In experiments 3–7 the presented objects were geometrical solids, which varied, respectively, for weight, volume, intrinsic height, centre of mass and shape. Nevertheless, in all experiments the object portion where subjects' fingers grasped it had the same physical features. Finally, experiment 8 was a control experiment in which subjects reached and grasped equal handles of bells of the same shape, but different size. Volume, shape, and familiarity of the object influenced the grasp kinematics, even if the features of the grasped object part did not change. Variation in intrinsic object height and weight influenced final reach kinematics. Variation in centre of mass influenced neither grasp nor reach kinematics. Data are discussed in support of the hypothesis that a single object motor representation, which codes all the object affordances, is involved in grasp kinematic implementation. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Reaching–grasping kinematics; Humans; Intrinsic object properties; Object familiarity

1. Introduction

When grasping an object, a particular type of grip has to be selected. In addition, when hand approaches the target, the fingers are shaped (grip aperture phase) and, then closed on the object (grip closure phase). Behavioural studies [8,11–13] showed that intrinsic object properties influence both the selection of the type of grip and the grasp kinematic implementation. These properties are referred as to object affordances, i.e. motor representations eliciting particular types of interaction with the object. Object features can be related to a single object affordance, and, consequently, to a specific type of grip and grasp motor pattern. Conversely, object features can be related to different affordances, hence to different types of grip and grasp motor patterns. For example, the wineglass shape and volume are usually related to affordances eliciting grasping its goblet or its stem. Thus, which visual analysis occurs when an object is about to be grasped? A first hypothesis assumes that the visual analysis extracts separately each affordance from the object. As a consequence, it analyses the same object from different motor points of view in order to code multiple and indepen-

dent representations of the same object. If this hypothesis is correct, when an object portion is selected in order to be grasped, according to the agent's intention, only the corresponding affordance will activate a specific type of grip and will affect the grasp implementation. A second hypothesis assumes that the visual analysis extracts concurrently all the affordances from the same object and codes a single motor representation formed by all the types of interaction with the object. If this hypothesis is correct, the activated type of interaction with the object will be influenced also by object affordances different from the congruent one.

The behavioural predictions arising from the two hypotheses will be the following. If the first hypothesis is correct, the kinematics of reaching–grasping a complex object will be affected only by the affordance related to the opposition space [2,3]. Opposition space is the space surrounding the object portion, which the hand interacts with. It is characterised by the axis along which the fingers and/or the hand palm approach and touch the object. Should the second hypothesis be correct, the reaching–grasping kinematics would be affected also by other object affordances. The two hypotheses were tested in the present kinematic study. In all experiments the opposition space of the reaching–grasping the target–object did not change. However, the features, and the corresponding affordances of the whole object changed.

* Tel.: +39-521-903899; fax: +39-521-903900.

E-mail address: gentiluc@unipr.it (M. Gentilucci).

In addition, in some experiments familiar objects were presented. It was assumed that familiar objects automatically elicit habitual type of interactions, which the agent inhibits with difficulty. These potential interactions could influence a different actual grasp. Results of the present study showed that features of the whole object differentially affected the kinematics of the reach and the grasp components.

2. Experiment 1

The target-objects of the present experiment were two fruits (apple and strawberry). Subjects grasped their stalks, which were of the same volume and shape. In contrast, the two fruits differed for both volume and shape. These elicited different affordances and, consequently, different types of interaction. Familiar objects were chosen in order to elicit the habitual types of grasp. If the actual grasp was different, these were probably inhibited with difficulty by the agent.

2.1. Materials and methods

Six right-handed (according to the Edinburgh Inventory) [16] subjects (four women and two men, age 22–24 years)

participated in the experiment to which they gave their informed consent. They had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

In a dark and soundproof room subjects sat in front of a black table. They placed their right thumb and index finger, held in the pinch position, on a flat disk located on the table plane (starting position, SP), 15 cm distant from its edge. The presented objects were two plastic fruits: a green apple and a red strawberry (the rightmost panel in the lower row of Fig. 1). The diameters of the apple and the strawberry were approximately 7.0 and 3.0 cm. The stalks of the two fruits were green wooden rods of equal dimensions (diameter 0.5 cm, height 2.0 cm). The weights of the apple and the strawberry were 42.0 and 5.0 g, respectively. One fruit was placed on the plane of the table along the subject's sagittal axis. The lowest part of the fruits touched the plane and, in addition, the strawberry had three thin rods in order to allow a sure placement. The distance of the objects from SP along the subject's sagittal axis could be at random either 15 cm (near position) or 30 cm (far position).

Subjects were required to reach and grasp the stalk of the fruit with their right thumb and index finger and to lift it. Objects were visible to the subject as soon as the room was illuminated. Illumination was commanded by a PC and

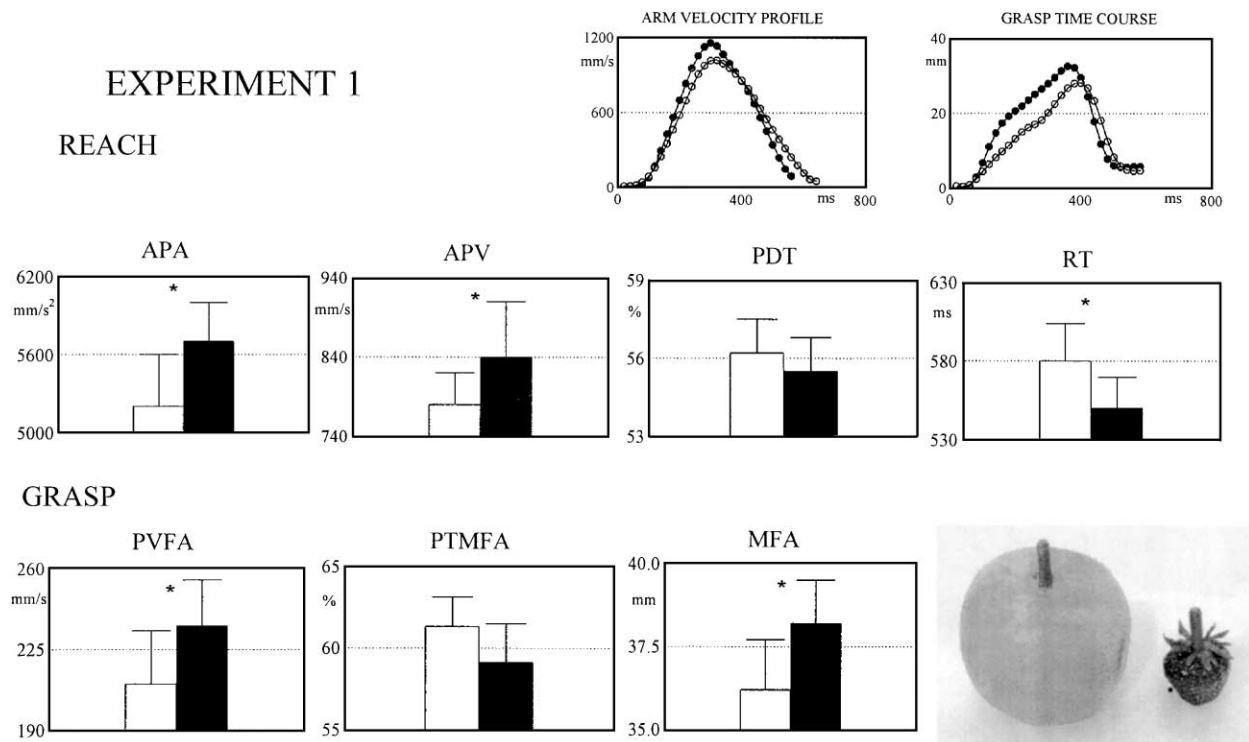


Fig. 1. The presented target-objects and the kinematic parameters analysed in experiment 1. Upper row: examples of arm velocity profiles and of grasp time course during reaching-grasping the stalks of the apple (black circles) and of the strawberry (white circles). Middle row: mean kinematic parameters of reach. APA: arm peak acceleration; APV: arm peak velocity; PDT: percentage of deceleration time; RT: reach (movement) time. Lower row: mean kinematic parameters of grasp and the presented target-objects (the rightmost panel). PVFA: peak velocity of finger aperture; PTMFA: percentage of time to maximal finger aperture; MFA: maximal finger aperture. White and black bars refer to reaching-grasping the stalks of the apple and of the strawberry, respectively. Bar markers are S.E. Asterisks indicate statistical significance. Note that, for a better object presentation, the strawberry is shown with only one supporting rod.

Table 1
Effects of target distance along sagittal axis from SP on reaching–grasping parameters

	Experiment 1		Experiment 2		Experiment 3		Experiment 4		Experiment 5		Experiment 6		Experiment 7		Experiment 8	
	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm	15 cm	30 cm
APA (mm/s ²)	$F(1,5) = 132.7$, $P < 0.0001$		$F(1,5) = 32.8$, $P < 0.002$		$F(1,5) = 60.0$, $P < 0.0006$		$F(1,11) = 49.2$, $P < 0.00001$		$F(1,5) = 24.1$, $P < 0.004$		$F(1,5) = 15.8$, $P < 0.01$		$F(1,5) = 19.8$, $P < 0.007$		$F(1,10) = 48.9$, $P < 0.00001$	
APV (mm/s)	4376.3	6567.3	5418.2	7410.7	4897.4	6455.3	4261.8	5591.3	4840.3	4903.7	4765.0	6099.4	4261.8	5591.3	5555.2	7365.8
	$F(1,5) = 331.9$, $P < 0.00001$		$F(1,5) = 383.8$, $P < 0.00001$		$F(1,5) = 504.9$, $P < 0.00001$		$F(1,11) = 791.0$, $P < 0.00001$		$F(1,5) = 184.4$, $P < 0.00001$		$F(1,5) = 95.5$, $P < 0.0001$		$F(1,5) = 96.4$, $P < 0.007$		$F(1,10) = 1115.0$, $P < 0.00001$	
	592.5	1020.4	662.0	1070.8	657.8	1056.4	573.9	917.0	586.4	941.7	856.1	920.5	573.9	917.0	655.3	1054.6
PDT (%)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
RT (ms)	$F(1,5) = 135.5$, $P < 0.0001$		$F(1,5) = 296.1$, $P < 0.00001$		$F(1,5) = 55.6$, $P < 0.0007$		$F(1,11) = 118.1$, $P < 0.00001$		$F(1,5) = 316.3$, $P < 0.00001$		$F(1,5) = 78.6$, $P < 0.005$		$F(1,5) = 62.2$, $P < 0.0005$		$F(1,10) = 69.3$, $P < 0.00001$	
	508.7	624.4	491.7	624.4	564.7	647.8	519.4	609.5	622.9	711.1	538.5	633.9	584.2	694.7	560.7	645.9
PVFA (mm/s)	n.s.	n.s.	$F(1,5) = 7.0$, $P < 0.05$		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$F(1,5) = 6.9$, $P < 0.05$		n.s.	n.s.
	–	–	251.6	225.2	–	–	–	–	–	–	–	–	216.0	185.2	–	–
PTMFA (%)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MFA (mm)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$F(1,5) = 6.6$, $P < 0.05$		$F(1,10) = 7.4$, $P < 0.02$	
	–	–	–	–	–	–	–	–	–	–	–	–	32.7	34.5	37.5	40.1

APA: arm peak acceleration; APV: arm peak velocity; PDT: percentage of deceleration time; RT: reach time; PVFA: peak velocity of finger aperture; PTMFA: percentage of time to maximal finger aperture; MFA: maximal finger aperture.

it was the signal for the movement to begin. Subjects were required to move with the maximal velocity compatible with the accuracy required by the task. The experimental session consisted of 24 trials. Six trials for each of the two positions and for each of the two fruits were run in pseudo-random order.

Movements of arm and hand were recorded using the three-dimensional optoelectronic ELITE system (B.T.S. Milan, Italy). It consists of two TV cameras detecting infrared reflecting markers at the sampling rate of 50 Hz. Three-dimensional movement reconstruction and computation of the kinematic parameters are described in a previous work [9].

In the present study four markers were used. The first marker was placed on the styloid process of the radius at the wrist; the second and the third markers were placed on the base of the nail of the thumb and the index finger, respectively. The fourth marker was placed on the plane of the table along the subject's sagittal axis, 5 cm from the chest, in order to provide a reference point. The marker placed on the subject's wrist was used to analyse the reach component. The following kinematic parameters were analysed: arm peak acceleration (APA), arm peak velocity (APV), percentage of deceleration time with respect to reach time (PDT), and reach (movement) time (RT). The grasp component was studied by analysing the time course of the distance between the thumb and the index finger. The measured grasp kinematic parameters were peak velocity of finger aperture (PVFA), percentage of time to maximal finger aperture with respect to grasp time (PTMFA), and maximal finger aperture (MFA). The procedure to calculate beginning and end of reaching–grasping is described in a previous work [10].

The experimental design included two within-subjects factors (fruit: apple versus strawberry; object position: near versus far). Separate ANOVAs were carried out on mean values of the analysed reaching–grasping parameters. The Newman–Keuls post-hoc test ($P < 0.05$) was used.

2.2. Results

2.2.1. Reach component

The upper left panel of Fig. 1 shows examples of arm velocity profiles during reaching the apple stalk and the strawberry stalk. APA showed a trend to increase ($F(1, 5) = 5.8$, $P = 0.06$), and APV ($F(1, 5) = 40.4$, $P < 0.001$) increased when reaching the apple stalk in the comparison with reaching the strawberry stalk (Fig. 1, middle row). Correspondingly, RT ($F(1, 5) = 6.2$, $P = 0.05$) decreased. The statistical effects of target position on reaching–grasping are shown in Table 1.

2.2.2. Grasp component

The upper right panel of Fig. 1 shows examples of the time course of grasping the apple stalk and the strawberry stalk. PVFA ($F(1, 5) = 6.2$, $P = 0.05$) and MFA ($F(1, 5) =$

6.8 , $P < 0.05$) were greater when grasping the apple stalk (Fig. 1, lower row).

2.3. Discussion

Although the opposition space of the two target–objects (i.e. the stalks) was the same, the reaching–grasping kinematics changed. This finding supports the hypothesis that affordances related to other object features influenced reaching–grasping kinematics implementation. It is known that hand shaping is enlarged, and reach is fastened when reaching and grasping larger objects [8,12]. The same results were found when the fruit was larger. Consequently, it is possible that the volume (three-dimensional size) of the whole object influenced reaching–grasping. This hypothesis was verified in experiment 4 in which subjects reached and grasped equal rods fixed to the top of two spheres of different volume.

However, two further alternative hypotheses can account for the results of experiment 1. First, the two stalks were differently high with respect to SP (Fig. 1). It is known that reach and grasp are influenced by target position [8,12,13]. The hypothesis that height, and consequently, the position of the object opposition space with respect to SP (extrinsic height) influenced reaching–grasping, was verified in experiment 2 in which the stalks of the two fruits were equally high. Second, the two fruits had a different weight. The weight could influence reaching–grasping since accuracy requirement during approaching the target can vary, due to the different grip force requested to hold the object to be lifted. This hypothesis was tested in experiment 3, in which subjects reached and grasped two spheres of the same volume, but different weight.

3. Experiment 2

It was verified whether in experiment 1 the height (position) of the opposition space with respect to SP (object extrinsic height) affected the kinematics of reaching–grasping. In experiment 1 the position (height) of both the object opposition space and the object centre of mass (COM) with respect to SP differed (Fig. 1). In experiment 2, the position of the object opposition space did not differ, whereas that of the object COM differed. As in experiment 1, familiar objects (i.e. fruits) were presented.

3.1. Materials and methods

A new sample of six right-handed (according to the Edinburgh Inventory) [16] subjects (four women and two men, age 21–25 years) participated in the experiment to which they gave their informed consent. They had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

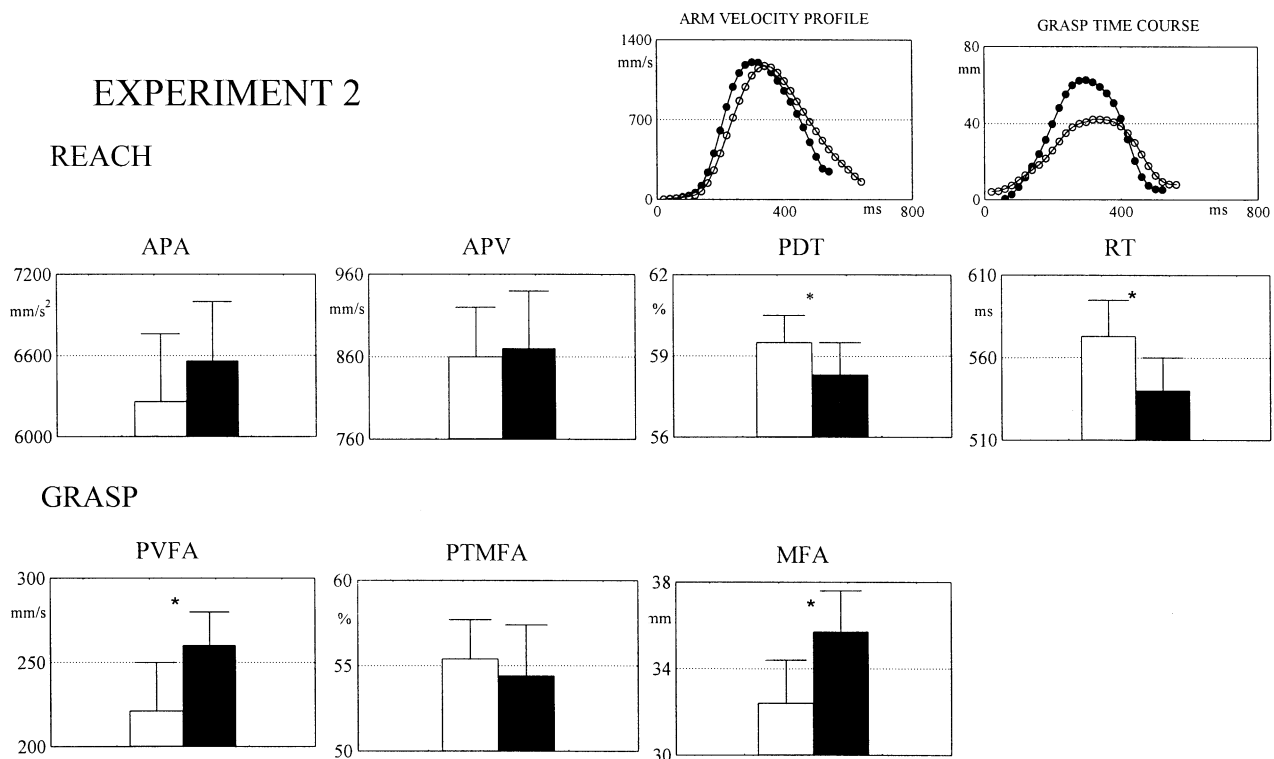


Fig. 2. The kinematic parameters analysed in experiment 2. Conventions as in Fig. 1.

Apparatus and target-objects were the same as in experiment 1. One of the two fruits could be randomly placed at two positions whose distances from SP along the subject's sagittal axis were the same as in experiment 1. However, the strawberry was located on a 4 cm high support-plane placed on the plane of the table in order to equalise the height of the two fruit stalks with respect to SP.

Procedure, data recording and analyses were the same as in experiment 1.

3.2. Results

3.2.1. Reach component

Examples of arm velocity profiles during reaching the apple stalk and the strawberry stalk are shown in the upper left panel of Fig. 2. Note no fruit effect on peak velocity. Percentage of deceleration time ($F(1, 5) = 6.1, P = 0.05$), and RT ($F(1, 5) = 17.9, P < 0.01$) decreased when reaching the apple stalk with respect to the strawberry stalk (Fig. 2, middle row). Table 1 shows the effects of target position on reach parameters.

3.2.2. Grasp component

Examples of the time course of grasping the apple stalk and the strawberry stalk are shown in the upper right panel of Fig. 2. PVFA ($F(1, 5) = 10.3, P < 0.05$) and MFA ($F(1, 5) = 16.5, P < 0.01$) were greater when grasping

the apple stalk with respect to the strawberry stalk (Fig. 2, lower row). PVFA decreased when grasping the far targets (Table 1).

3.3. Discussion

The comparison between the results of experiments 1 and 2 suggests that in experiment 1 the different height of the two stalks with respect to SP affected initial reach kinematics. It is known that target position affects initial reach kinematics [8,13]. Initial reach kinematics varied when the positions of the object opposition space with respect to SP (i.e. stalks) were different (experiment 1), whereas it did not vary for equal positions of the object opposition space (experiment 2). In contrast, initial reach kinematics was not affected by varying position of the object COM with respect to SP (experiment 2). Summing up, position of the opposition space, but not that of the object COM, affects initial reach kinematics.

4. Experiment 3

Did the weight of the target-objects affect the reach and/or the grasp kinematics in experiment 1? This possibility was verified in the present experiment in which subjects reached and grasped the rods fixed on the top of two spheres of the same volume, but different weight.

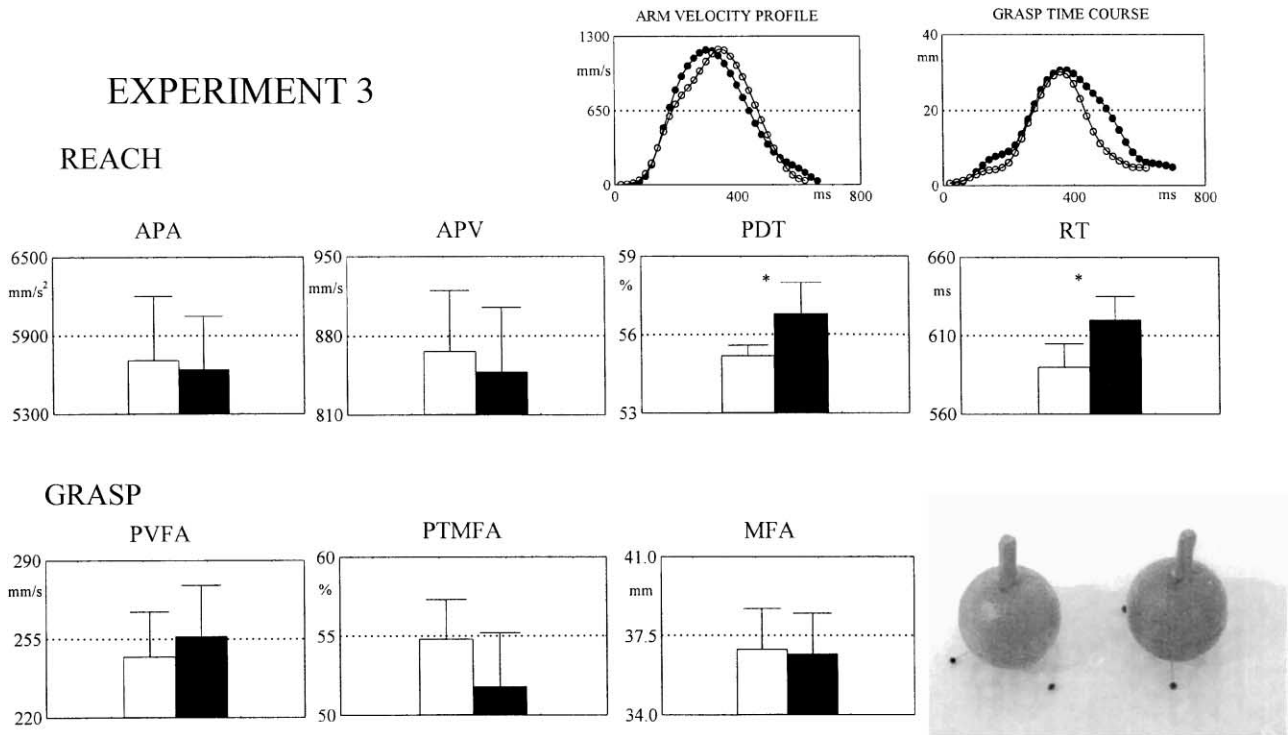


Fig. 3. The presented target-objects and the kinematic parameters analysed in experiment 3. Black and white symbols refer to reaching-grasping the rods of the heavy and the light sphere, respectively. Other conventions as in Fig. 1.

4.1. Materials and methods

A new sample of six right-handed (according to the Edinburgh Inventory) [16] subjects (four women and two men, age 20–24 years) participated in the experiment to which they gave their informed consent. They had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

Apparatus was the same as in experiment 1. Subjects reached and grasped the rods fixed on the top of two spheres of identical volume (the rightmost panel in the lower row of Fig. 3). The volume was approximately that of the strawberry (sphere diameter = 3.0 cm). The rods were the same stalks used in experiments 1 and 2. The weights of the two spheres were those of the apple (42 g) and of the strawberry (5 g) grasped in experiments 1 and 2. The heavy sphere was coloured in green (like the apple), whereas the light sphere was red (like the strawberry). One of the two spheres could be randomly placed at the same positions used in experiment 1.

Procedure was the same as in experiments 1 and 2. However, before the experimental session subjects performed a training session constituted by 20 trials in which they randomly grasped the heavy and the light sphere. The experimental session started only when subjects reported that the green sphere was heavier than the red one. Data recording and analyses were the same as in experiments 1 and 2. In the ANOVAs the within-subjects factors were object weight (heavy versus light) and object position (near versus far).

4.2. Results

4.2.1. Reach component

The upper left panel of Fig. 3 shows examples of arm velocity profiles during reaching the rods of the heavy and the light sphere. Note no weight effect on peak velocity. Percentage of deceleration time showed a trend to increase ($F(1, 5) = 5.2, P = 0.06$), and movement time ($F(1, 5) = 6.0, P = 0.05$) increased when reaching the rod of the heavy sphere (Fig. 3, middle row). Reach parameters were significantly affected by object position (Table 1).

4.2.2. Grasp component

The upper right panel of Fig. 3 shows examples of the time course of grasping the rods of the heavy and the light sphere. Object weight did not significantly affect grasp kinematics.

4.3. Discussion

Target weight did not influence the grasp kinematics. This datum indicates that modification in grasp kinematics observed in experiments 1 and 2 did not depend on fruit weight.

Final reach lengthened when reaching the heavier sphere. In experiment 2, the final reach significantly lengthened when reaching the strawberry. Also in experiment 1 it lengthened even if this was not significant probably because of an opposite effect due to the lower extrinsic height (i.e. nearer position) of the strawberry with respect to SP. Strawberry was lighter than the apple. The comparison of the results of

the present experiment with those of experiments 1 and 2 indicates that the variation in the final reach observed in experiments 1 and 2 were not due to target–object weight. In the present experiment lengthening of the final reach directed to the heavier sphere could be consequent to the fact that the variation in weight corresponded to no variation in size. This could induce uncertainty in exactly evaluating target weight before holding it, even if subjects were aware that the green object was heavier than the red one. This could increase accuracy requirement and slow down final reach, especially for the heavier object. In fact, the object had to be firmly held when it was lifted. This possibility is supported by the finding that the lack of congruence between size and weight induces the well known size–weight illusion [4]. It can explain also the reason why in experiments 1 and 2 in which there was congruence between size and weight, the heavier fruit did not cause an increase in accuracy requirement. In addition, it is possible that in experiments 1 and 2 other factors masked an object weight effect (see experiment 5).

5. Experiment 4

It is known that hand shaping enlarges when grasping larger objects and final reach lengthens when reaching to grasp smaller objects [8,13]. Consequently, it is possible that in experiments 1 and 2 the volume of the two fruits affected the control of reaching–grasping their stalks. In other words, subjects might automatically activate a reaching–grasping

program directed to the fruit, which influenced the control of reaching–grasping the stalk. The possibility of a volume effect was tested by requiring subjects to reach and grasp two equal rods fixed on the top of two spheres of different volume.

5.1. Materials and methods

A new sample of twelve right-handed (according to the Edinburgh Inventory) [16] subjects (seven women and five men, age 19–23 years) participated in the experiment to which they gave their informed consent. A larger sample than that employed in the previous experiments was tested in order to increase the power level of the statistical analyses (see Section 5.2). Subjects had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

Apparatus was the same as in experiment 2. Subjects reached and grasped the green rod fixed on the top of two plastic spheres of different volume (the rightmost panel in the lower row of Fig. 4). The volumes were approximately those of the apple (sphere diameter = 7.0 cm) and of the strawberry (sphere diameter = 3.0 cm). Weight and colour of the spheres were the same as those of the corresponding fruits. The green rods were of the same dimensions as those used in experiments 1–3. One of the two spheres could be randomly placed at the same positions as in experiment 2.

Procedure, data recording and analyses were the same as in experiments 1 and 2. In the ANOVAs the within-subjects factors were object volume (small versus great) and object

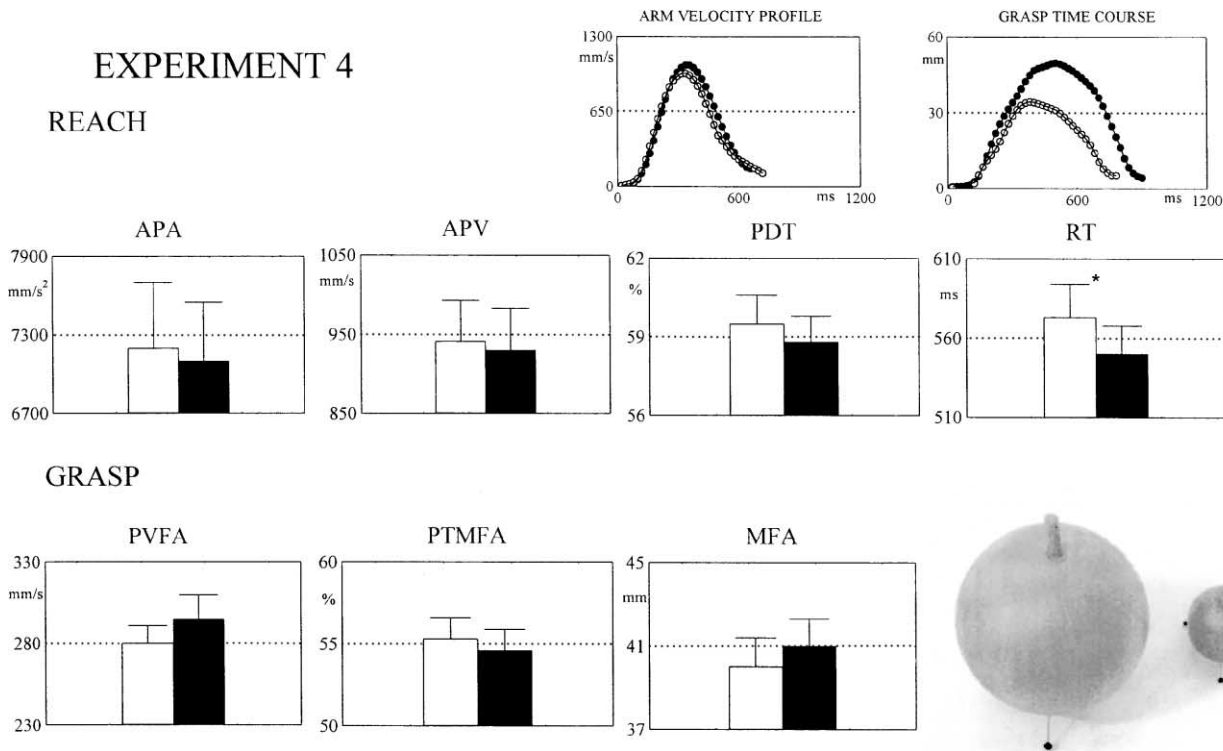


Fig. 4. The presented target–objects and the kinematic parameters analysed in experiment 4. Black and white symbols refer to reaching–grasping the rods of the great and the small sphere, respectively. Other conventions as in Fig. 1.

position (near versus far). In addition, values of the grasp parameters were compared with those collected in experiment 2. In the new ANOVAs the between-subjects factor was object (fruit versus sphere) and the within-subjects factors were object volume (small versus great) and object position (near versus far).

5.2. Results

5.2.1. Reach component

The upper left panel of Fig. 4 shows examples of arm velocity profiles during reaching the rods of the great and the small sphere. RT ($F(1, 11) = 6.4$, $P < 0.05$) increased when reaching the small sphere (Fig. 4, middle row). Note in Fig. 4 a not significant increase in percentage of deceleration time when reaching the small sphere. The statistical effects of object position on reach parameters are shown in Table 1.

5.2.2. Grasp component

The upper right panel of Fig. 4 shows examples of the time course of grasping the rods of the great and the small sphere. PVFA ($F(1, 11) = 4.4$, $P = 0.06$) and MFA ($F(1, 11) = 4.0$, $P = 0.07$) increased when grasping the rod of the great sphere. However, only a trend to statistical significance was observed, even if the sample of subjects was larger than that tested in the previous experiments. The comparison of data with those collected in experiment 2 showed a trend to significance for the interaction between object and object volume (PVFA, $F(1, 16) = 3.3$, $P = 0.08$, MFA, $F(1, 16) = 3.8$, $P = 0.07$). The factor object volume was significant (PVFA, $F(1, 16) = 16.1$, $P < 0.001$, small object 248.6 mm/s, great object 275.4 mm/s, MFA, $F(1, 16) = 12.7$, $P < 0.005$, small object 36.2 mm, great object 38.5 mm).

5.3. Discussion

The volumes of the two spheres influenced the grasp and the final reach similarly to the fruits presented in experiment 2. However, the volume effect on grasp was less evident than the fruit effect. In fact, even if statistical power level was increased, only a trend to significance was observed in the ANOVAs performed on the grasp parameters. In addition, a trend to a greater volume effect for the fruit was found in the comparison with data of experiment 2. These results suggest that additional factors could be involved along with object volume in the kinematic modification observed in experiment 2. They could be the following: the first factor is intrinsic height of the fruit. Although stalk heights were equal, height of the fruit (intrinsic height) was different. It is possible that intrinsic target height is computed when implementing reaching–grasping. This possibility was tested in experiment 5. The second factor is the centre of mass (COM). Goodale et al. [11] observed that when an object is grasped the final finger position is influenced by its COM. Indeed, they found that the line joining thumb and index finger at the end of a precision grip usually crossed

the COM. In experiments 1, 2, and 4, the final finger position was nearer to the COM when the object was smaller. It is possible that the relative position between final finger position and object COM influenced grasp. This possibility was tested in experiment 6. The third factor is target shape. Although similar, the shapes of the two fruits could automatically activate different reach and grasp programs, which interfered with reaching–grasping the stalks of equal volume and shape. This possibility was tested in experiment 7. The fourth factor is object familiarity. Since the fruits, but not their stalks, are usually grasped, their presentation could automatically activate the usual reach and grasp program, which influenced reaching–grasping the stalks. This possibility was tested in experiment 8.

6. Experiment 5

The possible influence of object intrinsic height on reaching–grasping movements was tested. Objects to be reached were two rods of different height. Their upper part whose contact surface was equal was grasped. The variation in volume of the two target–objects was minimal.

6.1. Materials and methods

A new sample of six right-handed (according to the Edinburgh Inventory) [16] subjects (three women and three men, age 21–25 years) participated in the experiment to which they gave their informed consent. Subjects had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

Apparatus was the same as in experiment 2. The green upper part of two wooden rods was reached and grasped (dark part of the rods in Fig. 5, the rightmost panel in the lower row). The area of the rod section and the length of the green upper part were the same as those of the stalks grasped in experiments 1 and 2. The white lower parts (light part of the rods in Fig. 5) were as high as the apple and the strawberry, respectively. The weights of the high and low rods were 3.2 and 2.6 g, respectively. The support bases of the two rods had equal dimensions (3.0 cm × 3.0 cm × 0.1 cm). One of the two rods could be randomly placed at the same positions used in experiment 2.

Procedure, data recording and analyses were the same as in experiments 1 and 2. In the ANOVAs the within-subjects factors were intrinsic target height (small versus great) and object position (near versus far).

6.2. Results

6.2.1. Reach component

The upper left panel of Fig. 5 shows examples of arm velocity profiles during reaching the low and the high rod. APV ($F(1, 5) = 9.7$, $P < 0.05$), PDT ($F(1, 5) = 38.8$, $P < 0.005$), and RT ($F(1, 5) = 5.8$, $P = 0.06$) were greater

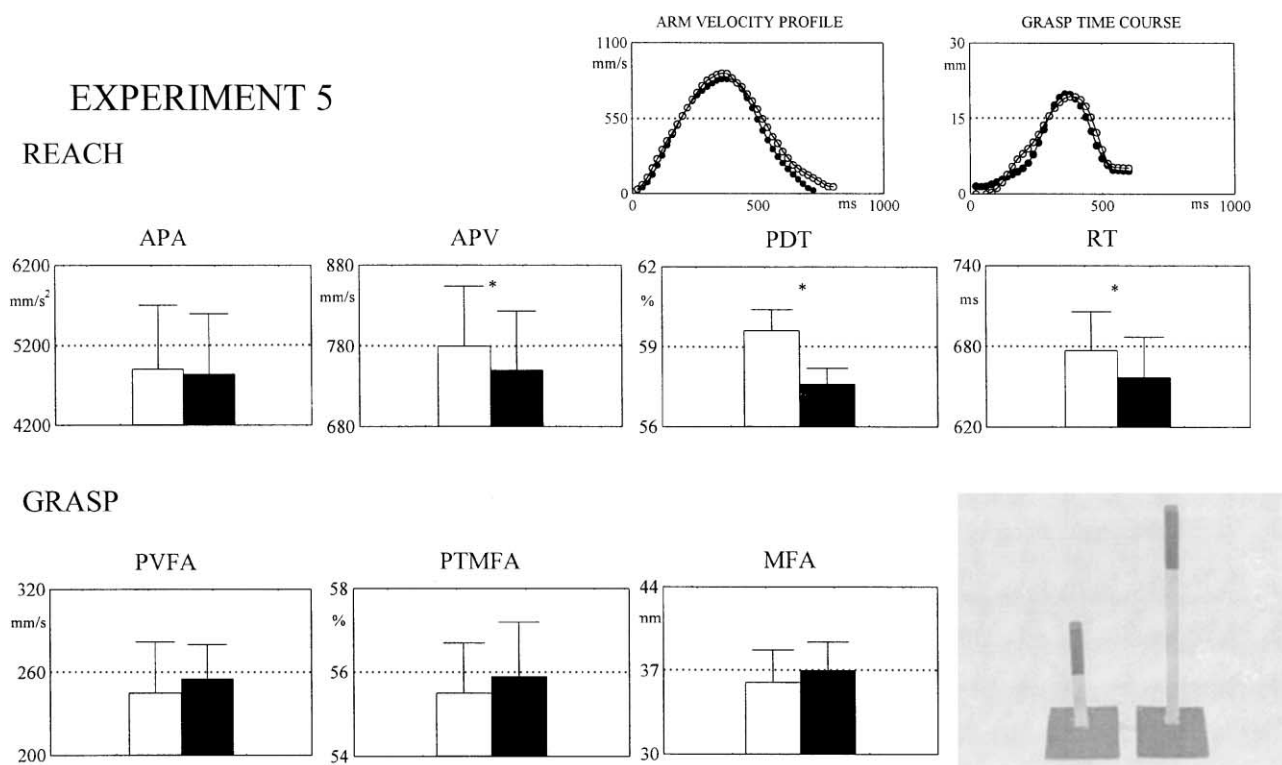


Fig. 5. The presented target-objects and the kinematic parameters analysed in experiment 5. Black and white symbols refer to reaching-grasping the high and the low rod, respectively. Other conventions as in Fig. 1.

when reaching the low rod (Fig. 5, middle row). The effect of rod height on PDT was more evident for the far object (interaction between intrinsic target height and object position, $F(1, 5) = 8.4$, $P < 0.05$). Object position significantly affected reach parameters (Table 1).

6.2.2. Grasp component

The upper right panel of Fig. 5 shows examples of the time course of grasping the low and the high rod. Intrinsic target height affected no parameter (Fig. 5, lower row).

6.3. Discussion

Although intrinsic target height is an intrinsic object property, it appeared to affect reach, but not grasp. The high rod probably increased difficulty in precisely localising its upper part during initial reaching. This can explain the decrease in APV. This effect was not observed in experiments 1, 2, and 4 probably because the lower object part was larger and it was a more reliable reference in order to localise precisely the end point of fingers. The low rod could induce an increase in accuracy requirement during final reach. This could be due to the necessity of the agent's hand to avoid the contact with the table plane. This can explain the increase in reach deceleration time. Summing up, the results concerning the final reach found in experiments 1, 2, 4 were probably due to intrinsic target height.

The difference in volume of the two objects did not influence grasp. In fact, the sizes of the sides by which the rod lower parts could be grasped were equal. They probably elicited an equal affordance in both the objects. In experiments 1, 2, and 4 the sizes of the graspable sides of the object lower parts varied, and, probably, different object affordances were elicited.

7. Experiment 6

The aim of the experiment was to determine whether in experiments 1 and 2 the different position of the COM (centre of mass) of the fruits with respect to the opposition space was responsible for the modifications observed in the reaching-grasping kinematics. Subjects reached and grasped the upper part of two objects of the same volume and intrinsic height. The positions of the object COMs with respect to the opposition space were different.

7.1. Methods

A new sample of six right-handed (according to the Edinburgh Inventory) [16] subjects (three women and three men, age 23–27 years) participated in the experiment to which they gave their informed consent. Subjects had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

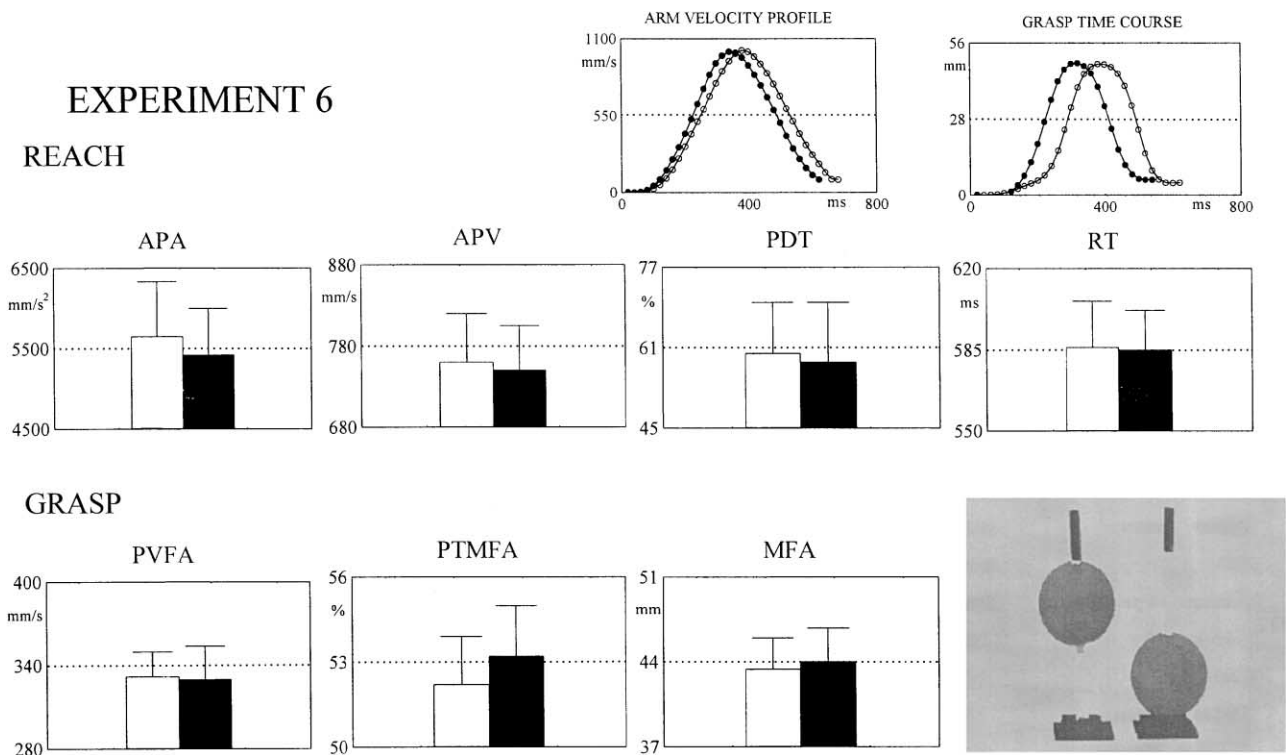


Fig. 6. The presented target-objects and the kinematic parameters analysed in experiment 6. Black and white symbols refer to reaching-grasping the object with high and low COM, respectively. Other conventions as in Fig. 1.

Apparatus was the same as in experiment 2. The green upper part of two wooden rods was reached and grasped (dark part of the rods in Fig. 6, the rightmost panel in the lower row). The area of the rod section and the length of the green upper part were the same as those of the stalks grasped in experiments 1 and 2. The white lower parts (light part of the rods in Fig. 6, the rightmost panel in the lower row) were as high as the apple and passed through the centre of a red sphere (diameter = 4.0 cm). The sphere could be positioned either on the high part (left object in Fig. 6, the rightmost panel in the lower row) or in the low part (right object in Fig. 6, the rightmost panel in the lower row) of the white rod. The support bases of the two rods had equal dimensions (3.0 cm × 3.0 cm × 0.1 cm). Consequently, the two objects were of the same volume, and intrinsic height, but the COMs were differently located. That of the right object shown in Fig. 6 (the rightmost panel in the lower row) was higher than that of the left object. In other words, the COM of the right object was nearer to the grasped object part with respect to that of the left object, like the COM of the strawberry was nearer to the grasped object part with respect to that of the apple. One of the two objects could be randomly placed at the same positions used in experiment 1.

Procedure, data recording and analyses were the same as in experiments 1 and 2. In the ANOVAs the within-subjects factors were COM position (low versus high) and object position (near versus far).

7.2. Results

7.2.1. Reach component

The upper left panel of Fig. 6 shows examples of arm velocity profiles during reaching the two objects. COM position affected no reach parameter (Fig. 6, middle row), whereas object position significantly affected reach parameters (Table 1).

7.2.2. Grasp component

The upper right panel of Fig. 6 shows examples of the time course of grasping the two objects. COM position affected no parameter (Fig. 6, lower row).

7.3. Discussion

The COM position affected neither reach nor grasp parameters. Note that the distance between the COMs of the two objects presented in the present experiment was greater than that of the two fruits presented in experiments 1 and 2. Consequently, if the COM locations were responsible for the kinematic modification observed in experiments 1 and 2, the same modification should be observed also in the present experiment. This did not occur.

By the comparison of the results of the present experiment with those found by Goodale et al. [11] it can be suggested that only the COM of the object part related to the opposition space influences grasp.

8. Experiment 7

The aim of the experiment was to determine whether in experiments 1 and 2 the shape of the two fruits influenced reaching–grasping. In general, the aim of the present experiment was to dissociate the possible effects of object shape on grasp from those of object volume. Subjects reached and grasped the rods fixed on the top of two objects of the same volume, but different shape. Shapes different from those of the apple and the strawberry were chosen because shapes equal to the two fruits could be automatically associated to the corresponding familiar objects. Consequently, in this case shape could not be dissociated from familiarity.

8.1. Materials and methods

A new sample of six right-handed (according to the Edinburgh Inventory) [16] subjects (three women and three men, age 22–25 years) participated in the experiment to which they gave their informed consent. Subjects had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

Apparatus was the same as in experiment 2. Subjects reached and grasped the rod fixed on the top of a green sphere and a red disk (Fig. 7, the rightmost panel in the lower row). The major and the minor axes of the disk were 9.0 and 3.6 cm long, respectively. The sphere diameter was 6.5 cm long. The volume of the two objects was equal. Since objects were made by the same material (plastic), also their

weight did not differ. The rods were those used in experiments 1–5. A flat circular surface (diameter = 2.9 cm) allowed placement of the disk on the table plane, whereas the heads of three thin rods arranged at the vertices of a triangle (side = 1.5 cm) allowed placement of the sphere. One of the two objects could be randomly placed at the same positions as in experiment 2.

Procedure, data recording and analyses were the same as in experiments 1 and 2. In the ANOVAs the within-subjects factors were object shape (disk versus sphere) and object position (near versus far).

8.2. Results

8.2.1. Reach component

The upper left panel of Fig. 7 shows examples of arm velocity profiles during reaching the rods of the disk and of the sphere. PDT showed a trend to increase ($F(1, 5) = 5.8$, $P = 0.06$) when reaching the rod of the disk (Fig. 7, middle row). Also RT increased, although not significantly. Target position significantly affected reach parameters (Table 1).

8.2.2. Grasp component

The upper right panel of Fig. 7 shows examples of the time course of grasping the rods of the disk and of the sphere. Factor object shape affected PVFA ($F(1, 5) = 48.8$, $P < 0.001$) and MFA ($F(1, 5) = 112.6$, $P < 0.0001$). Hand shaping was larger when grasping the rod of the sphere than the rod of the disk (Fig. 7, upper right panel and lower

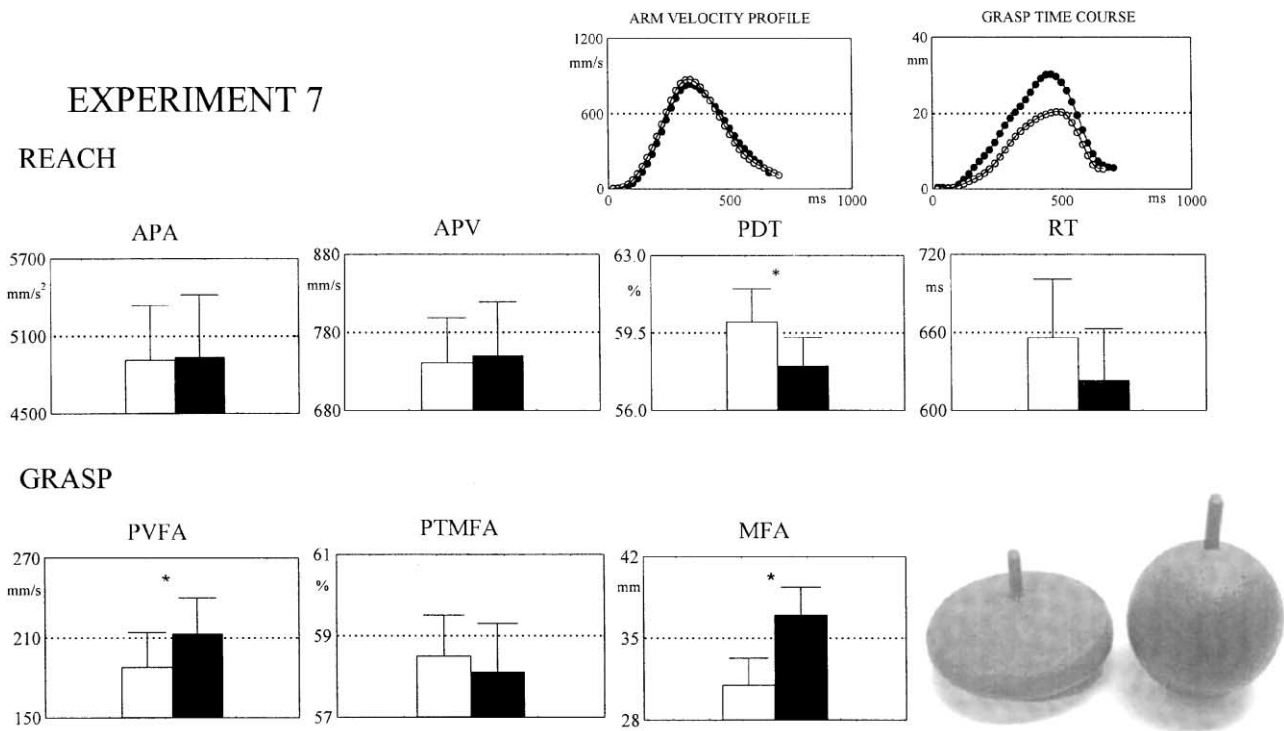


Fig. 7. The presented target–objects and the kinematic parameters analysed in experiment 7. Black and white symbols refer to reaching–grasping the rods of the sphere and the disk, respectively. Other conventions as in Fig. 1.

panels). Hand shaping was affected also by object position (Table 1).

8.3. Discussion

Hand shaping was smaller when grasping the disk rod with respect to the sphere rod. This result can be interpreted in the following way. The sphere evoked only one affordance related to the sphere diameter. This affordance influenced grasping the upper placed rod. In contrast, the disk evoked two affordances related to the lengths of the two disk axes. The lengths of the major and minor axes were, respectively, greater and less than the sphere diameter. Probably, grasping the disk by using the minor axis as opposition space was automatically chosen, affecting the control of grasping the rod. Indeed, such a grasp allows a larger contact surface at the end of grasp and requires the use of the thumb and index finger (precision grip) like grasping the upper rod. In contrast, the natural grasp of the disk by the major axis requires the use of more than two fingers. Note that in experiment 6 the two objects had different shapes. Nevertheless, they did not modify grasp kinematics. This result can be explained by considering that the two objects, although different for shape, afforded the same types of interactions.

It can be suggested that in experiments 1, 2, and 4 the probability that the small object slipped and/or fell on the table plane could be higher, if one finger inadvertently knocked against the rod during the last phase of grasp. This possibility could induce subjects to close more slowly their fingers and to use smaller grip apertures. Results of the present experiment and of experiments 3 and 5 disprove this possibility. Smaller contact surface between object and table plane and/or lighter objects increase the possibility of slipping since friction force is lower. Smaller contact surface when the two objects were of the same weight (sphere in comparison with disk in the present experiment) and smaller weight when the two objects had the same contact surface (light in comparison with heavy sphere in experiment 3) did not induce a decrease in hand shaping. Higher ratio between object height and contact surface area increases the possibility of falling when object weights do not vary. Indeed, the threshold for a rotation movement due to a force applied to the top of an object decreases. Higher ratios in the present experiment (sphere in comparison with disk) and in experiment 5 (high in comparison with low rod; the weight of the two objects poorly varied) did not induce a decrease in hand shaping.

9. Experiment 8

The results of experiments 4 and 7 suggest that the fruit effects (experiments 1 and 2) observed on the grasp kinematics can be due to both volume and shape of the whole object. However, also familiarity of the object could be responsible for the observed grasp kinematic modification. In

fact, the object volume was less effective than the fruit in modifying grasp, even if the difference in volume of the two fruits was the same as that tested in experiment 4. Moreover, in experiment 7 the tested object shapes were very different, whereas those of apple and strawberry were similar. Indeed, both of them could be approximately associated to spherical shapes. The hypothesis that object familiarity affects grasp was again tested by presenting two familiar objects of the same shape, but different volume. Alternatively, an experimental paradigm might be chosen in which two objects of the same shape and volume, but different familiarity were presented. However, volume and shape are the main features characterising a familiar object. Consequently, two objects of the same shape and volume even if differing for other features (i.e. material, colour, weight, texture), can be automatically perceived as belonging to the same semantic category, and, probably, activate the same type of interaction.

9.1. Materials and methods

A new sample of 12 right-handed (according to the Edinburgh Inventory) [16] subjects (seven women and five men, age 21–26 years) participated in the experiment to which they gave their informed consent. Subjects had normal or correct-to-normal vision, and were naive as to the purpose of the experiment.

Apparatus was the same as in experiment 2. Objects to be reached and grasped were the handles of a great green bell and of a small red bell (Fig. 8, the rightmost panel in the lower row). The volumes of the two bells corresponded approximately to those of the apple and the strawberry presented in experiments 1 and 2. The handle dimensions were the same as those of the previously presented stalks. One of the two bells could be randomly placed at the same positions as in experiment 2.

Six subjects were required to reach and grasp the bell handle and to lift it. The other six were required to reach and grasp the bell and to ring it by shaking the handle. Procedure, data recording and analyses were the same as in experiments 1 and 2. In the ANOVAs the between-subjects factor was action (grasp-and-lift versus grasp-and-ring) and the within-subjects factors were bell volume (great versus small) and bell position (near versus far).

9.2. Results

At the end of the experimental session each subject was required to show how she or he would spontaneously grasp the two bells. All subjects grasped the small bell by the handle, and the great bell by the vessel.

9.2.1. Reach component

The upper left panel of Fig. 8 shows examples of arm velocity profiles during reaching the handles of the small and the great bell. PDT ($F(1, 10) = 6.9, P < 0.02$) and RT ($F(1, 10) = 69.3, P < 0.00001$) increased when reaching

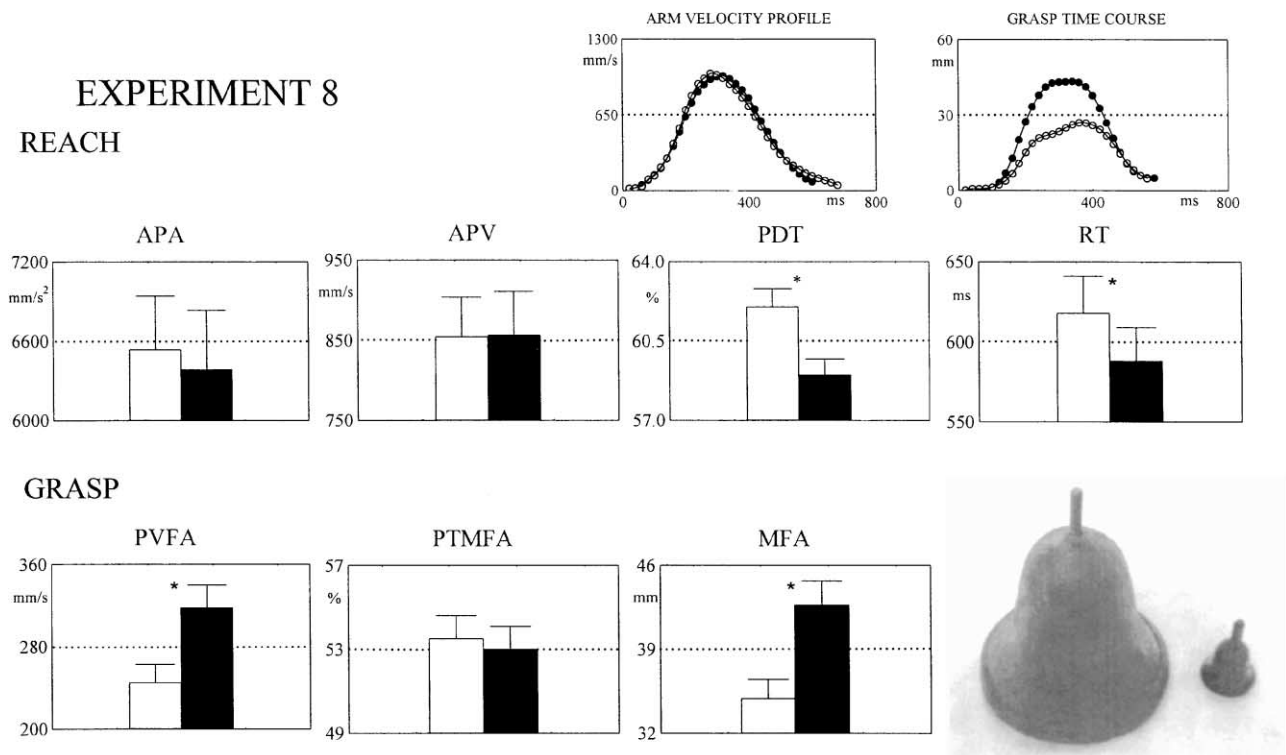


Fig. 8. The presented target-objects and the kinematic parameters analysed in experiment 8. Black and white symbols refer to reaching-grasping the handles of the great and the small bell, respectively. Other conventions as in Fig. 1.

the handle of the small bell (Fig. 8, middle row). Bell position significantly affected APA, APV, and RT (Table 1).

9.2.2. Grasp component

The upper right panel of Fig. 8 shows examples of the time course of grasping the handles of the small and great bell. PVFA ($F(1, 10) = 23.6, P < 0.0007$) and MFA ($F(1, 10) = 45.8, P < 0.00001$) increased when grasping the handle of the large bell (Fig. 8, lower row). MFA was affected also by bell position (Table 1). Factor action was not significant in all analyses.

9.3. Discussion

The following arguments are in favour of the hypothesis that object familiarity affects grasp. The effects of bell volume on grasping their handle were the same as those of fruits on grasping their stalks (experiments 1 and 2). The effects of sphere volume on grasping the upper fixed rods (experiment 4) were lower than those of the fruits (experiments 1 and 2) and the bells. The two fruits differed in volume and slightly in shape, whereas the two bells differed only in volume.

The bell effect can be explained by postulating that vision of the two bells could automatically afford two different types of interaction, which influenced grasping the handle. Indeed, subjects spontaneously grasped the small bell by the handle and the large bell by the vessel. Grasping the large bell by the vessel could be due to the fact that subjects

automatically estimated the rod too short with respect to the vessel and not enough reliable for a stable pinch.

10. General discussion

The results of the present study show that object affordances different from that related to the actual opposition space [2,3] influenced the kinematics of reaching-grasping. This finding may be interpreted as an interference effect similar to that found when a target is presented simultaneously with a distractor [5,6,7,20]. However, the following differences with respect to the other studies should be considered. First, those studies found that movement frequently slowed down in presence of a distractor, probably because of an inhibition of the motor program towards it, in agreement with Tipper's interpretation [20]. Slowing down was stronger for higher distractor salience [6,7,20]. This was not observed in the present study. In fact, movement did not slow down when the whole object was larger, and, consequently more salient. Second, in the present study the effects of the whole object on grasp were highly consistent. In contrast, in the previous experiments [6,7,20] they depended on extrinsic (position) and intrinsic (lightness, colour) properties of the distractor and on the experimental conditions (i.e. on the possibility that the distractor could be either the actual movement target or the target of a successive movement). More importantly, if in the present study an interference effect similar to that

observed during the simultaneous presentation of target and distractor was present, the effect should be evident when the interfering part of the object was nearer to the object portion related to the finger opposition space. This condition was present in experiment 6 in which the possibly interfering part of the object (the red sphere) was differently located with respect to the object part related to the opposition space. Nevertheless, no interference effect was observed on reaching–grasping. Finally, the aim of the present study was different from that of the other studies. The present study aimed to determine whether the actual interaction with an object is influenced by other potential types of interaction with the same object, whereas the other studies aimed to determine whether the interaction with an object is influenced with the potential interaction with another object. In other words, the present study aimed to determine whether, when an object is visually presented, a single motor representation of the whole target–object is coded. Conversely, the other studies aimed to determine how a target–object is isolated from environment (process of selection-for-action) [1].

The results of the present study might be interpreted as determined by an attraction of attention towards the object core which was meaningful to the viewer, i.e. the fruit which could be eaten, and the bell vessel which could ring. However, the effect was found also when the object core was semantically meaningless, that is when a sphere or a disk was presented. In addition, the grasp modification was always congruent with the type of interaction with the object core. In brief, if attention played a role, this was strictly related to the processes of visuo-motor transformation [6].

Intrinsic object properties of the whole target–object affected reach and grasp even if in all experiments the properties of the object portion related to the opposition space did not vary. Object volume (in particular the size of the graspable side) and shape affected grasp. The influence of object volume on grasp kinematics is well known (for a review see [13]). Consequently, it is plausible that the affordances related to the volume of the fruits (experiments 1 and 2), spheres (experiment 4), and bells (experiment 8) interfered with the affordance related to the rod. Till now, the influence of object shape on grasp kinematics has been poorly studied [11]. However, the presented object shapes (i.e. sphere and disk) elicited stereotyped types of grasp. The results were congruent with their possible influence on the control of the actual grasp. In the present study enlarging hand shaping was associated to presentation of a green object. However, if colour played a role [7], enlarging hand shaping should be observed for red objects.

Intrinsic height of the object affected the final reach, but not the grasp. It is interesting to note that extrinsic height of the opposition space, i.e. height with respect to the agent, affected the initial reach. Although extrinsic height is likely to affect the reach planning phase, whereas intrinsic object height likely affected the control of reach execution, both properties related to the location of the opposition space affected reach, but not grasp. Both these results and those

concerning the effects of the whole object volume and shape on grasp are in favour of the hypothesis that the “visuo-motor channels” for the reach and grasp control are independent [8,13].

The volume effect was stronger when grasping familiar objects (fruit, bell) than spheres (geometrical solid). These results can be explained as due to a greater subjects’ capability to separate visually the rod from the sphere rather than the stalk from the fruit or the handle from the bell. In fact, the latter stimuli are semantically single objects. At variance with this explanation the shape effect was strong even if geometrical solids were presented. A complementary explanation is that familiar objects automatically activate habitual types of interactions, which very strongly influence grasp implementation. It can be argued that, from a motor point of view, familiar objects can be represented by the type/types of interaction that we habitually have with them.

Neurophysiological studies showed that both AIP (anterior part of intraparietal sulcus) [15,19] and F5 premotor [14,17] areas of monkey are involved in the control of grasp movements. The two areas are reciprocally connected [18]. The majority of AIP neurons are active during the entire motor act of grasp (motor-dominant neurons). Many neurons have visual responses (visual-dominant neurons). They fire during target–object fixation, and some of them fire also without a subsequent grasping act. Frequently, their discharge is selective for target size and/or shape. Others require other visual stimuli, such as the view of the moving hand. Conversely, F5 neurons are active during specific phases of grasp and are selective for a particular type of grip. Some of them respond to visual stimuli. Three-dimensional objects are effective in eliciting neuron discharge provided that their sizes are congruent with the type of grip coded by the neuron.

In agreement with these data it has been proposed a model according to which area AIP sends visual signals of object properties to area F5 for selecting the type of grip and the pattern of hand movements, and area F5 sends back the reference copy of the selected motor command to area AIP [19]. This feedback loop plays a role in the control of movement execution, i.e. in matching, during grasp, the pattern of hand-grip with the features of the target–objects and, in particular, with the corresponding affordance. However, usually more affordances can be extracted from the same object. Does the AIP-F5 circuit extract each affordance separately or a motor representation of the whole object is coded? Data of the present study support the second hypothesis. The AIP-F5 circuit concurrently extracts all the possible affordances from the object when it is presented. It is possible that this occurs at level of single AIP neuron. However, I propose that, when an object is presented, AIP neurons code separately each object affordance. They send information on affordances to F5 neurons involved in both selecting different types of grip and implementing different grasp kinematics. The large distribution of affordance information to F5 neurons is due to the possibility of choosing grasps even different from that

congruent with the actual affordance. For example, large objects are occasionally grasped with only the thumb and index finger. In addition, the concurrent activation of different affordances and the large distribution of information can have an adaptive function. In the case the grasp cannot be completed, other interactions with the object can be activated (e.g. in experiments 1 and 2 the apple rolls from the table and needs to be fetched at its base). However, I assume that the connection between neurons coding an affordance and neurons coding the congruent type of grip and grasp kinematics is stronger. Signals are sent back to AIP from F5 and again to F5 from AIP till grasp is accomplished. Consequently, in some circumstances this reverberating circuit can be strengthened until achieving activation of grasp patterns different from the actual one.

Acknowledgements

I wish to thank C. Secchi, S. Grimaldi, and L. Caselli for the help in carrying out the experiments. I thank G. Cossu, P.F. Ferrari and V. Gallese for the comments on the manuscript. I thank also Dr. S. Vogt, and an anonymous reviewer for the useful comments on this work. The work was supported by grant from MURST (Ministero dell' Università e della Ricerca Scientifica e Tecnologica) to M.G.

References

- [1] Allport DA. Selection-for-action: some behavioral and neurophysiological considerations of attention and action. In: Heuer H, Sanders AF, editors. *Perspectives on perception and action*. Hillsdale, NJ: Lawrence Erlbaum, 1987. p. 395–419.
- [2] Arbib MA. Programs, schemas and neural networks for control of hand movement: beyond the RS frameworks. In: Jeannerod M, editor. *Attention and performance XIII: motor representation and control*. Hillsdale, NJ: Lawrence Erlbaum, 1990. p. 111–38.
- [3] Arbib MA, Iberall T, Lyons D. Coordinated control programs for movements of the hand. In: Goodman AW, Darian-Smith I, editors. *Hand function and the neocortex*. Berlin: Springer, 1985. p. 135–70.
- [4] Charpentier A. Analyse expérimentale de quelques éléments de la sensations de poids. *Archives de Physiologie Normale et Pathologique* 1891;3:122–35.
- [5] Chieffi S, Gentilucci M, Allport A, Sasso E, Rizzolatti G. Study of selective reaching and grasping in a patient with unilateral parietal lesion. Dissociated effects of residual spatial neglect. *Brain* 1993;116:1119–37.
- [6] Gangitano M, Daprati E, Gentilucci M. Visual distractors differentially interfere with the reaching and grasping components of prehension movements. *Exp Brain Res* 1998;122:441–52.
- [7] Gentilucci M, Benuzzi F, Bertolani L, Gangitano M. Influence of stimulus color on the control of reaching–grasping movements. *Exp Brain Res* 2001;137:36–44.
- [8] Gentilucci M, Castiello U, Corradini ML, Scarpa M, Umiltà C, Rizzolatti G. Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia* 1991;5:361–78.
- [9] Gentilucci M, Chieffi S, Scarpa M, Castiello U. Temporal coupling between transport and grasp components during prehension movements: effects of visual perturbation. *Behav Brain Res* 1992;47:71–82.
- [10] Gentilucci M, Toni I, Chieffi S, Pavesi G. The role of proprioception in the control of prehension movements: a kinematic study in a peripherally deafferented patient and in normal subjects. *Exp Brain Res* 1994;102:483–94.
- [11] Goodale MA, Meenan JP, Bühlhoff HH, Nicolle DA, Murphy KJ, Racicot CI. Separate neural pathways of object shape in perception and prehension. *Curr Biol* 1994;4:604–10.
- [12] Jakobson LS, Goodale MA. Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Exp Brain Res* 1991;86:199–208.
- [13] Jeannerod M. *The neural and behavioural organization of goal-directed movements*. Oxford: Oxford University Press, 1988.
- [14] Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G. Object representation in the ventral premotor cortex (area F5) of the monkey. *J Neurophysiol* 1997;78:2226–30.
- [15] Murata A, Gallese V, Luppino G, Kaseda M, Sakata H. Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *J Neurophysiol* 2000;83:2580–601.
- [16] Oldfield RC. The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia* 1971;9:97–113.
- [17] Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M. Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res* 1988;71:491–507.
- [18] Rizzolatti G, Luppino G, Matelli M. The organization of the cortical motor system: new concepts. *Electroencephalography Clin Neurophysiol* 1998;106:283–96.
- [19] Sakata H, Taira M, Murata A, Mine S. Neural mechanisms of visual guidance in the parietal cortex of the monkey. *Cerebral Cortex* 1995;5:429–38.
- [20] Tipper SP, Howard LA, Jackson SR. Selective reaching to grasp: evidence for distractor interference effects. *Vision Cognition* 1997;4:1–38.