UNIVERSITÀ DEGLI STUDI DI PADOVA

Sede Amministrativa: Università degli Studi di Padova

Dipartimento di Psicologia Generale

Scuola di Dottorato di Ricerca in Scienze Psicologiche
Indirizzo di Percezione e Psicofisica

CICLO XX

REACHING BEYOND GRASP

Direttore della Scuola: Ch.mo Prof. Luciano Stegagno

Supervisore: Ch.mo Prof. Umberto Castiello

Dottorando: Caterina Ansuini

DATA CONSEGNA TESI
31 gennaio 2008

Table of contents

CHAPTER 3

CONTROL OF HAND SHAPING IN RESPONSE TO OBJECT SHAPE PERTURBATION

CHAPTER 4

DISTRACTOR OBJECTS AFFECT FINGERS' ANGULAR DISTANCES BUT NOT HAND SHAPING DURING GRASPING

CHAPTER 5

EFFECT OF END-GOAL ACCURACY ON HAND SHAPING

CHAPTER 6

AN OBJECT FOR AN ACTION, THE SAME OBJECT FOR OTHER ACTIONS

CHAPTER 7

BREAKING THE FLOW OF ACTION

CHAPTER 8

GENERAL CONCLUSIONS

1. General introduction

1.1 The static aspects of grasping

The modern study of human hand movements has been pioneered by the British evolutionary biologist John Napier (1956). He provided a classification of hand prehensile activities which has greatly simplified the analysis of such complex movements. In particular, he identified two anatomically distinct patterns of prehension that seem to be at the basis of all manipulative hand movements, namely precision and power grip (Napier, 1960) (see Figure 1.1a-b). Precision grip, executed between the terminal digital pad of the opposed thumb and the pads of the fingertips, is predominantly employed for accurate movements (Figure 1.1a). Power grip, executed between the surface of the fingers and the palm, with the thumb acting as a reinforcing agent (Figure 1.1b), has in the application of force its dominant feature (Napier, 1960). An important tenet of Napier's theorization (1956) is that the selection of one or the other type of grip not only depends on object features, but it also depends on what we aim to do with the object following grasping. This latter issue is at the core of the experimentation included in the present thesis.

A B

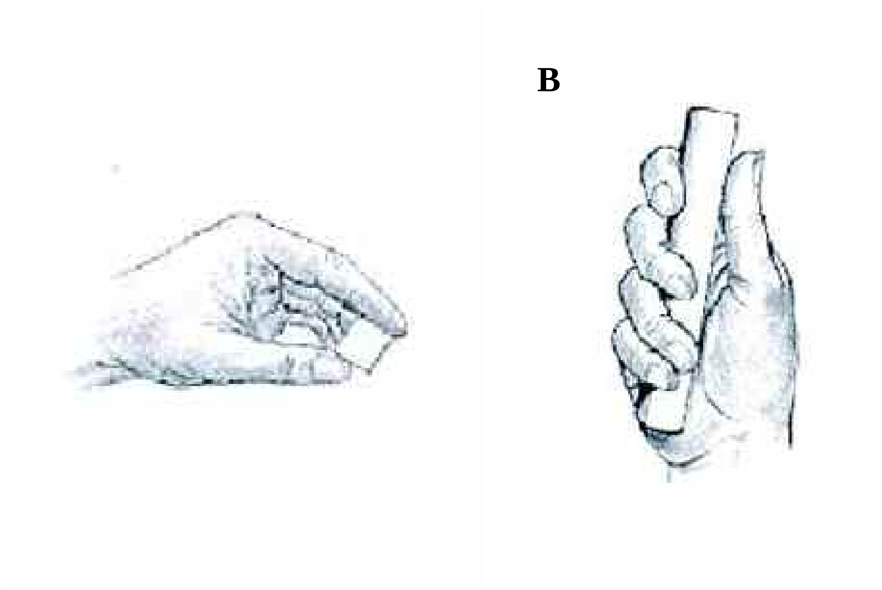

Figure 1.1 Precision grip between index finger and thumb and power grip (Panel A and B, respectively). Modified from: Marzke, 1994.

The taxonomy of prehensile movements proposed by Napier is qualitative and primarily relies on the inspection of images representing 'static' hand gripping. However, the type of grip configuration assumed by the hand in contact with the object represents the end result of a motor sequence which starts well ahead the act of grasping itself. The process of grip formation is an important aspect to consider, because it shows how the static posture of the hand is achieved in a dynamical domain. In this respect, the first account of the dynamic aspects of prehension has been famously provided by Marc Jeannerod (1981; 1984) in a series of experiments based on filming techniques. These experiments are detailed in the following section.

1.2 The dynamic aspects of grasping

With the use of high speed cinematographic techniques, Marc Jeannerod (1981; 1984) was one of the first to systematically analyze the dynamic aspects of prehension, providing a quantitative description for such movements.

Jeannerod (1981; 1984) described two major components for prehensile behaviour: the transport and the grasp components. The transport component brings the hand in the vicinity of the object. The grasp component is concerned with fingers' preshaping during transport and fingers' closing around the object. The kinematics of the transport component was obtained by recording arm movement (i.e., wrist), whereas the kinematics of the grasp component was primarily characterized by the maximum distance reached by the thumb and the index fingertip during transport (i.e., maximum grip aperture).

In his original observations, Jeannerod (1981, 1984, 1986) noticed that during a reach-to-grasp movement, the transport component is characterized by a single-peak asymmetrical velocity profile (see Figure 1.2). Specifically, during the deceleration phase of the movement - from peak velocity (PV) to the end of the movement - the velocity decreases rapidly up to a point (i.e., peak deceleration; 70 – 80 % of reach duration) and then decreases less rapidly (Figure 1.2).

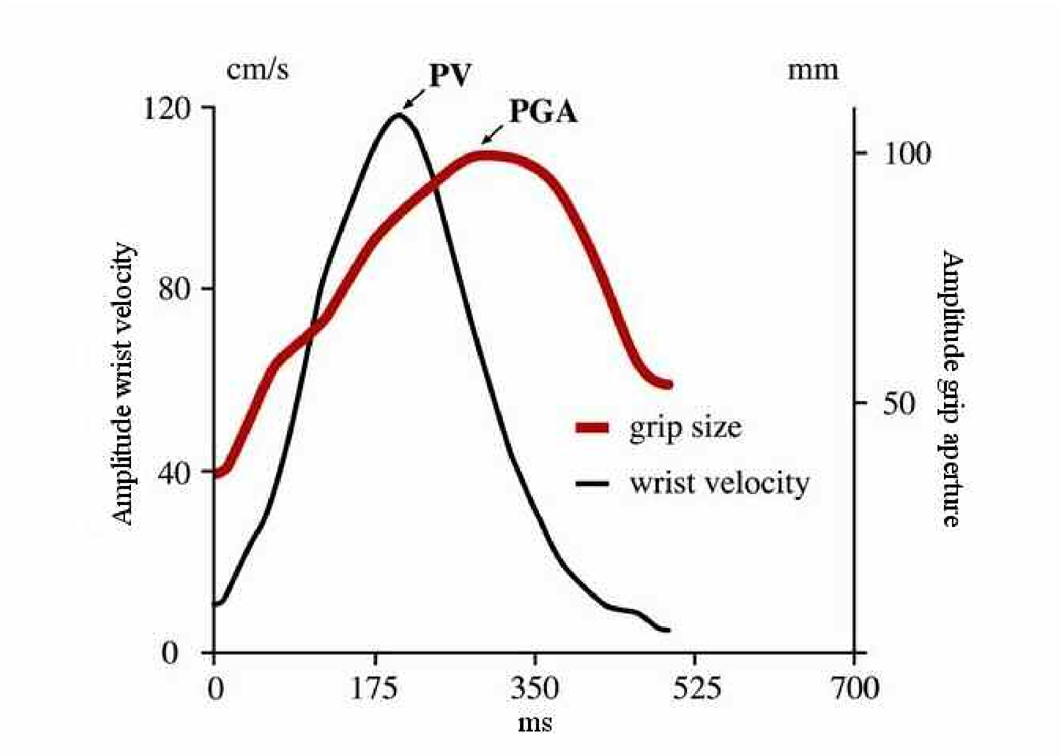

Figure 1.2 The velocity profile of the wrist (i.e. transport component) and the amplitude of the grip (i.e., grasp component) are shown as a function of time in a prehension movement towards a dowel (1.5 cm Ø), located 30 cm from the participant. Arrows indicate peak velocity (PV) and peak grip aperture (PGA), respectively. Modified from: Paulignan & Jeannerod, 1996.

Regarding the grasp component, the fingers open up to a point of maximum grip aperture and then close around the object (see Figure 1.2). Maximum peak grip aperture (PGA) exceeds the real size of the object and occurs at around the time peak deceleration occurs (Jeannerod, 1981, 1984, 1986).

Jeannerod's early work was not limited to the individuation and description of the landmarks characterizing a reach-to-grasp movement, but he went a step further by making inferences regarding the control mechanisms underlying such movements. Particularly, on the basis of the obtained data, Jeannerod (1981) postulated that the transport and the grasp components were controlled by two independent visuomotor channels (Jeannerod, 1981). This proposal, known as “visuo-motor channels hypothesis”, has been extremely influential and it is described in the following section.

1.3 The visuo-motor channels hypothesis

In Jeannerod’s original proposal (1981; 1984) a visuo-motor channel is conceived as a specialized input-output structure that extracts from the visual world a limited number of features which are relevant to produce a response. According to Jeannerod (1981, 1984), the inputs for the visuo-motor channels are not objects but features, or properties. He hypothesized two independent visuo-motor channels concerned with the processing of specific object’s features. The visuo-motor channel controlling the transport component would only be sensitive to features relating the object and its environment such as object’s orientation or spatial location (i.e., extrinsic properties). Conversely, the channel responsible for the grasp component would only detect the ‘intrinsic’ features of objects such as size, texture and weight. In this view, changing an object extrinsic property should not affect grip formation, whereas changing an object intrinsic property should not alter transport of the hand (Jeannerod 1981, 1988; Paulignan & Jeannerod, 1996). This prediction, which is critical for evaluating the validity of Jeannerod’s hypothesis, has been tested in a large number of studies which have varied either object location or size (Castiello, Bennett, & Stelmach, 1993; Chieffi, Fogassi, Gallese, & Gentilucci, 1992; Chieffi & Gentilucci, 1993; Gentilucci, Castiello, Corradini, Scarpa, Umiltà, & Rizzolatti, 1991; Gentilucci, Chieffi, Scarpa, & Castiello, 1992; Jakobson & Goodale, 1991; Marteniuk, Leavitt, MacKenzie, & Athenes, 1990; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991). This body of data is discussed within the following section.

1.4 Testing the visuo-motor channels hypothesis

To test the 'impermeability' of the visuo-motor channels hypothesis two types of paradigm have been chiefly used. For one, either the location or the size of the object was changed from trial to trial (Chieffi et al., 1992; Chieffi & Gentilucci, 1993; Gentilucci et al., 1991; Jakobson & Goodale, 1991; Marteniuk et al., 1990). For another, the change in object properties occurred during the reaching movement (i.e., perturbation paradigm) (Paulignan et al., 1991a,b; Castiello et al., 1993; Gentilucci et al., 1992).

In particular, they provided some evidence that challenged the visuo-motor channels hypothesis (Jeannerod, 1981). The main finding was that both the transport and the grasp components were sensitive to the intrinsic and extrinsic properties of objects (Castiello et al., 1993; Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991; Marteniuk et al., 1990; Chieffi et al., 1992; Gentilucci et al., 1991, 1992). For instance, when targeting the transport component, by varying the distance between the initial hand position and the target, the PV was higher and PGA was brought forward for longer than for shorter distances (Chieffi et al., 1992; Gentilucci et al., 1991; 1992). When targeting the grasp component PGA varied linearly with object size, occurring proportionally later in time for larger than for smaller objects. Further the velocity profile also modulated with respect to object size. PV was lower and deceleration time was longer for smaller than for larger objects (Chieffi & Gentilucci, 1993; Gentilucci et al., 1991; Marteniuk et al., 1990; Jakobson & Goodale, 1991) (see Figure 1.3).

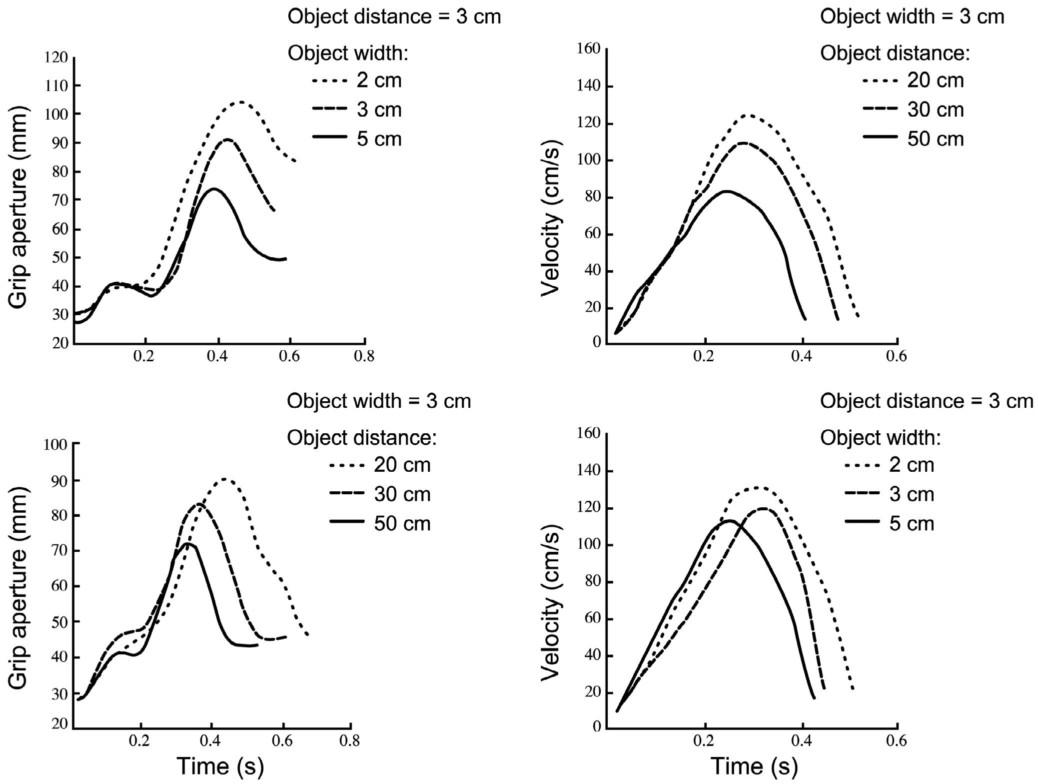

Figure 1.3 Representative data from a single participant demonstrating the scaling of maximum grip aperture and velocity to either object distance (bottom-left and top-right panels, respectively) and to object size (top-left and bottom-right panels, respectively). Modified from: Jakobson & Goodale, 1991.

Altogether these results do not completely disprove the existence of two independent visuo-motor processes, rather they suggest that some form of coupling between the two systems may exist (Castiello et al., 1993; Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991).

Although not fully conclusive, the above mentioned experiments had represented the starting point for a vast body of theoretical developments and research on human prehension (e.g., Hoff & Arbib, 1993; Zaal & Bootsma, 1993; Smeets & Brenner, 1999; Meulenbroek, Rosenbaum, Jansen, Vaughan, & Vogt, 2001). In particular, such developments have considered how reach-to-grasp kinematics is modulated by a number of object properties such as weight, fragility, texture and contact surface size (for review see Smeets & Brenner, 1999). Because of the issues at stake in the present thesis in the ensuing section I shall review some of this literature paying particular attention only to those studies which have targeted specific intrinsic object's properties.

1.5 Effects of Intrinsic object properties on grasp parameters

1.5.1 Effects of object's weight

A possible confound characterizing a number of studies which have investigated the effects of object size on hand kinematics was that, although object weight varied depending on object size, the 'weight' variable was not assessed (Gentilucci et al., 1991; Castiello et al., 1993). Therefore, the reported results may not only be a reflection of the object size manipulation, but also of a possible object weight manipulation. In order to isolate the possible effects of weight, Weir, MacKenzie, Marteniuk, Cargoe and Frazer (1991a) asked participants to reach, grasp, and pick up between the thumb and the index finger one of four dowels that were identical in appearance but had different weights. This task could be performed under two different conditions of weight presentation, random trials (i.e., weight unknown) and blocked trials (i.e., weight known). The authors report that changing object weight did not change any key variable for the grasp component in neither condition (Weir et al., 1991a). However, more recent studies seem to suggest that the object's weight has an effect on hand aperture (Steenbergen, Marteniuk, & Kalbfleisch, 1995; Smeets & Brenner, 1999). PGA was earlier and larger for heavier than for lighter objects. The proposal is that because a heavy object requires a more accurate grasp as to avoid slippage, such accuracy requirement would call for a greater safety margin (obtained by a greater aperture) and a longer time to determine more firm contact points (obtained by an anticipated PGA) (Smeets & Brenner, 1999).

1.5.2 Effects of object's texture

Another object's property which has attracted the interest of scientists is object texture. For instance, Johansson and Westling (1984) asked participant to reach, grasp, and pick up between the thumb and the index finger one of three dowels covered in either plain metal (i.e., 'normal'), Vaseline (i.e., 'slippery'), or rough sandpaper (i.e., 'rough'). When reaching to grasp the slippery object, a larger grip earlier in the movement was evident compared with grasping rough-surfaced object (Johansson & Westling, 1984). These results have been confirmed in subsequent studies (Weir, MacKenzie, Marteniuk, & Cargoe, 1991b; Fikes, Klatsky, & Lederman, 1994) and interpreted as a kinematic response to the accuracy requirement embodied in grasping slippery objects (Smeets & Brenner, 1999).

1.5.3 Effects of object's fragility

The level of accuracy with which an object is grasped depends also on how fragile the object is. The effect of object's fragility has been investigated by Savelsbergh, Steenbergen and van der Kamp (1996). In this study, the target object was either transparent or black. The impression of the participants was that the transparent object was more fragile than the black object. From a kinematic perspective, no differences were found on either time or amplitude of PGA; however the 'fragile' object was associated with longer movement duration with respect to the object appearing more firm (Savelbergh et al., 1996).

1.5.4 Effects of contact surface size

It is possible that not all the surface of a graspable object would be suitable for hand-object contact. Therefore, the effect of contact surface size has been investigated in a series of studies in which participants were requested to reach, grasp, and pick up between the thumb and the index finger similar objects having different contact surface (e.g., rounded vs. flattened objects) (Zaal & Bootsma, 1993; Bootsma, Marteniuk, MacKenzie, & Zaal, 1994). It was found that PGA occurred earlier and it was bigger when reaching to grasp objects with smaller contact surfaces (Zaal & Bootsma, 1993).

Altogether the studies on the effects of intrinsic object properties on reach-to-grasp kinematics had shown that, regardless the type of property being manipulated, a greater level of grasp stability determined a magnification of PGA (i.e., an increase of the thumb-index linear distance), and an increase in reach duration. In other words, the need for more firm hand-object contact points translates into the determination of a safety margin which is operationalized through a lengthening of the time window within which contact points can be selected. A point worth noting is that in these studies participants were requested to grasp the target object by using a precision grip. By definition this type of grip is applied when the object manipulation requires precision rather than steadiness. Therefore, the above reported effects might not represent a comprehensive description of what the hand was actually doing when reaching towards objects having different intrinsic properties. The requirement for a precision grip might have also posed severe limitations on the type of object properties which could be actually investigated. The possible limitations dictated by the 'two-digit' approach will be discussed in deep within the following section.

1.6 Limitations of the 'Two-digit' Approach

Although the above mentioned studies had represented a tremendous development for the research on grasping behaviour, they all share at least two important limitations.

The first has to be ascribed to the type of measure being used to characterize grasp kinematics. In all studies the amplitude and the time of PGA was the only kinematic descriptor for the grasp component (i.e., 'two-digit' approach). The second is that none of these studies had considered the possibility that the shape of the to-be-grasped object may influence grasp kinematics. These two limitations might be mutually linked. Indeed, two differently shaped objects can be grasped by using the same PGA if the selected contact points are located at the same distance. Therefore, what is needed is an approach which allows for the investigation of the kinematic patterning concerned with the entire hand rather than solely two digits: a ‘multi-digits’ approach.

1.7 OBJECT’S SHAPE AND HAND SHAPING PHENOMENON

The question of whether and how hand posture during reach might depend on object’s shape was first addressed by Santello and Soechting (1998). In this study, participants were requested to reach, grasp, and lift differently shaped objects with the four fingers opposed to the thumb (i.e., whole-hand grip). The posture of the hand was defined as the pattern of angular excursion at the joints of the fingers (i.e., both metacarpal-phalangeal and proximal interphalangeal joints). It was found that the extent to which hand posture resembles object’s geometry increased in a monotonic fashion as the hand approached the object, reaching a maximum at the time of object’s contact (i.e., hand shaping phenomenon). Although no differences were evident in terms of PGA while reaching towards differently shaped objects – that were similar in size – such an effect emerged when considering the posture assumed by specific and individual fingers (Santello & Soechting, 1998) (see Figure 1.4).

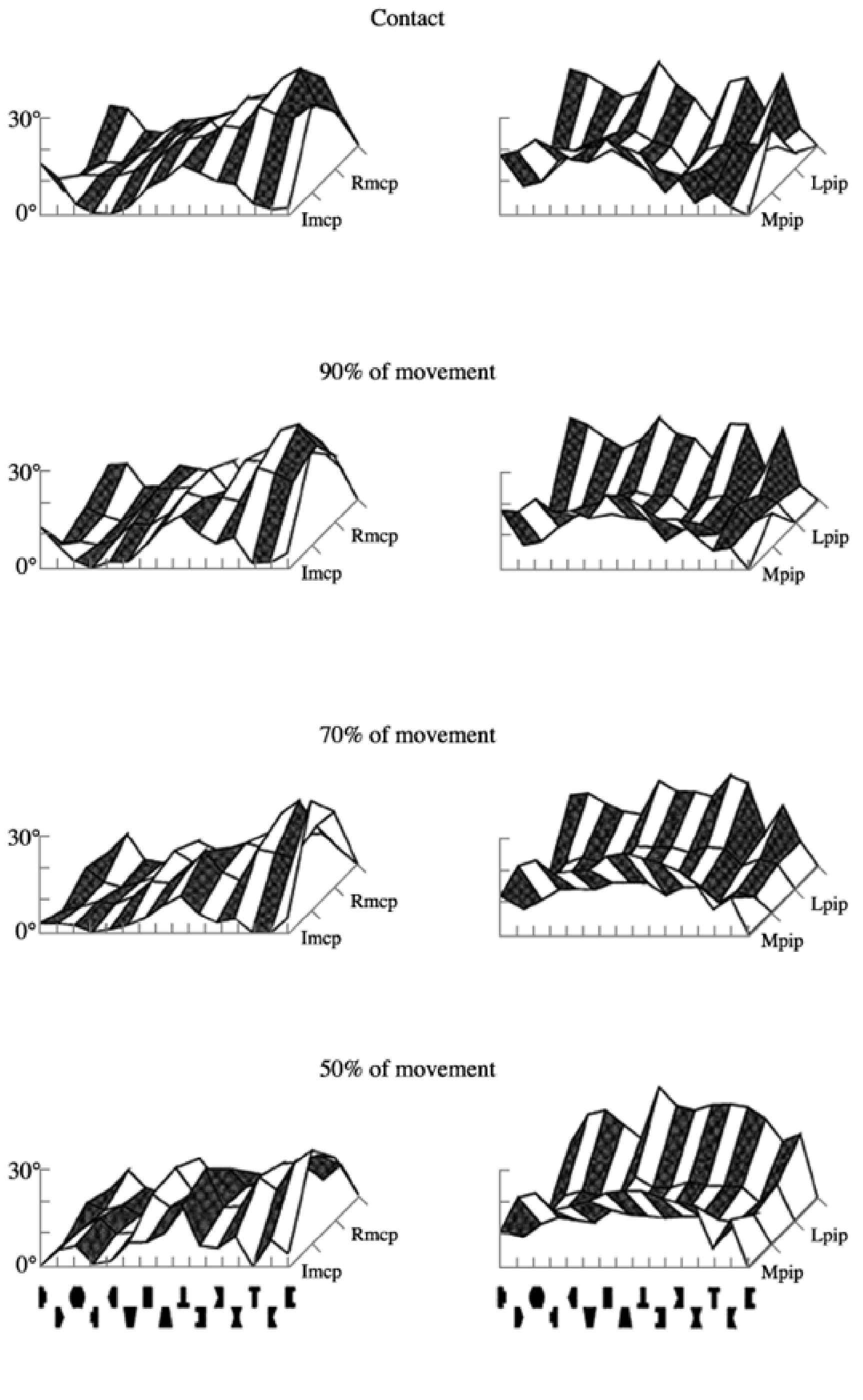

Figure 1.4 Hand postures measured at different epochs during the movement (50, 70, 90, 100% of reach duration) are illustrated for each of the objects. Objects are arranged on the horizontal axis, with a progression from convex shapes (left) to concave ones (right). Oblique axis denotes metacarpal (mcp) (*left*) and proximal interphalangeal (pip) joints (*right*) for index, middle, ring, and little finger. Value 0° denotes the most extended posture for the 15 objects at each joint. Modified from: Santello & Soechting, 1998.

Furthermore, at the time PGA occurred (i.e., about mid-way in the reaching movement), hand posture was only partially influenced by the shape of the object, suggesting that processes underlying prehension are still in their evolution when PGA is reached.

These results were confirmed and extended in a subsequent series of studies in which it was shown that the hand shaping phenomenon was evident even when the object to be grasped was not physically presented but just remembered (Santello, Flanders, & Soechting, 2002). Furthermore, when participants were not allowed to see both the hand and the to-be-grasped object hand pre-shaping still occurred (Winges, Weber, & Santello, 2003).

1.8 The present research

When grasping an object, the hand can assume different postures during reaching; these postures are obtained by modulating the motion of all digits and not necessarily the distance between the thumb and the index finger. Therefore, this would signify that a 'two-digit' approach may prevent the full elucidation of the mechanisms underlying grasping movements.

Here I applied the multi-digits approach to investigate a few processes underlying the organization of hand movements which has yet to be fully elucidated. First, I investigated whether and how a sudden and unexpected change in object shape affects hand posture during reaching movement towards that object (Chapter 3). This study would allow to understand how the central nervous system (CNS) controls the organization of individual digits for differently shaped objects and how it deals with the requirement of a fast reorganization. Then I translated these notions within a more cognitive domain considering the processes of selection-for-action (Allport, 1987) by looking at the effects that distractor objects, of a similar or a different shape than the target object, may have on hand shaping (Chapter 4). Continuing on this analysis, I investigated the effects that the implicit demands embedded in a 'second' action may have on the kinematics of the 'first' action (Chapters 5 and 6). Specifically, the experiment described in Chapter 5 tested whether hand posture modulates according to the accuracy constraints dictated by the task to be performed after grasping (i.e., accurate versus inaccurate placement). Another experiment (Chapter 6) went a step forward by manipulating not simply the accuracy requirements of the task following grasping, but also its functional nature (i.e., grasping the same object for different functional purposes). Finally, in order to test whether or not temporal contiguity between two segments of a coordinate action is a prerogative for performing a successful action, I carried out an experiment in which the time interval between the first (i.e., reach-to-grasp) and the second actions was systematically changed (Chapter 7).

The obtained results have been discussed in light of current theories proposed to explain how the CNS controls a complex motor behaviour such as prehension and how contextual information may influence such control (see 'Discussion' sections for each experimental chapter and Chapter 8).

2. General methods

In this chapter the methods and the procedures which are common to all the experiments included in the present thesis will be described.

2.1 Participants' characteristics

All the participants who took part in the present series of experiments showed right-handed dominance and reported normal or corrected-to-normal vision. They were naïve as to the purpose of the experiments and gave informed consent to participate in the study. The experimental procedures were approved by the Institutional Review Board at the University of Padova and were in accordance with the declaration of Helsinki.

2.2 Procedures

In all the experiments, the participant sat on a height-adjustable chair in front of a rectangular table with the elbow and wrist resting on the table, the forearm horizontal, the arm oriented in the parasagittal plane passing through the shoulder, and the right hand on a starting platform (see Figure 2.1).

Figure 2.1 The hand starting position adopted by each participants at the beginning of each trial. Note that the starting platform was designed with slight convexities dictating a natural flexed posture of the fingers as to make sure that the initial posture of hand was similar for all participants across trials.

Participants were instructed to maintain the initial hand position until they heard a tone (Hz = 800; duration = 200 ms) signalling the start of the trial. Then, they were requested to reach and grasp at a natural speed the target object by opposing the thumb to the four fingers. The target object was aligned with the participant's body midline and located at about 30-cm-distance from the hand starting position. The hand starting position was located slightly to the left of the participant's right shoulder. This allowed for a comfortable reach to grasp movement by avoiding the necessity to adopt an extreme extension of the wrist during the movement. An experimenter visually verified that participants complied with all task requirements during each trial. Trials which did not meet set criteria were discarded and repeated.

2.3 Recording techniques

At the beginning of each experimental session, participants were requested to wear in their right hand a glove (CyberGlove, Virtual Technologies, Palo Alto, CA) (see Figure 2.2a-b).

A B

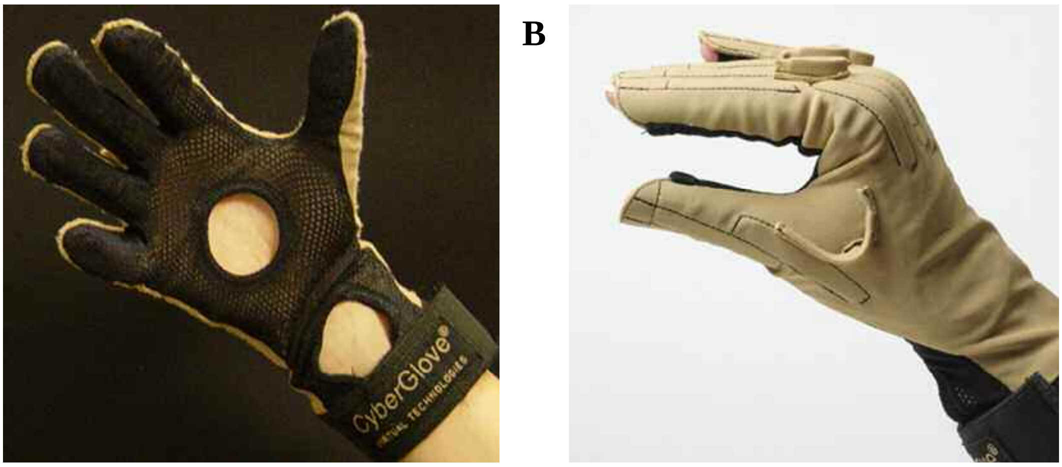

Figure 2.2 Bottom and side views of the Cyberglove worn by each participants at the beginning of each trials (Panel A and B, respectively).

The resistive sensors embedded in the glove are extremely thin and flexible being virtually undetectable and allow for recording hand posture. In particular, it is possible to record the angular excursion at the level of both metacarpal-phalangeal (*mcp*) and proximal interphalangeal (*pip*) joints of the thumb, index, middle, ring, and little fingers (see Figure 2.3). Furthermore, the sensors placed between the digits allow for recording the adduction-abduction angles for each pair of adjacent digits (i.e., thumb-index, index-middle, middle-ring, and ring-little) (Figure 2.3).

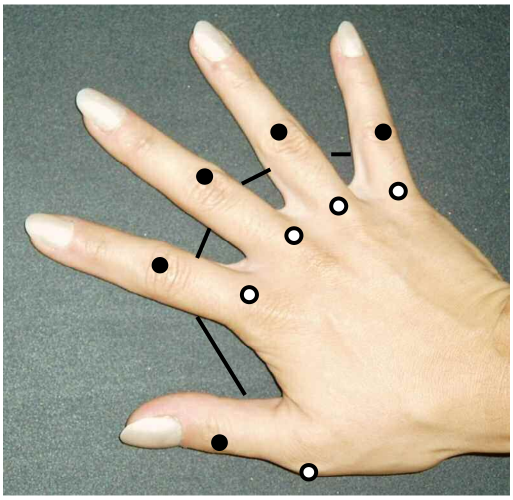

Figure 2.3 A schematic view of metacarpal phalangeal (white dots) and proximal inter phalangeal joints (black dots), and distances between adjacent digits (black segments) from which angular excursion and adduction-abduction angles can be recorded by means of the CyberGlove.

In order to obtain a reference hand posture, once the glove was worn, participants were requested to position their right hand flat on the table on a predetermined position and to maintain it in that position while *mcp* and *pip* joints angle of all digits were recorded. The *mcp* and *pip* joints' angles were defined 0° when the fingers were straight in the plane of the palm ('reference' hand posture), and flexion was assigned positive values. The 'reference' adduction-abduction angles were set as 0° when the hand was on the pre-determined position with pre-set adduction-abduction angles (i.e., thumb-index fingers 22°; index-middle fingers 32°; middle-ring fingers 45°; ring-little fingers 50°)[1]. Fingers' aperture was assigned negative values.

[1] While abduction-adduction angles were always recorded, results from these measures will be not reported for the Experiments described in Chapter 3, 5, and 7 respectively.

The linearity of the sensors embedded in the CyberGlove is 0.62% of maximum nonlinearity over the full range of hand motion and their resolution is 0.5 degrees. These characteristics remain constant over the entire range of motion joint. The output of the transducers is sampled at 12-ms interval.

In order to record movement duration, we used two pressure switches. The first switch was embedded in the hand starting platform (see Figure 2.1). When the participants placed their hand on this position, at the beginning of each trial, this switch was pressed. The release of this switch indicated the onset of the reaching movement.

The second switch was placed underneath the to-be-grasped object. The weight of the target object maintained the switch pressed whereas the object's lift triggered the switch release. This event determined the end of the reaching movement. Reach duration was taken as the time interval between the release of the first and second switch.

2.4 Kinematic data pre-processing

After data collection, the raw data for all trials for each participant were pre-processed by means of a custom software (Matlab, MathWorks, Natick, MA). Specifically, the absolute duration of reaching was first converted in relative terms (as a percentage of movement duration). Then percentage time points were computed in 10 temporal intervals. Within each of these ten intervals, both joints' angular excursions and adduction-abduction angles were then averaged. An example of the time normalization procedure is represented in Figure 2.4a-b.

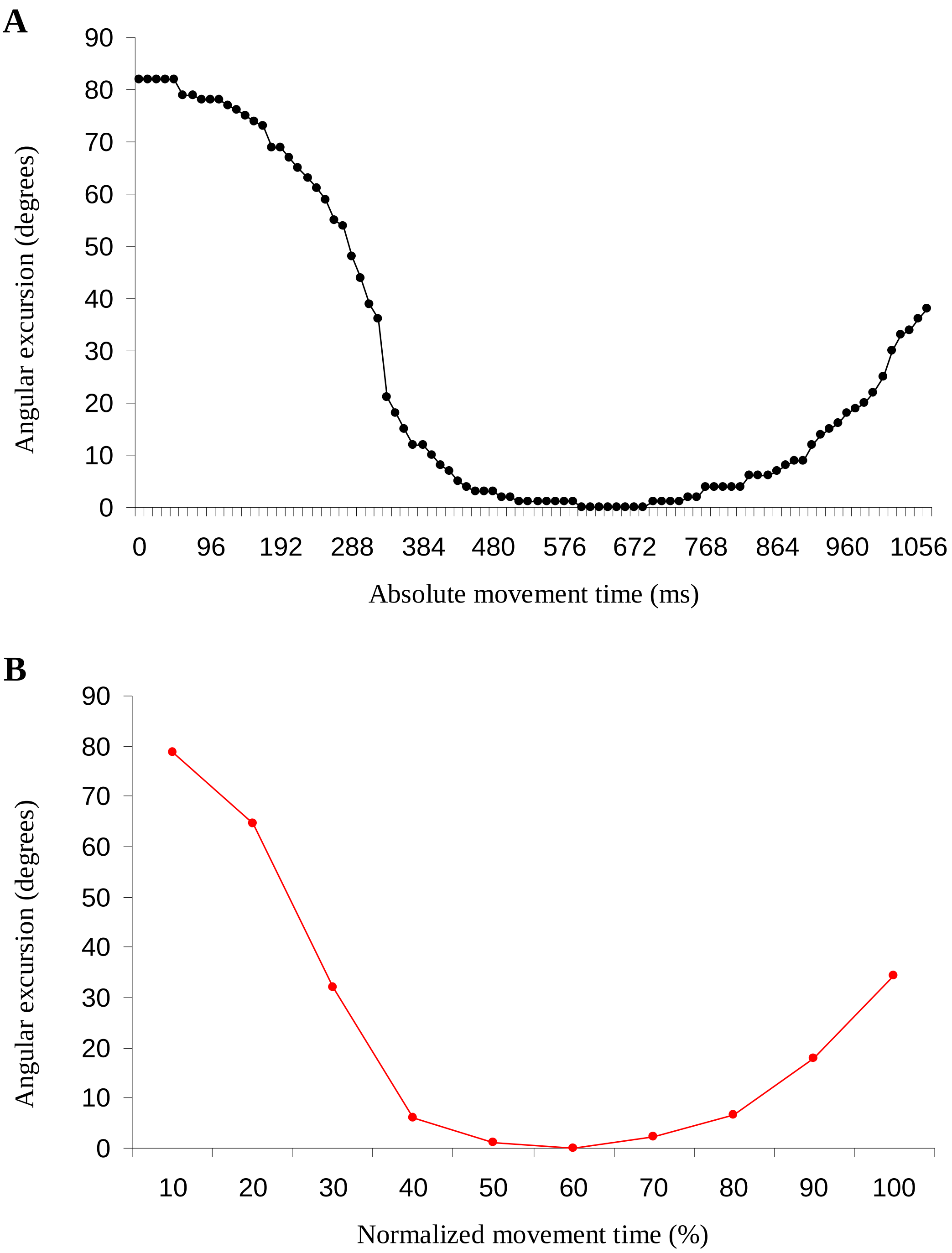

Figure 2.4 Panel A shows exemplificative data for metacarpal phalangeal joint of the index finger plotted against absolute time. Panel B shows the same data in relative time (%).

Please note that the waveform does not differ when expressing kinematic variable against absolute (i.e., milliseconds) and relative (i.e., percentage) reaching time. Since the sampling time for kinematic data recording was constant (i.e., 12 ms; see Paragraph 2.3), no curve fitting by interpolation algorithms was requested.

2.5 Measures of interest

After time normalization procedures, statistical analyses were performed on the following dependent measures:

1) The absolute duration of reaching movement (milliseconds)

2) Angular excursion recorded at the level of both *mcp* and *pip* joints for thumb, index, middle, ring, and little fingers of the participants' right hand at each epoch of normalized reaching duration (i.e., from 0 to 100%, at step of 10%).

3) The abduction/adduction angles recorded at the level of adjacent digits' pair of the participants' right hand at each epoch of normalized reaching duration (i.e., from 0 to 100%, at step of 10%).

2.6 Data analysis

The measures of interest have been inserted in two types of statistical model: a linear regression and a generalized linear model. The linear regression model has been applied in order to determine whether the posture assumed by the hand during reaching would correlate with the posture assumed by the hand at object's contact. Specifically, I applied the Person's linear correlation (Pearson's coefficient) to compare hand posture at different epochs during reaching (from 10 to 90% of normalized reach duration) with hand posture at the end of the reaching movement (100% of normalized reach duration). Since this analysis provides a quantifiable index of the relationship between hand posture and the shape of the to-be-grasped object, it has been applied in the experiments specifically targeting the investigation of such relationship (see Chapters 3 and 5).

The generalized linear model has been applied in order to determine whether the experimental manipulations characterizing each of the experiments reported in the present thesis significantly affected the measures of interest. In particular, I applied a series of repeated measures analyses of variance (ANOVA). Simple effects were used to explore the means of interest and Bonferroni corrections (alpha level: $P<0.05$) were applied. Given the high number of levels for the factors included in these ANOVAs, statistical significant interactions were explored by means of profile analysis. This analysis was applied in order to avoid an increase of Type I error that classically stems from a high number of post-hoc comparisons.

For both the linear regression and the generalized linear model, the analyses have been carried out by using Statistical Package for Social Sciences (SPSS).

3. Control of hand shaping in response to object shape perturbation[2]

Abstract

This study assessed how hand shaping responds to a perturbation of object shape. In blocked trials (80%), participants were instructed to reach, to grasp and lift a concave or a convex object. In perturbed trials (20%), a rotating device allowed for the rapid change from the concave to the convex object or vice versa. In this situation participants grasped the last presented object. In the blocked condition we found that most joints of the fingers were modulated by the type of the to-be-grasped object during the reach. When object shape was perturbed, reach duration was longer and angular excursion of all fingers differed with respect to blocked trials. For the 'convex → concave' perturbation, a greater degree of finger extension was found than during the blocked 'concave' trials. In contrast, for the 'concave → convex' perturbation, fingers were more flexed than for the blocked 'convex' trials. The thumb reacted to the perturbation showing a similar pattern regardless the 'direction' of the perturbation. The present results suggest that applying an object shape perturbation during a reach-to-grasp action determines a reorganization of all digits. This pattern is suggestive of a control strategy which assign to opposing digits different roles.

---

[2] *Published*: Ansuini, C., Santello, M., Tubaldi, F., Massaccesi, S., & Castiello, U. (2007). Control of hand shaping in response to object shape perturbation. *Experimental Brain Research, 180,* 85-96.

3.1 INTRODUCTION

The hand is a very complex biomechanical system with 27 bones, 18 joints and 39 intrinsic and extrinsic muscles and over 20 degrees of freedom (Kapandji, 1970; Tubiana, 1981). This biomechanical complexity raises the question of how the CNS controls the motion and forces at the digits. Within this theoretical framework there are two main viewpoints. The more traditional view has emphasized a strategy based on controlling individual muscles and joints as to generate the needed forces (for review see Schieber, 1990; Lemon, 1999). Another view has emphasized the need for control strategies that may result in a reduction of the large number of degrees of freedom and thereby, simplify the control problem (Arbib, Iberall, & Lyons, 1985; Bingham, Iberall, & Arbib, 1986; Iberall & Fagg, 1996; Santello & Soechting, 1998; Santello, Flanders, & Soechting, 1998).

A test to understand how the CNS coordinates the motion of multiple degrees of freedom of the hand during reach-to-grasp can be provided by applying a perturbation paradigm which allows for the observation of how the system is able to modify an initial motor plan in order to successfully perform a different end-grasp response. Previous perturbation studies have largely confined the analysis of the grasping component to the time and amplitude of PGA (e.g., Castiello, Bennett, & Paulignan, 1992; Castiello et al., 1993; Castiello, 1998; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1990; Paulignan et al., 1991a; Savelsbergh, Whiting, & Bootsma, 1991) (see Chapter 1). So far, no consideration has been given to how the evolving shape of all digits for a particular shaped object is modified during the reach when a sudden change in object shape requires hand posture to be modified accordingly. Given the demonstration that fingers' posture during reaching is highly dependent on the shape of the to-be-grasped object (Santello & Soechting, 1998) (see Chapter 1), it is of interest to ask whether the adaptive response of the hand to this type of perturbation involves all digits and not only kinematic parameters such as, for example, the time and amplitude of PGA as previously reported.

Here we tackle this issue by providing a description of how hand shaping (i.e., angular excursion at both *mcp* and *pip* joints for all digits) reacts to an object shape perturbation. In the present experiment, participants were instructed to reach towards and grasp a concave or a convex object. For blocked trials a concave or convex object was presented from the start to the end of the movement. For perturbed trials, the originally presented object was replaced by an object of a different shape (i.e., either from concave to convex or vice versa) as soon as the movement started. We first determined how the hand was shaped during the reach when the object to be grasped (i.e., concave or convex) was presented in the blocked condition. These kinematic patterns were then used as 'baseline' measurements to which hand kinematics for the perturbed conditions was compared. This comparison allowed us to address the following questions: will the object shape perturbation elicit a different hand kinematic pattern from the 'baseline' hand shaping found for blocked trials ending with the same object shape? If so, will the response to the perturbation occur at the level of all or some of the joints?

3.2 METHODS

3.2.1 Participants

Twenty five participants (13 females and 12 males, ages 21-29) took part in the experiment.

3.2.2 Stimuli and apparatus

The stimuli were a concave and a convex wooden objects (Fig. 3.1a). The concave object was 12 cm high, 2.4 cm deep and 2 cm wide at the point of maximum concavity. The convex object was 12 cm high, 2.4 cm deep and 8 cm wide at the point of maximum convexity. Both objects measured 5 cm at the base and weighted ~ 100 g. Both the concave and convex objects were accommodated back to back within a device (see Figure 3.1a-b). A rectangular black paperboard was placed between objects so that only one object at the time was visible (Fig. 3.1a-b). The device included a little disk engine controlled by a software which allowed for 180° clockwise or counterclockwise rotation of the platform on which the objects were seated (Figure 3.1b).

The onset of object rotation was triggered by a pressure switch released at the onset of the reach (see Chapter 2). The release of this switch was the signal for the personal computer to trigger the target object perturbation. A metal contact was inserted in the base of the objects. This contact made a connection with a metal contact on the device. When the target object was lifted, the connection between these contacts was interrupted. Reach duration was defined as the time interval between the release of the pressure-switch and the interruption of that connection. There was no delay from movement start to the beginning of the rotation. The time taken by the device to perform the 180° rotation was 104 ms.

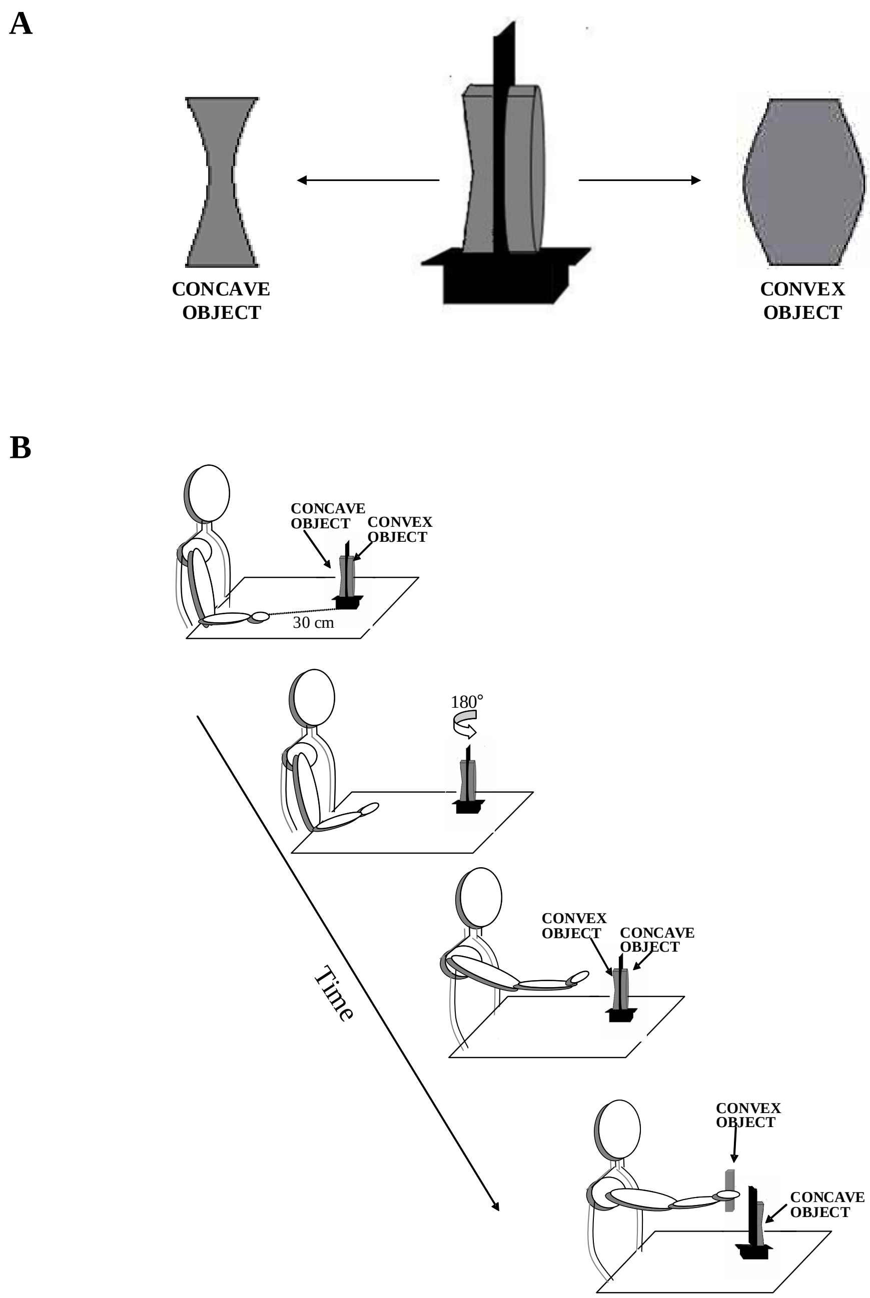

Figure 3.1 Panel A shows the objects used as targets in the present experiment and the device by which the perturbation was produced. Panel B shows a schematic representation of the participant's posture and an example of the time course for a perturbed trial. Figure is not on scale.

3.2.3 Procedures

Participants were required to reach, grasp and lift either the concave or the convex object. This task could be performed under two different conditions:

1. Blocked condition. The target object (concave or convex) remained the same from the onset to the end of the reaching movement. We define trials performed in this condition as 'blocked' trials.

2. Perturbed condition. After the beginning of the movement, as soon as the starting switch was released, the device rotated so that the first presented object (concave or convex) was replaced with the other object (concave or convex) (Fig. 3.1b). The latter object was then the actual target for the reach and grasp movement (Fig. 3.1b). We define trials performed in this condition as 'perturbed' trials.

Four types of trial within two 50 trials blocks were administered: (a) blocked concave (n = 40) in which the participants reached towards and grasped the concave object; (b) blocked convex (n = 40) in which the participant reached towards and grasped the convex object; (c) perturbed convex → concave (n = 10) in which the participant was originally confronted with the convex object, but at movement onset the device rotated and the concave object became the to-be-grasped object; (d) perturbed concave → convex (n = 10) in which the participant was originally confronted with the concave object, but at movement onset the device rotated and the convex object became the to-be-grasped object. The 'perturbed' trials were pseudo random and interspersed with 'blocked' trials (ratio 20/80%). Prior to each recording session the participants were given ten practice trials, including two examples of perturbation. To avoid fatigue and lack of concentration/attention, participants were given a pause after 50 trials.

3.2.4 Data analysis

To test for possible differences in the absolute duration of reaching movements as a function of experimental condition and type of target object an analysis of variance (ANOVA) with type of object (concave and convex) and experimental condition (blocked and perturbed) as within-participants factors was performed. To assess whether the pattern of linear correlation changed across experimental conditions we performed linear regression analysis (Pearson's coefficient) to compare hand posture at different epochs of the reach (from 10 to 90% of the reach) with hand posture at the end of the reaching movement (100% of the reach). This regression analysis was performed on the joint excursions averaged across all participants (see Chapter 2).

Finally, to assess how and to what extent the angular excursion at the analyzed joints for each digit differed between 'blocked' and 'perturbed' trials, relative values for the dependent measures of interest were entered into five repeated measures multivariate analyses of variance (MANOVAs). The MANOVAs' model consisted of two joints (*mcp* and *pip*) for each digit separately. The within-subjects factors were experimental condition (blocked and perturbed) and time (from 10% to 100% of the reach, 10% intervals).

3.3 Results

This section is organized in three main parts. In the first part we describe the differences in reach duration, the pattern of linear correlation, and the pattern of angular excursion between the concave and the convex objects for the blocked condition. The assessment of differences in hand kinematics between the two object shapes was crucial to validate our perturbation paradigm. In the second and the third parts we describe the results obtained for the 'convex → concave' perturbation and for the 'concave → convex' perturbation, respectively. Each of these latter parts are presented separately for reach duration (ANOVA), the pattern of linear correlation, and the pattern of fingers' angular excursion (MANOVAs).

3.3.1 Concave vs. convex object: blocked condition

For 'blocked' trials, the ANOVA revealed a difference between reach duration directed to the concave or the convex object ([$F_{(1,24)} = 6.913$, $P<0.05$]). Reach duration was longer for the concave than for the convex object (1366 vs. 1326 ms; $P<0.05$). Although for both considered objects the strength of the linear correlation increased during reaching time (see Figure 3.2), correlation analysis revealed some differences.

For instance, for the concave object a significant level of correlation was reached from the beginning (10 – 20%) and maintained until the end of the movement for both the *mcp* and the *pip* joints of all digits (Fig. 3.2). When the to-be-grasped object was convex a significant level of correlation was also evident from the beginning (i.e., 10 – 20%) to the end of the reaching action, but not for all digits. For the *pip* of index, middle, and ring finger *r* values became significant at 50, 70, and 30% of reaching, respectively, and remained significant up to the end of the movement (Fig. 3.2). Differences between the two patterns of angular excursion for the considered objects were also evident when looking at patterns of angular excursions (MANOVA); profile analysis revealed that both the *mcp* and the *pip* joints of the thumb and the *pip* joint of little finger showed similar profiles for both the concave and the convex objects (Figure 3.3). In contrast, after 30 – 40% of the reaching movement, the remaining joints were more flexed for the concave than for the convex object (Fig. 3.3).

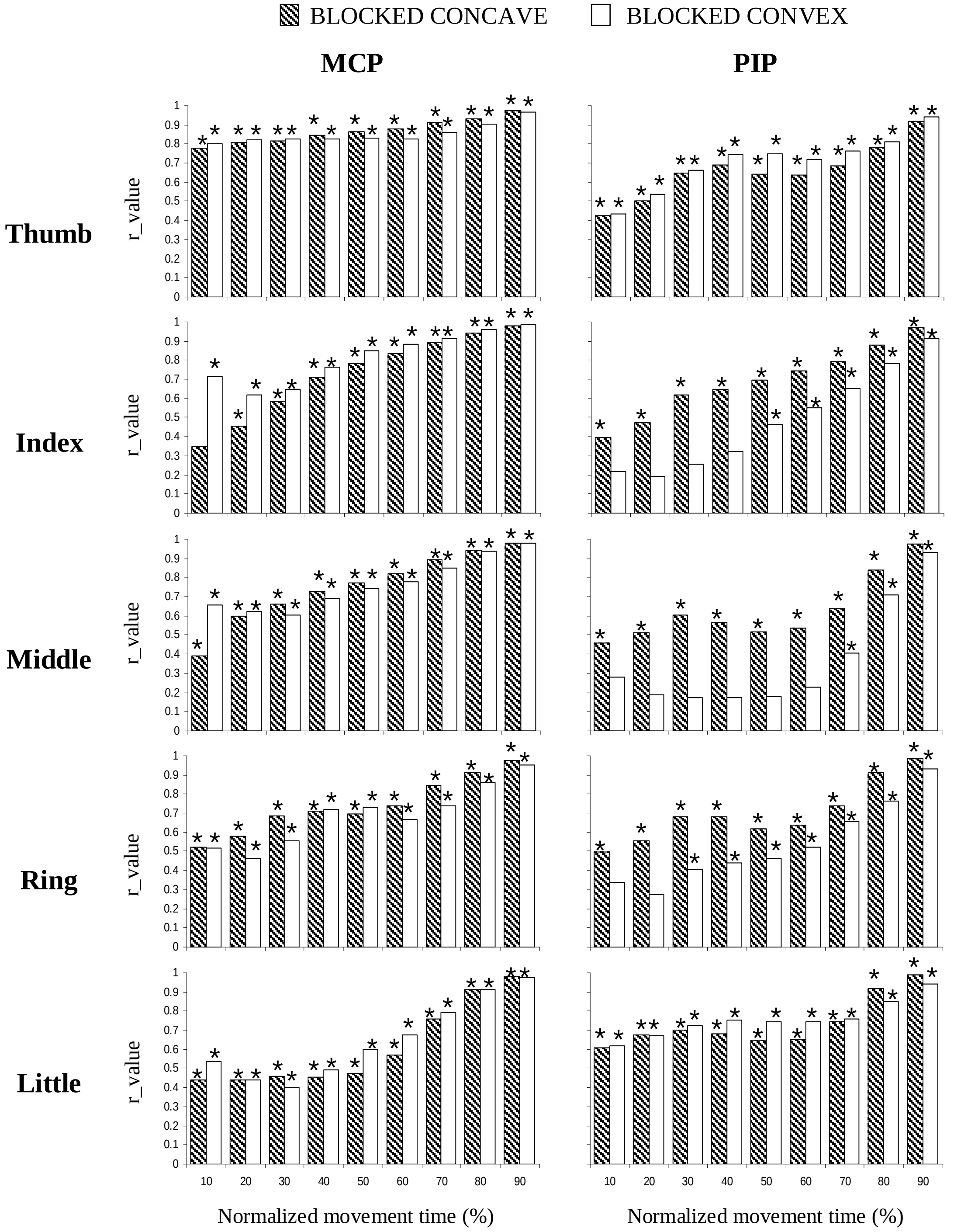

Figure 3.2 Each panel shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at the reaching end for the concave (patterned bars) and the convex (white bars) objects. Data on the left and right columns correspond to metacarpal and proximal interphangeal joints' correlation coefficients, respectively, for each digit. An r value > 0.397 is significant at $P < 0.05$. Asterisks indicate the significant correlation values.

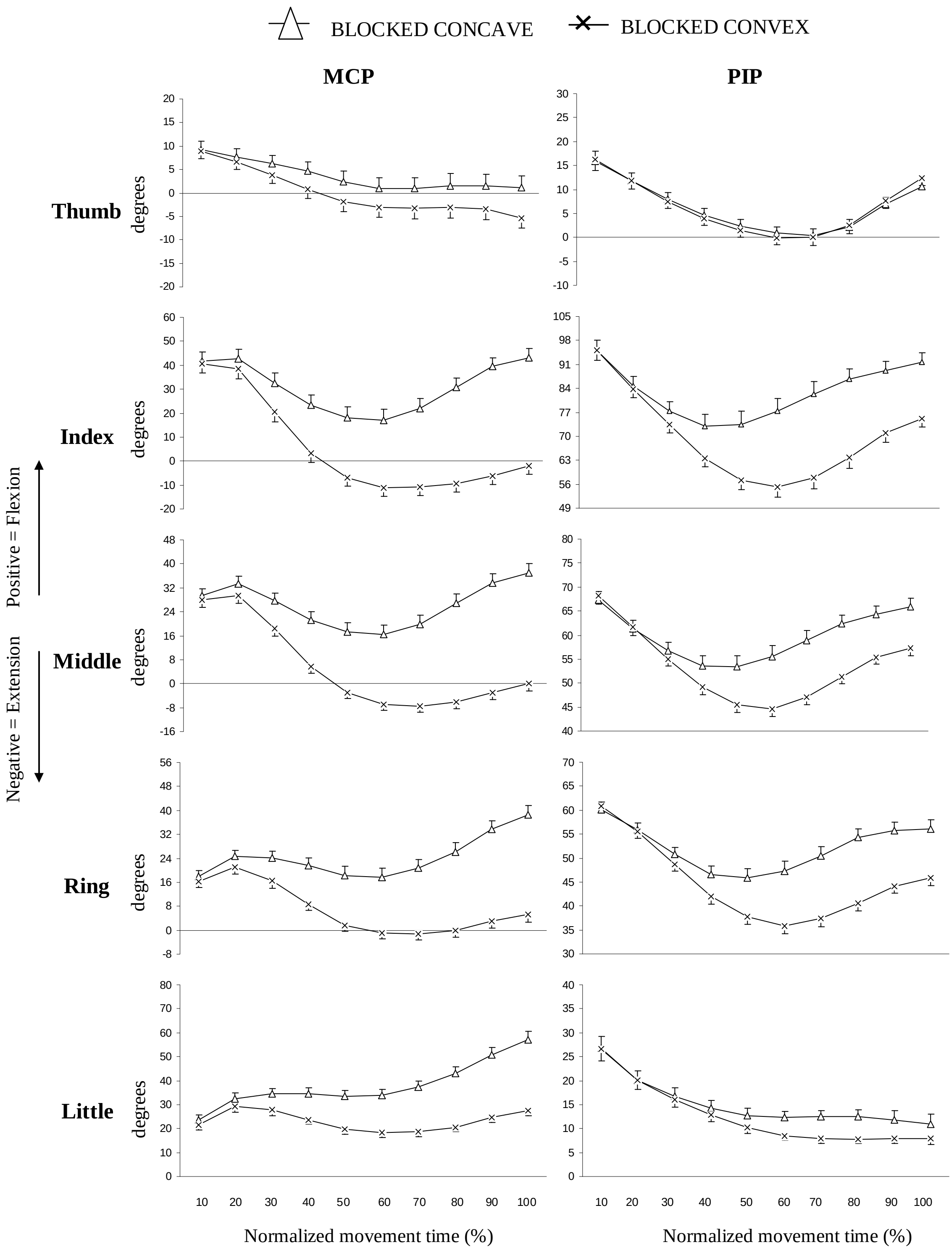

Figure 3.3 Each trace denotes average angular excursion across trials and participants of metacarpal (left panels) and proximal interphalangeal (right panels) joints of the thumb, index, middle, ring, and little finger performed in 'blocked' trials for the concave (empty triangles) and the convex (crosses) object. Bars represent the standard error.

3.3.2 Convex → concave perturbation

The main factor 'Experimental Condition' was significant ([$F_{(1,24)} = 36.475$, $P < 0.0001$]). Reach duration was longer for 'perturbed' (1498 ms) than for 'blocked' trials (1366 ms).

Results from linear regression analysis revealed that *r* values obtained for 'perturbed' trials were generally lower than those obtained for 'blocked' trials (see Figure 3.4). Although the presence of the perturbation did not severely modify the gradual increase of linear correlation found in 'blocked' trials, it introduced a delay in the time where the level of correlation started to be significant ($P < 0.05$). For instance, the *mcp* joint of index, ring, and little finger and *pip* joint of middle finger reached firmly a significant level of correlation at 30%, 40%, 50%, and 60% respectively, which was maintained up to the end of the movement (Fig. 3.4).

For the *pip* joint of the thumb a significant level of correlation was reached at 30% of reaching duration. For 'blocked' trials the above mentioned joints reached a significant level of correlation from the very beginning to the end of the movement (Fig. 3.4).

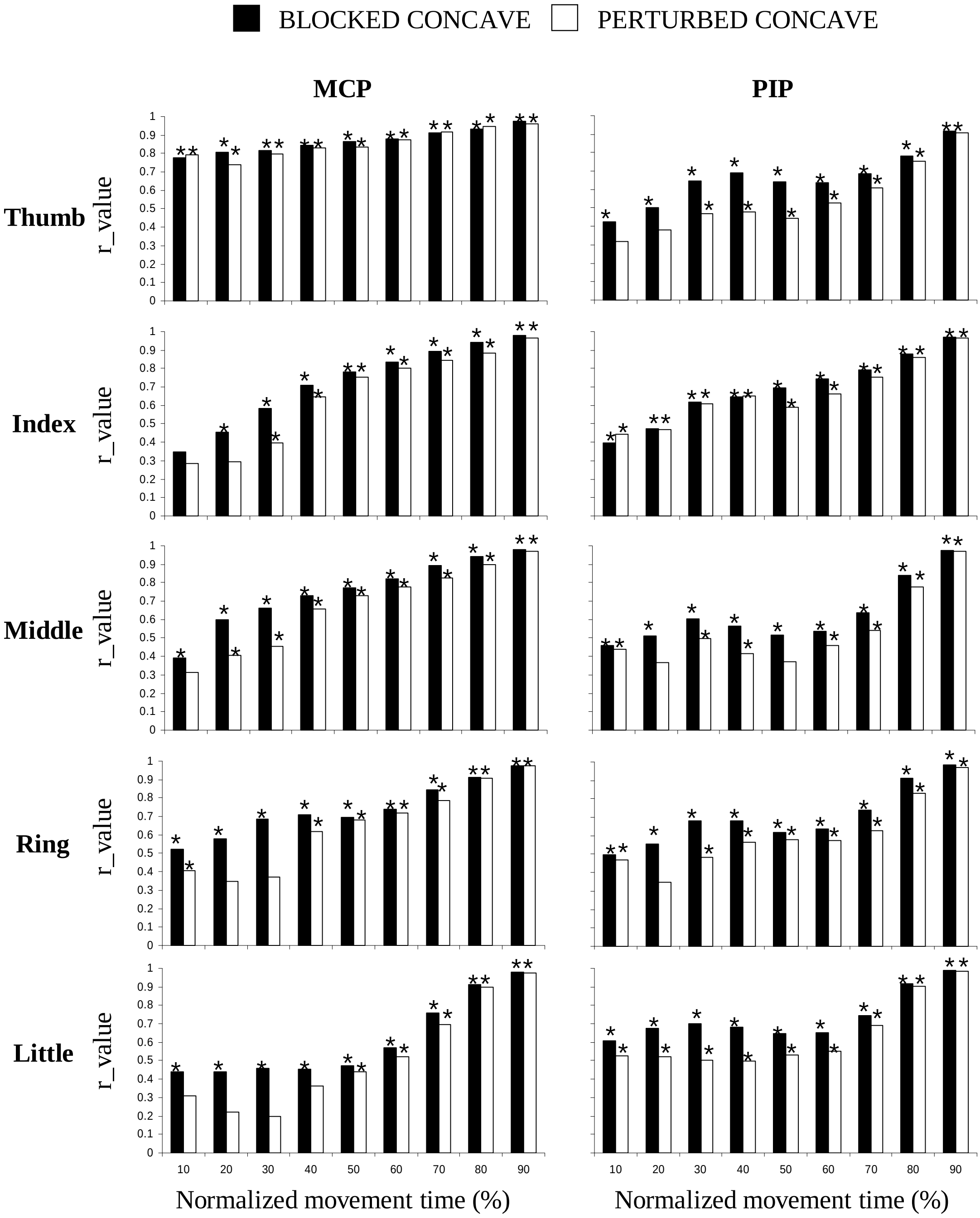

Figure 3.4 Each panel shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at the reaching end for the 'blocked' concave (black bars) and the 'perturbed' concave (white bars) trials. Data on the left and right columns correspond to the metacarpal and the proximal interphalangeal joints' correlation coefficients, respectively, for each digit. An *r* value > 0.397 is significant at $P < 0.05$. Asterisks indicate the significant correlation values.

When comparing 'blocked' and 'perturbed' trials ending with the concave object, the MANOVAs revealed that, except for the *mcp* of the index finger, angular excursion for all analyzed joints was significantly affected by the presence of the perturbation (see Appendix A).

For example, the *mcp* of the ring finger showed a greater extension for ‘perturbed’ (22.6 degrees) than for ‘blocked’ trials (24.3 degrees) (main factor ‘Experimental Condition’; see Appendix A). For the remaining joints, the two – ways interaction ‘Experimental Condition x Time’ was significant (see Appendix A). These results indicated that both *mcp* and *pip* joints for the thumb, the middle finger and the little finger, the *pip* joint for both the index and ring finger were affected at some points in time by the occurrence of the perturbation.

The profile analysis showed that at the very beginning and at the end of movement no differences between ‘blocked’ and ‘perturbed’ trials were evident (see Fig. 3.5). However, for the thumb both *mcp* and *pip* joints showed a greater flexion for ‘perturbed’ than for ‘blocked’ trials between 30% and 70% of the reaching movement. In addition, both *mcp* and *pip* joints for the middle, and the *pip* joint for both the index and the ring finger, and the *mcp* joint for the little finger were generally more extended for ‘perturbed’ than for ‘blocked’ trials from 30-40% to 70-80% of the reaching movement (Fig. 3.5).

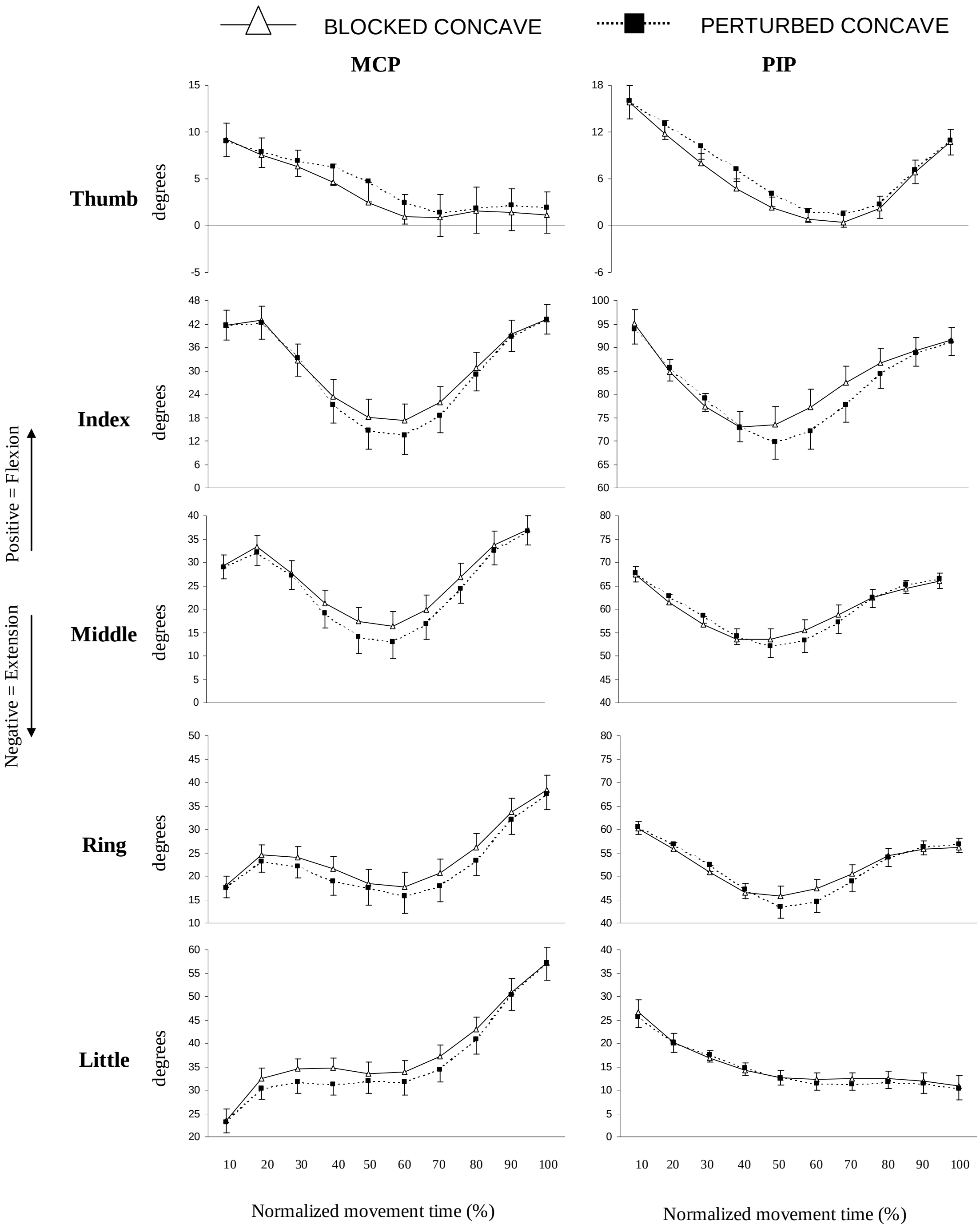

Figure 3.5 Each panel shows the angular excursion averaged across trials and participants of metacarpal (left panels) and proximal interphalangeal (right panels) joints of the thumb, index, middle, ring, and little finger performed in 'blocked' concave (empty triangles) and 'perturbed' concave (filled squares) trials. Bars represent the standard error.

3.3.3 Concave → convex perturbation

The main factor 'Experimental Condition' was significant ([$F_{(1,24)} = 36.475$, $P<0.0001$]). Reach duration was longer for 'perturbed' (1450 ms) than for 'blocked' trials (1326 ms). Results from the linear regression analysis revealed that *r* values were lower for 'perturbed' than for 'blocked' trials (see Figure 3.6). Furthermore, for some of the analyzed joints a significant level of correlation ($P<0.05$) was reached later in 'perturbed' than in 'blocked' trials. For instance, the *pip* joint of thumb, index and middle finger reached a significant level of correlation later in 'perturbed' than in 'blocked' trials (i.e., 30 vs. 10, 60 vs. 50%, and 80 vs. 70, respectively) (Fig. 3.6). Finally, the *r* value for the *pip* joint of the ring finger reached a significant level at 70% of reaching duration for 'perturbed' and at 30% for the 'blocked' trials (Fig. 3.6).

The five MANOVAs performed to compare 'blocked' and 'perturbed' trials ending with the convex object revealed a significant two – ways interaction (i.e., 'Experimental Condition' x 'Time') (see Appendix B) for all analyzed joints the effect of the perturbation on hand shaping varied along reaching time. As depicted in Figure 3.7 both the *mcp* and the *pip* joints for all digits were more flexed for 'perturbed' than for 'blocked' trials from the beginning up to 50-60% of the movement. After 50-60% of movement duration, differences in hand shaping between 'blocked' and 'perturbed' trials started to decrease and disappeared at the end of the movement (see Fig. 3.7).

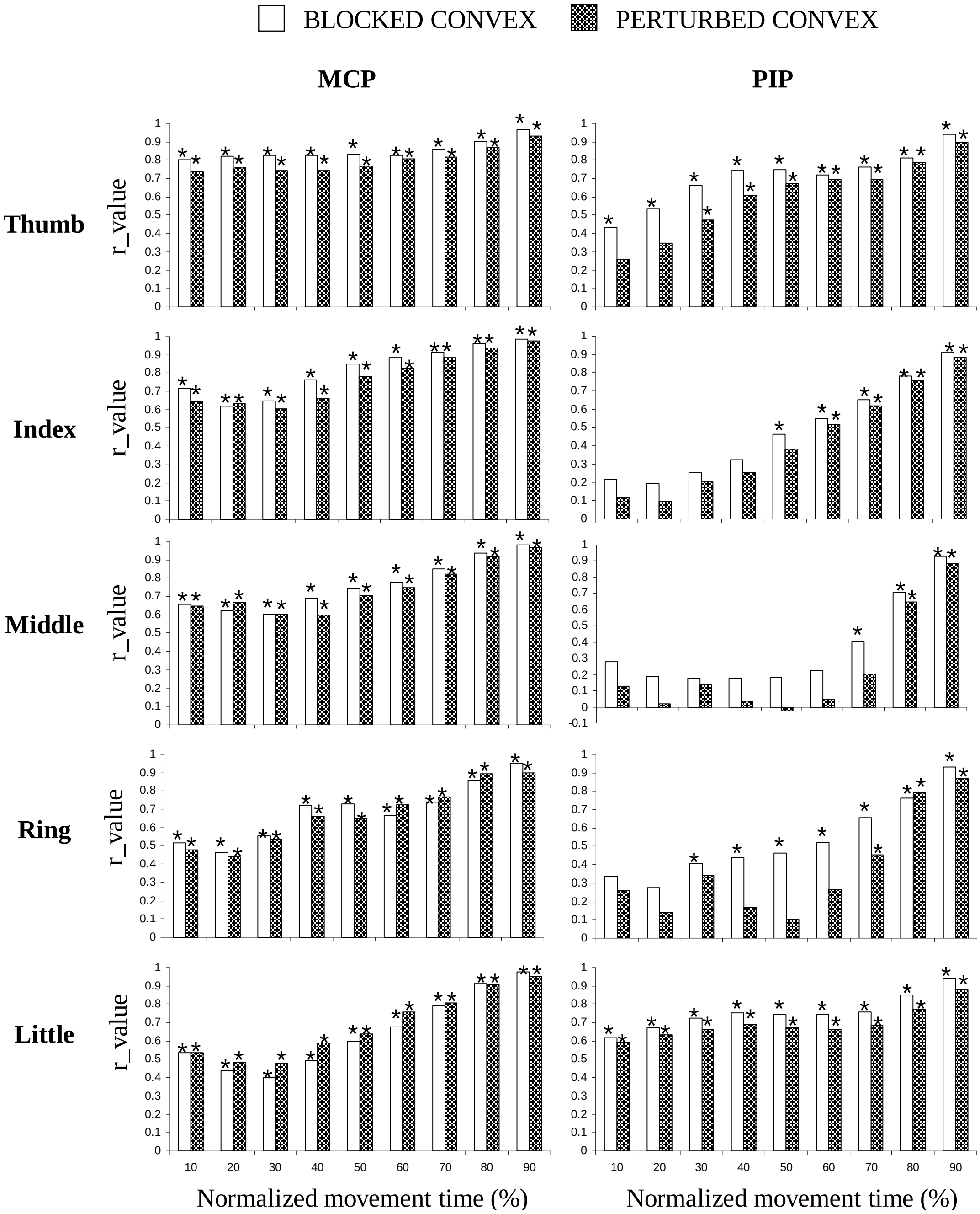

Figure 3.6 Each panel shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at the reaching end for the 'blocked' convex (white bars) and the 'perturbed' convex (grey bars) trials. Data on the left and right columns correspond to the metacarpal and the proximal interphalangeal joints' correlation coefficients, respectively, for each digit. An r value > 0.397 is significant at $P < 0.05$. Asterisks indicate the significant correlation values.

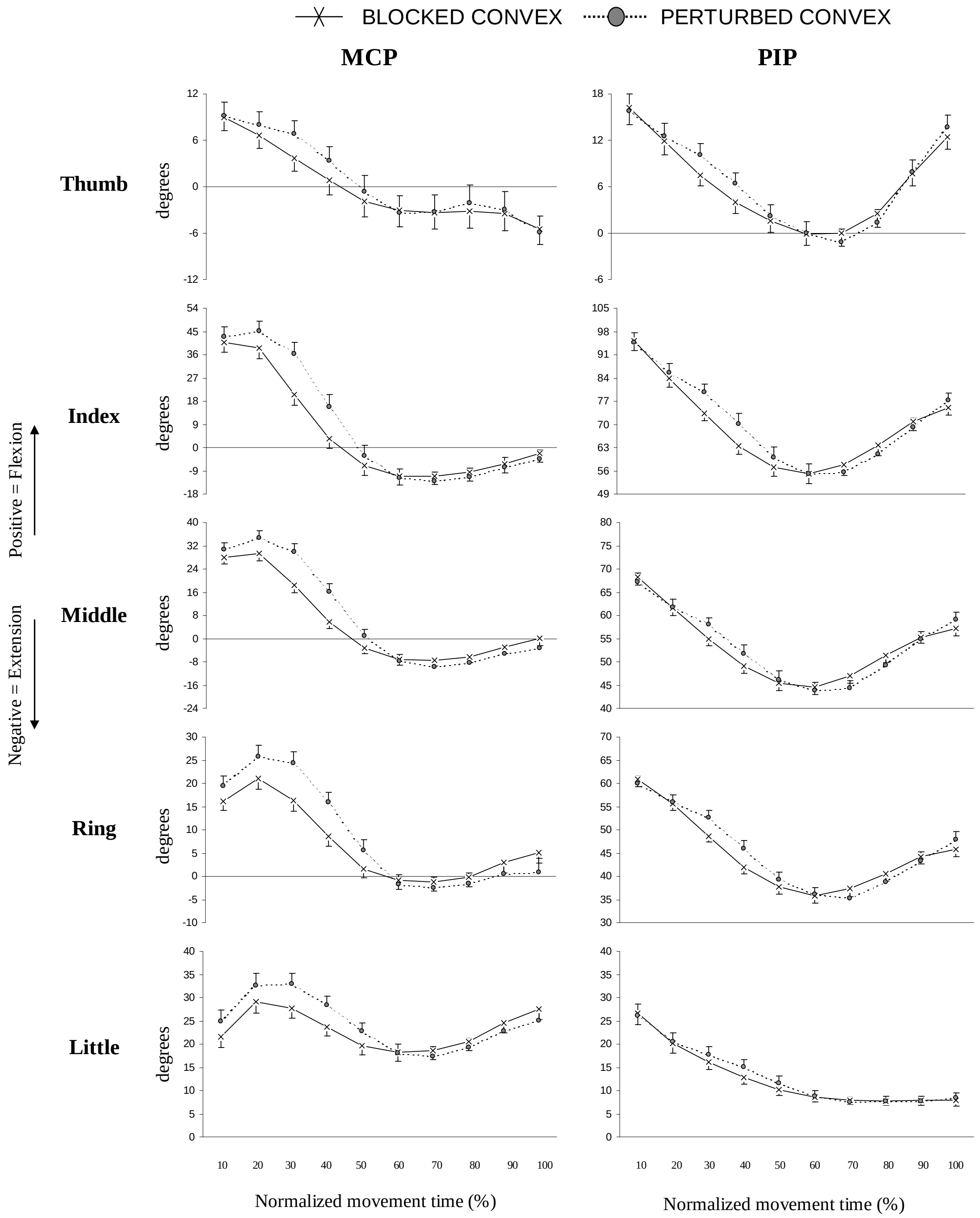

Figure 3.7 Each panel shows the angular excursion averaged across trials and participants of metacarpal (left panels) and proximal interphalangeal (right panels) joints of the thumb, index, middle, ring, and little finger performed in 'blocked' convex (crosses) and 'perturbed' convex (filled circles) trials. Positive values correspond to fingers' flexion whereas negative values correspond to fingers' extension. Bars represent the standard error.

3.4 Discussion

The goal of the present study was twofold. First, we aimed to address whether the hand reaction to an object shape perturbation involves digits' posture. Second, whether the kinematic response to the perturbation was evident at the level of the fingers which were specifically modulated with respect to the shape of the objects (i.e., as identified in the 'blocked' trials) or required a less specific reorganization which involved all digits similarly. Our results suggest that object shape perturbation has an effect on reach duration and on hand shaping during reaching. Specifically, reach duration was longer for 'perturbed' than for 'blocked' trials and the linear regression analysis revealed that the perturbation reduces the strength of the relation between hand shape during the reach and hand configuration at object contact. With respect to joint angular excursions, for both types of perturbation (i.e., from convex to concave and concave to convex), changes were evident for all joints with the exception of index finger *mcp* joint in the perturbation from convex to concave object. All fingers that exhibited a modulation to object shape in the blocked condition were affected by the perturbation. The kinematic patterning of the thumb was very different from that observed for the fingers. Specifically, *mcp* and *pip* joints of this digit were not modulated to object shape in the blocked condition. Nevertheless, they responded to object shape perturbation and they did so in the same way (i.e., over-flexion relative to the blocked condition) regardless of the 'direction' of the perturbation.

3.4.1 Effect of object shape perturbation on reach duration and hand shaping

In agreement with previous perturbation studies (e.g., Castiello et al., 1993; Paulignan et al., 1991a), we found that reach duration was significantly longer in 'perturbed' than in 'blocked' trials. This finding confirms that the initial planning of movement duration has been altered and that reach duration is a parameter which is subject to continuous on-line change according to end-task requirements (e.g., Castiello et al., 1993; Paulignan et al., 1991a).

The effects of the perturbation were also evident when looking at the degree of fingers flexion/extension and at the correlation patterns between hand shaping during reach movement and hand shaping at the end of the movement. For instance, the *mcp* and *pip* joints for the thumb and fingers (except for the *mcp* joint of index finger for the convex to concave perturbation) showed a different pattern of angular excursion between 'blocked' and 'perturbed' trials. Specifically, both *mcp* and *pip* joints of the thumb were more flexed in the 'perturbed' than in 'blocked' trials for both types of perturbation. On the contrary, the response to the perturbation for all fingers was sensitive to the 'direction' of the perturbation. In particular, for the 'convex → concave' perturbation, fingers were more extended than for the 'blocked' concave trials (see Fig. 3.5). In contrast, for the 'concave → convex' perturbation, fingers were more flexed than for the 'blocked' convex trials (see Fig. 3.7). We interpret these patterns of over flexion/extension for 'perturbed' trials as evidence that the motor plan for the initially presented object remains and interacts with the implementation of the motor plan for the newly presented object. The persistence of the original motor plan while adapting for the new motor plan, may result in a kind of 'hybrid' hand shaping for the to-be-grasped object, which is not specifically tuned to the type of object to be grasped.

3.4.2 Differences between the two 'directions' of perturbation

Although all fingers (except for the *mcp* joint of index finger for the convex to concave perturbation) showed a common pattern of response to the perturbation (i.e., over-extension or flexion in convex to concave and concave to convex trials, respectively), the timing and the magnitude of this response differed with respect to the type of perturbation. For the 'convex → concave' perturbation, both *mcp* and *pip* joints for all fingers started to show a differential degree of extension for 'perturbed' with respect to 'blocked' concave trials from 30% of reach duration. This differential extension pattern for 'perturbed' trials lasted up to 80% of reach duration. In contrast, for the 'concave → convex' perturbation a differential degree of flexion for 'perturbed' with respect to 'blocked' convex trials was noticed for all fingers from the very beginning of the movement and lasted up to 60% of reach duration.

These results give an estimate of the time period within which the first identifiable change in kinematic patterning following the perturbation is noticed. Therefore, it appears that although the re-organization in hand shaping as response to the perturbation lasted for a period of time similar for both perturbations, the beginning of such response occurred earlier for the 'concave → convex' than for the 'convex → concave' perturbation. Furthermore, the two 'directions' of perturbation seemed to be different also relatively to the magnitude of correction in the joint angular excursion in response to the perturbation. When looking at the differences between 'blocked' and 'perturbed' trials it can be noticed that a greater discrepancy was found for trials ending with the convex rather than with the concave object (see Figs. 3.7 and 3.5, respectively).

In terms of complexity several factors could contribute to the difference in response timing between the two types of perturbation. For instance, biomechanically there may be more advantage for closure (as happens for the present 'convex → concave' perturbation) than for opening (as happens for the present 'concave → convex' perturbation). Colebatch and Gandevia (1989) found, for example, that thumb and finger flexors were 2.8 – 3.5 times stronger than extensors. For a task focused upon a grasping action, the biomechanical setting for the flexors would be more favoured. This view seems to be supported by the results obtained in previous studies looking at the reprogramming of grip aperture following a perturbation of object size (Bock & Jungling, 1999; Castiello et al., 1993). These findings indicate that correction time was shorter when the perturbation required the passage from a large to a small object than from a small to a large object. A further contributory and inter-related factor and one which receives support from neural network modelling (Ulloa & Bullock, 2003; see also Hoff & Arbib, 1993) is concerned with the extent of motor plan inhibition as to avoid potential risk collision. Ulloa and Bullock (2003) implemented a model capable of simulating adaptation to perturbations of object size (Castiello et al., 1993; Paulignan et al., 1991a). Importantly they were able to simulate the differences in the extent of the correction for small vs. large and large vs. small perturbations. The crucial variable was the amount of self-inhibition put in place to halt the original motor plan. Their proposal is that when the change is made from a large to a small object, a change in fingers closing could easily be managed without compromising object grasp. Inhibitory gating then might be lower because the new motor plan can be partially incorporated within the existing plan. In contrast, when the change is made from a small to a large object the amount of inhibition, to halt the original motor plan, has to be higher and put in place more promptly. This is because if the inhibitory process is activated at a time which does not allow a certain degree of reorganization, fingers are at risk of collision with the object due to too little aperture.

Although the focus of the above-mentioned studies was on the maximum distance between index finger and thumb, and no emphasis was placed on the detailed measurements of all digits, they might account for the present results. For the 'convex → concave' perturbation the plan for the convex object, which includes a larger fingers aperture, could easily be adapted on-line to the plan for grasping the concave object which requires a smaller fingers aperture. In contrast, for the 'concave → convex' perturbation it could be assumed that if fingers shaping would remain unaltered, then the hand would collide with the object.

3.4.3 All digits react to the perturbation: one control strategy

As mentioned above, both *mcp* and *pip* joints of all fingers responded to the perturbation by either an over - extension or an over - flexion depending on whether object shape changed from convex to concave or from concave to convex, respectively. In particular, the *mcp* and *pip* joints of all fingers (with the only exception of the *pip* joint of the little finger) being affected by the perturbation were also the joints that in the blocked condition modulated to the shape of the to-be-grasped object. On the contrary, the thumb – which was not modulated to the shape of the target in blocked condition – reacts to the perturbation in the same way (i.e., more flexed in 'perturbed' that in 'blocked' trials) despite the 'direction' of the perturbation.

A likely explanation for these results is that the CNS could react to the perturbation by applying one control strategy on the hand. In the event of a fast reorganization following a sudden change in object shape, the CNS responds to the perturbation by either an over-flexion or an over-extension (depending by the direction of the perturbation) of the same joints involved in the 'unperturbed' shape discrimination. Noticeably, the temporal window for such 'shape – sensitive' fingers response was approximately the same for both types of perturbation (i.e., from 30 to 80% of the reaching movement for the convex to concave perturbation and from the beginning to 60% of the reaching movement for the concave to convex perturbation). At first sight, the proposal for one control strategy for all digits may not fit with the results obtained for the thumb. Remember that the thumb reacted in the same manner regardless of the 'direction' of the perturbation. With this in mind we are inclined to suggest that the type of response to the perturbation observed here for the thumb and the fingers may signify the expression of a control strategy within which opposing digits would play different roles. The invariance of the thumb being important in maintaining a suitable action guidance (Frak, Paulignan, & Jeannerod, 2001; Galea, Castiello, & Dalwood, 2001; Paulignan, Frak, Toni, & Jeannerod, 1997; Smeets & Brenner, 1999; Wing & Fraser, 1983) in the event of a perturbation. The modulation of fingers' shaping being important as to tune the hand to the newly presented object shape following the perturbation.

4. Distractor objects affect fingers' angular distances but not fingers' shaping during grasping[3]

Abstract

The aim of the present study was to determine whether and how hand shaping was affected by the presence of a distractor object adjacent to the to-be-grasped object. Participants were requested to reach towards and grasp a 'convex' or a 'concave' object in the presence or absence of a distractor object either of the same or different shape than the target object. The results indicate robust interference effects at the level of reach duration and the extent of fingers' abduction angles together with changes at the level of a single joint for the thumb. No distractor effects on individual fingers' joints except for the *mcp* of the middle and little fingers were found. These findings suggest that the presence of distractor object affects hand shaping in terms of fingers' abduction angles, but not at the level of 'shape dependent' fingers' angular excursions. Furthermore they support the importance of the thumb for the guidance of selective reach-to-grasp movements. We discuss these results in the context of current theories proposed to explain the object selection processes underlying the control of hand action.

---

[3] *Published*: Ansuini, C., Tognin, V., Turella, L., & Castiello, U. (2007). Distractor objects affect fingers' angular distances but not fingers' shaping during grasping. *Experimental Brain Research, 178*, 194-205.

4.1 Introduction

From everyday experience, we intuitively know that we carry out many visually guided actions on the objects that surround us. For example, when choosing a piece of fruit from a bowl, many fruits are visible and within reach, but only the one that we would like to pick up governs the particular pattern and the direction of reaching movement. This implies that to avoid the undesired fruits and instead to act selectively towards the desired fruit, at some stage (or stages) in the information stream some objects are filtered out from processing. In this respect, little is known about the limits governing the brain's ability to process information presented in parallel for the control of overt action towards three-dimensional (3D) stimuli.

The mechanisms underlying the control of such behaviours have been studied by having people reach for, point to, and grasp objects when non-target (i.e., distractor) objects were introduced into the workspace (e.g., Castiello, 1996; Deubel, Schneider, & Paprotta, 1998; Keulen, Adam, Fisher, Kuipers, & Jolles, 2002; Pratt & Abrams, 1994; Tipper, Lortie, & Baylis, 1992; Tipper, Howard, & Jackson, 1997). In the present article, we report an experiment that continues that tradition. Our interest is in the hand shape that people make while they grasp target objects in the presence of distractors. It is worth noting that much can also be learned about the underlying mechanisms by examining arm spatial trajectories and temporal aspects of the movement (e.g., Chang & Abrams, 2004). Such an approach is taken by a number of researchers (e.g., Chang & Abrams, 2004; Fischer & Adam, 2001; Tipper et al., 1997). However, here we were specifically concerned with kinematics of hand shaping during reach to grasp movement.

In previous attempts to target specifically the grasping component during a reach to grasp movement towards a target in the presence of distractor objects (for a review see Castiello, 1999) participants were requested to grasp a target presented in conjunction with a distractor of a different size, but similar in colour and positioned roughly in the same position as the target (Bonfiglioli & Castiello, 1998; Castiello, 1996, 1998). It was found that the participants' amplitude of PGA while en-route to the target was influenced by the size of the distractor. If the target was small, the amplitude of PGA was greater when the distractor was large than when no distractor was present. Conversely, the amplitude of PGA for the grasp of a large target was less when the distractor was small than when there was no distractor.

Common to these findings is the suggestion that if more than one grasping pattern is simultaneously kept active, this parallel activation triggers mutual interference. The proposal is that interference arose from the competition between the different types of grasp required by target and distractor having different size. Thus parallel computations for different types of grasp, one for the target and one for the attended distractor, may have been at the origin of the changes found for the kinematics of the action directed towards the target when presented alone. In these terms, both the target and the distractor evoke grasping representations which interact in a mutually suppressive or competitive way.

To date research on this topic has focused on the relationship between the thumb and the index finger giving little attention to differences in the shape assumed by individual fingers when performing grasping movements to target objects in the presence of distractors. It is not known whether and how the presence of a distractor object affects hand shaping for a target object at the level of single fingers' posture. Recent methodological and theoretical developments in the study of grasping make this a particularly timely and tractable issue. Santello and Soechting (1998) investigated hand shaping at the level of individual joints for all fingers for movements directed towards objects having different shapes and found a gradual modulation of hand posture to object's geometry (see Chapter 1). Therefore it may be reasonable to ask whether the presence of a distractor object affects hand kinematics only at the level of the thumb-index angular distance (as revealed by previous studies) or also at the level of hand shaping in terms of individual fingers' posture.

In the present experiment we contrasted the evolution of hand shaping during a grasping task directed towards objects of different shapes in three conditions: a no-distractor condition in which a 'convex' or a 'concave' target objects was presented in isolation, a congruent distractor condition in which the target object ('convex' or 'concave') was flanked by a distractor object of the same shape, and an incongruent distractor condition in which the target object was flanked by a distractor object of a different shape (e.g., either a 'convex' target with a 'concave' distractor or vice versa). Comparing the effects of distractor objects on the extent and timing of the abduction angles between fingers with the extent and timing of kinematical parameters concerned with hand shaping at the level of single digits may allow to ascertain if and at which level the distractor objects produce interference on the motor patterning for the target. If a distractor of a different shape than the target object is represented at a more generalized size level, then interference effects should be most evident at the level of abduction angles with particular reference to that involving the thumb and the index finger as previously demonstrated. In contrast, if the distractor representation is more fine-grained then it might be possible that the distractor being represented at the level of angular excursions of single fingers.

Our results indicate robust interference effects on reach duration, on the extent of fingers' abduction angles and at level of a single joint for the thumb. In contrast, no distractor effects on the pattern of angular excursion for the joints which were sensitive to object shape were found.

4.2 METHODS

4.2.1 Participants

Twenty right - handed participants (male = 10, female = 10, ages 19 - 34) took part in this experiment.

4.2.2 Stimuli and apparatus

In the present experiment, a convex and a concave wooden objects served as targets and distractors (see Figure 4.1a).

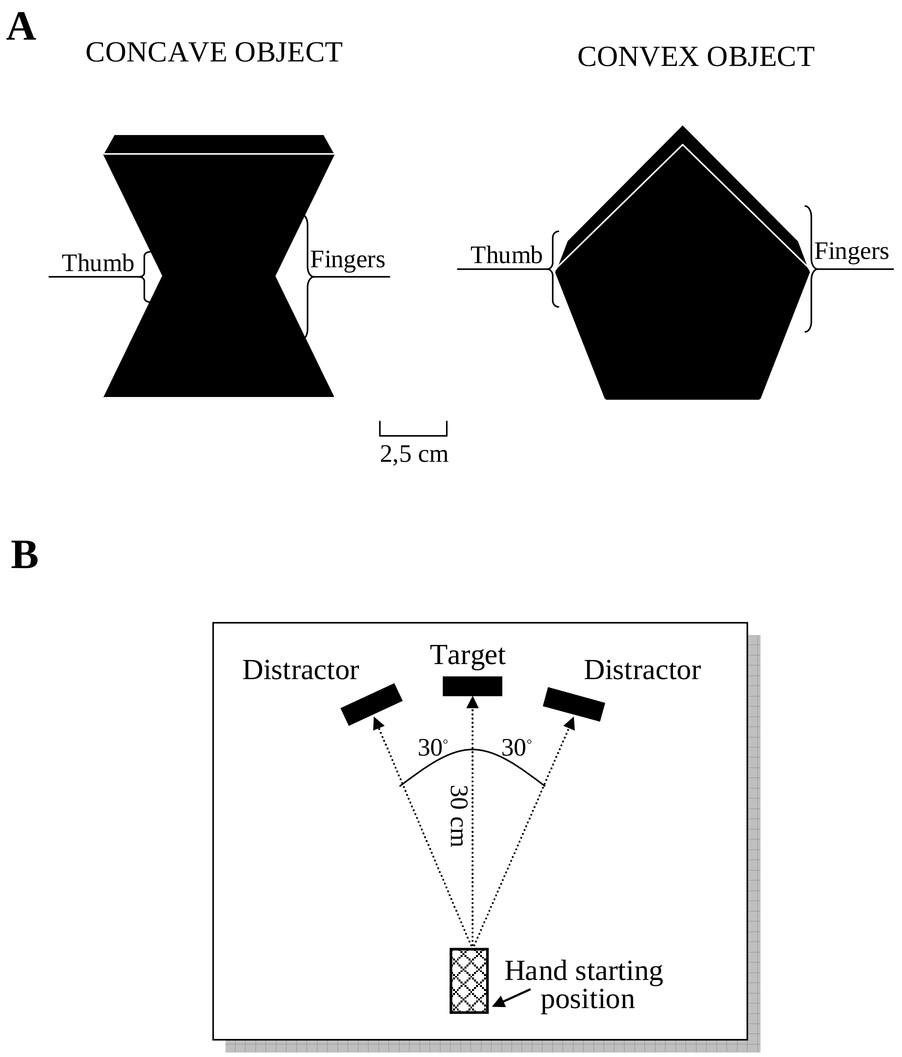

Figure 4.1 Panel A shows the objects used as targets and distractors in the present experiment. 2.5 cm refers to the drawing's scale. Parentheses depict the thumb and fingers' contact areas used by the participants as to naturally grasp the objects. Panel B shows a schematic representation of the workspace (top view).

The 'concave' object was characterized by two triangular indentations extending from each of four corners to its center (see Fig. 4.1a). It was 10 cm wide at the base and 5 cm wide at the point of maximum ‘concavity’ (i.e., the distance between the two vertices of triangular indentations; see Fig. 4.1a). The ‘convex’ object was characterized by a point at the top from which two triangular protrusions ended up at the base (see Fig. 4.1a). It was 5 cm wide at the base and 10 cm wide at the point of maximum ‘convexity’ (i.e., the distance between the two vertices of triangular protrusions; see Figure 4.1a). Both objects measured 3 cm in thickness, 9 cm in height and weighed ~ 100 g.

The participants naturally grasped these objects opposing the thumb to the fingers as shown in Figure 4.1a. The concave object was grasped by opposing the thumb with the other fingers around the area of maximum concavity (see Fig. 4.1a). In such circumstances, all fingers were near to each other. For the convex object the thumb/fingers opposition pattern was along the points of maximum convexity of the object (see Fig. 4.1a). In particular, the convex object was generally grasped with the index and the middle fingers above the point of maximum convexity and the ring and little fingers below this point; in some cases, also the ring finger was placed above the point of maximum convexity. When present, the distractor object was located at 30 cm from the hand start location either at ~ 30° to the right or left side of the target object (Fig. 4.1b).

Visual availability of the stimuli was controlled with Plato spectacles (Plato Technologies Inc.). These were lightweight and were fitted with liquid crystal lenses. The opacity of the lenses was controlled by the switch embedded within the hand starting position (see Chapter 2). When the hand was positioned on this switch the lenses were opaque, and cleared when the hand was lift from its starting position. Once the participant re-placed his/her hand on the starting position at the end of each trial, the LCD glasses were set to return in the opaque position.

4.2.3 Procedures

The main task of the participant was to reach towards and grasp the target object between the thumb and the four fingers on the vertical sides of the object, and briefly lift it from the working surface. This main task was performed under three different conditions:

1. No-distractor condition. The target object was presented centrally and in isolation;

2. Congruent-distractor condition. The target object was centrally placed and flanked by an identical object (e.g., ‘convex’ target/‘convex’ distractor; ‘concave’ target/‘concave’ distractor);

3. Incongruent-distractor condition. The target object was centrally placed and flanked by an object of a different shape (e.g., ‘convex’ target/‘concave’ distractor; ‘concave’ target/‘convex’ distractor).

Participants performed two blocks of 50 randomized trials over which all possible target/distractor combinations were presented (10 trials per each combination) and were given a rest at the end of the first block.

4.2.4 Data analysis

It is evident in the literature that the hemispace location of the target relative to the distractor has differential effects for left versus right hand reaches (e.g., Howard & Tipper, 1997; Jackson, Jackson, & Rosicky, 1995). However, preliminary analysis did not reveal differences due to the factor 'distractor location', consequently trials for the left and right distractor's position were collapsed. To address the possible differences in absolute duration of reaching movements due to the experimental manipulation, we performed an ANOVA with 'Distractor Type' (no-distractor, distractor congruent, distractor incongruent) and 'Type of Target' ('convex', 'concave') as within-subjects factors. To determine the effect of the experimental manipulation on the pattern of angular excursion we carried out repeated measures multivariate analyses of variance (MANOVAs), one for each digit for both *mcp* and *pip* joints. In these MANOVAs, the main within-subjects factors were 'Distractor Type' (no-distractor, distractor congruent, distractor incongruent), 'Type of Target' ('convex', 'concave'), and 'Time' (from 10% to 100% of the normalized movement duration, at 10% interval). A MANOVA including the same factors was carried out on the abduction angles between fingers.

4.3 RESULTS

This section will be organized in two parts. In the first part we shall describe the differences between 'convex' vs. 'concave' objects for the no-distractor condition for each of considered dependent measures (i.e., reach duration, fingers' angular excursion, and fingers' abduction angles). The determination of kinematical parameters which are object-shape specific when no distractor object was present, allows us to address whether the presence of the distractor affected these parameters. In the second part, we shall describe the results concerned with the impact that the presence of a congruent or incongruent distractor had on hand shaping for the considered measures. In this section we shall present the results for reach duration followed by the results concerned with the extent and timing of the patterns of fingers' angular excursion and abduction angle.

4.3.1 'Convex' vs. 'concave' object: no-distractor condition

Reach duration was similar when comparing the 'convex' with the 'concave' object (1339 vs. 1328 ms, respectively). When looking at the patterns of angular excursion, the profile analysis revealed that from the beginning to 50% of reach duration no differences depending on the type of target object for any of the recorded joints were noticed (see Figure 4.2). In contrast, after 50% of reach duration, the *pip* joint of the middle finger and the *mcp* joint of the ring finger were more extended for the 'convex' than for the 'concave' object (see Fig. 4.2). Furthermore, after 50% of reach duration, the *pip* joint of the index finger was more flexed for the ‘convex’ than for the ‘concave’ object (see Fig. 4.2). For the remaining joints the patterns of angular excursion were similar from the beginning up to the end of reach duration (see Fig. 4.2).

The type of hand configurations dictated by the type of target object also gave rise to some differences at the level of fingers’ abduction angles (see Figure 4.3). In particular, middle-ring and ring-little fingers’ abduction angles were similar from the beginning up to 50% of reach duration (Fig. 4.3). However, after 50% of reach duration, these angles became larger for the ‘convex’ than for the ‘concave’ object (Fig. 4.3). In contrast, as revealed by the profile analysis, the thumb-index and index-middle fingers’ abduction angles remained invariant with respect to the type of to-be-grasped object from the beginning to the end of the reaching movement (Fig. 4.3).

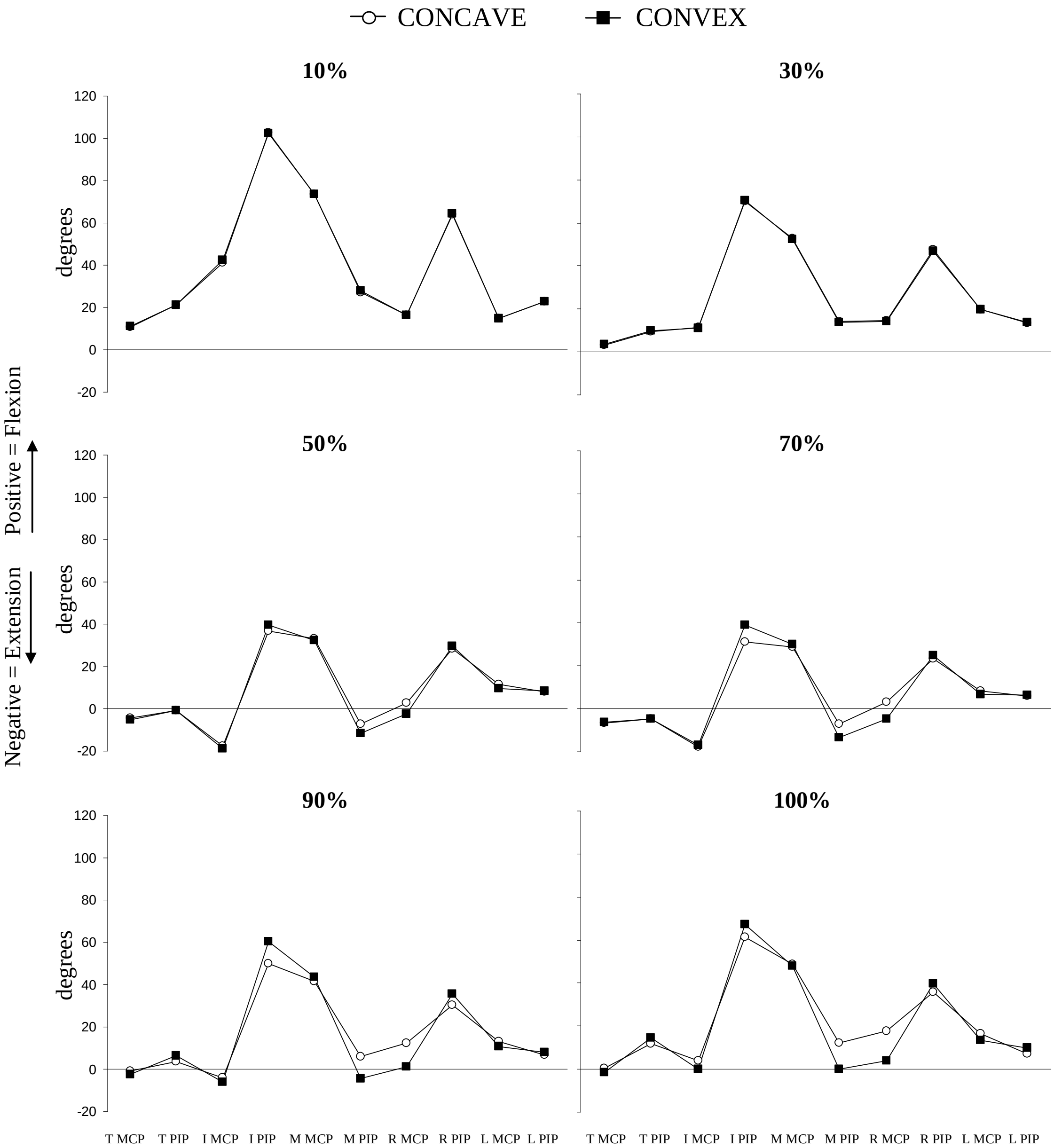

Figure 4.2 Patterns of angular excursion for no-distractor trials at different epochs during reaching (10, 30, 50, 70, 90, and 100% of the reach duration) for the concave (filled circles) and the convex (empty squares) objects. The represented angles correspond to the metacarpal (MCP) and proximal interphalangeal (PIP) joints for the thumb, index, middle, ring, and little fingers (T, I, M, R, and L, respectively). Data are averaged across participants and trials.

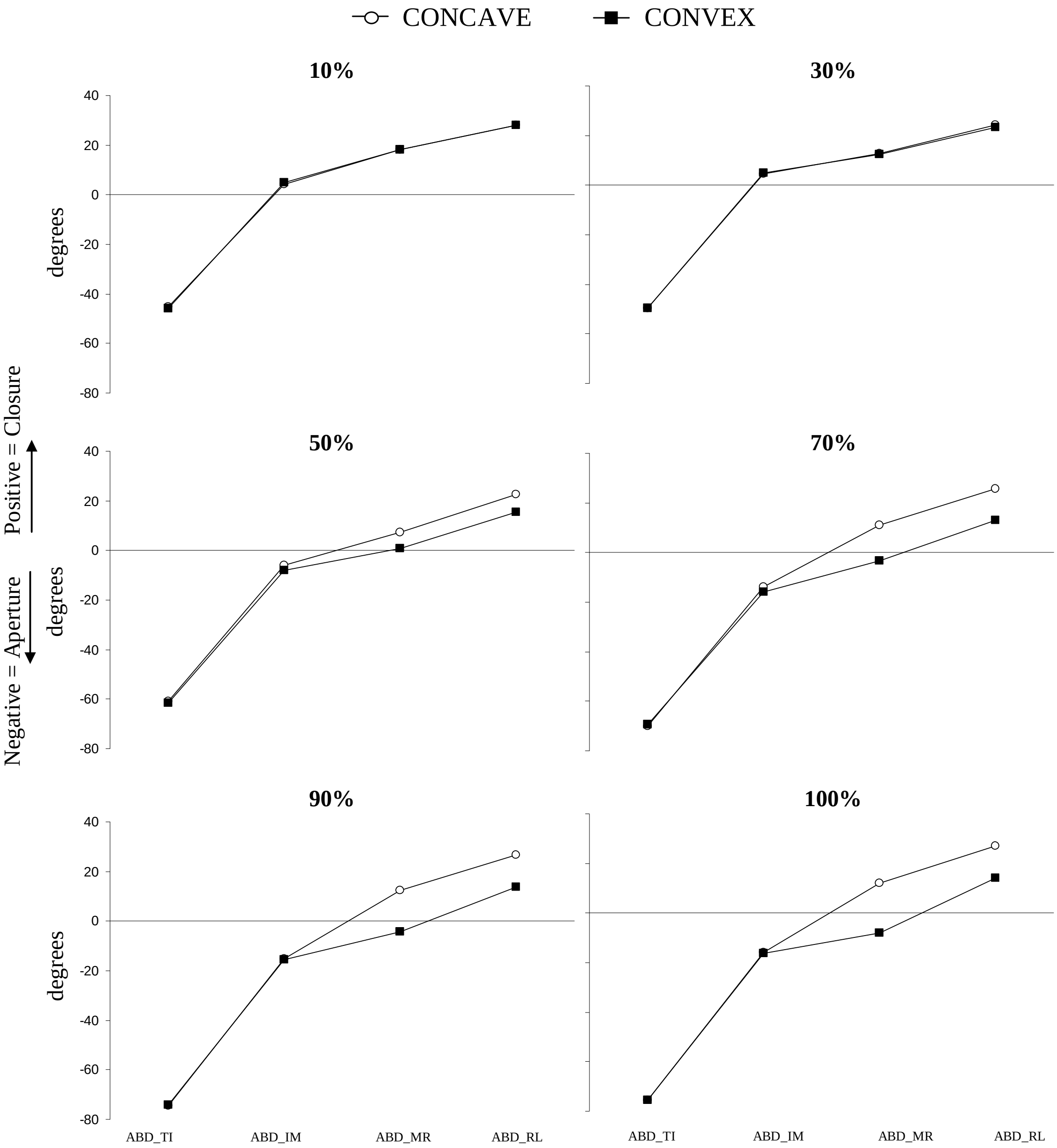

Figure 4.3 Patterns of abduction angle between fingers for the no-distractor condition at different epochs during reaching (10, 30, 50, 70, 90, and 100% of the reach duration) for the concave (filled circles) and the convex (empty squares) objects. The represented fingers' abduction angles (ABD) correspond to the angle between thumb and index, index and middle, middle and ring, and ring and little fingers (TI, IM, MR, and RL, respectively). Data are averaged across participants and trials.

4.3.2 No-distractor vs. congruent and incongruent distractor conditions

4.3.2.1 Reach duration

For reach duration the main factor 'Distractor Type' was significant ([$F_{(2,38)} = 4.374$, $P < .021$]). Post-hoc contrasts (Bonferroni's correction) revealed that reach duration was longer when the target was flanked by an incongruent distractor (1364 ms) than when the target was presented alone (1334 ms). The difference between the no-distractor and the congruent distractor (1357 ms) conditions was almost significant ($P = .058$). The two - ways interaction between 'Type of Target' and 'Distractor Type' was not significant ([$F_{(2,38)} = .728$, $P > .05$]).

4.3.2.2 Patterns of angular excursion

The results obtained from the MANOVAs performed on the angular excursion for each finger separately (e.g., each for both of *mcp* and *pip* joints) (see Appendix C) revealed that none of the joints which specifically modulated with respect to the shape of the target object ('convex' or 'concave') when presented in isolation (i.e., *pip* joint of both index and middle fingers, and *mcp* joint of ring finger; see Fig. 4.2) were significantly affected by the distractor type condition. However, the distractor type condition significantly affected the *pip* joint of the thumb, as revealed by the significance of the main factor 'Distractor Type' ([$F_{(2,38)} = 8.066$, $P < .002$]). In particular, this joint was more extended when the target object was presented alone (5.6 degrees) than when flanked by the congruent (6.5 degrees) or the incongruent distractor (6.2 degrees). As shown in Figure 4.4, this pattern of over – extension was evident from 20% to 70% of reach duration when the object to be grasped was 'concave' and from 40% to 80% when it was 'convex' (three - ways interaction between 'Type of Target', 'Distractor Type', and 'Time' [$F_{(18,342)}$=2.496, P <.002]) (see Appendix D).

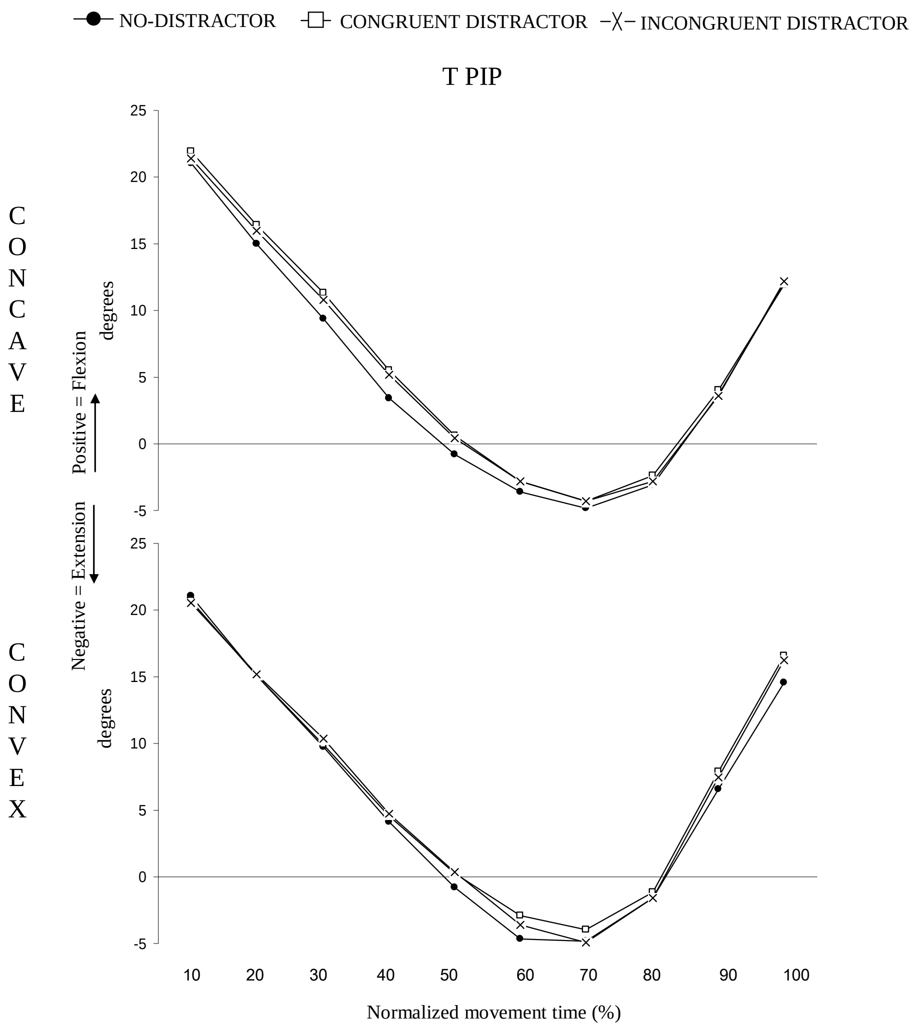

Figure 4.4 Angular excursion during reaching for the concave (top panel) and convex (bottom panel) objects in no-distractor, congruent distractor, and incongruent distractor conditions for the proximal interphalangeal (PIP) joint of the thumb (T).

The interaction between 'Distractor Type' and 'Time' was also significant for the *mcp* joint of both the middle and the little fingers ([$F_{(18,342)} = 1.692$, $P < .04$] and [$F_{(18,342)} = 1.730$, $P < .035$], respectively). Profile analyses for these two joints did not reveal a consistent pattern indicating the influence of the distractor's shape on the modulation of these joints during reaching (see Fig. 4.5). This latter observation might be ascribed to a generalized 'disturbance' effect due to the presence of the distractor or to the effect of experimental manipulation on fingers' abduction angles as explained below.

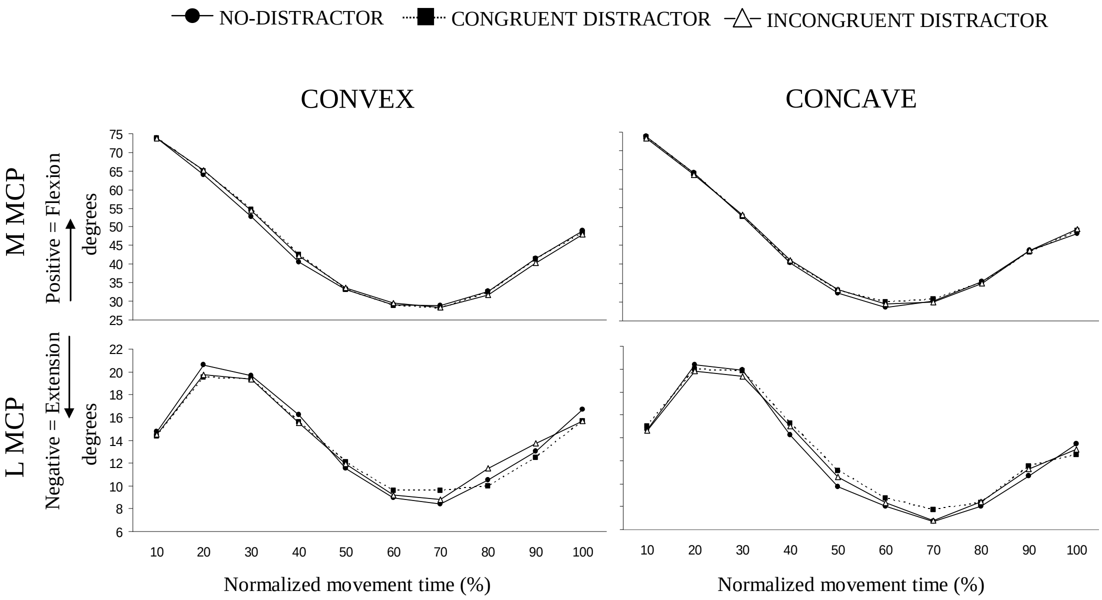

Figure 4.5 Time course of angular excursion during reaching for the convex (left column) and concave (right column) objects in no-distractor (filled circles), congruent distractor (filled squares), and incongruent distractor (empty triangles) conditions. The represented angular excursion refers to the metacarpal (MCP) joint of middle (M) (top panels) and little fingers (L) (bottom panels). Data are averaged across participants and trials.

4.3.2.3 Fingers' abduction angles

The MANOVA performed to address the effects of the experimental manipulation on the fingers' abduction angles revealed a significant main effect of the factor 'Distractor Type' for the angular distance between thumb and index ([$F_{(2,38)} = 4.665$, $P < .016$]) (see Appendix E). In particular, post-hoc contrasts revealed that this angle was smaller when the target object was presented alone (62 degrees) than when it was flanked by a congruent (61 degrees) or an incongruent (61 degrees) distractor. No significant differences were found when comparing the congruent and the incongruent distractor conditions. The interaction between 'Distractor Type' and 'Time' was significant for the abduction angles between the middle-ring ([$F_{(18,342)} = 1.645$, $P < .049$]) and the ring-little fingers ([$F_{(18,342)} = 1.616$, $P = .05$]) (see Appendix F). As revealed by the profile analysis, these angles were similar for each of the distractor type conditions at the very beginning of the movement (see Fig. 4.6), but became larger for the no-distractor than for the congruent and the incongruent distractor condition from 30-40% up to 60-70% of reach duration (Fig. 4.6). Further, from 60-70% up to 90% of reach duration the pattern inverted: these angles became smaller for the no-distractor than for the congruent and the incongruent conditions (Fig. 4.6). In particular, after 60-70% of reach duration when the distractor was incongruent these angles were larger than when the distractor was congruent. However, at object contact these angles were found to be similar for all distractor type conditions.

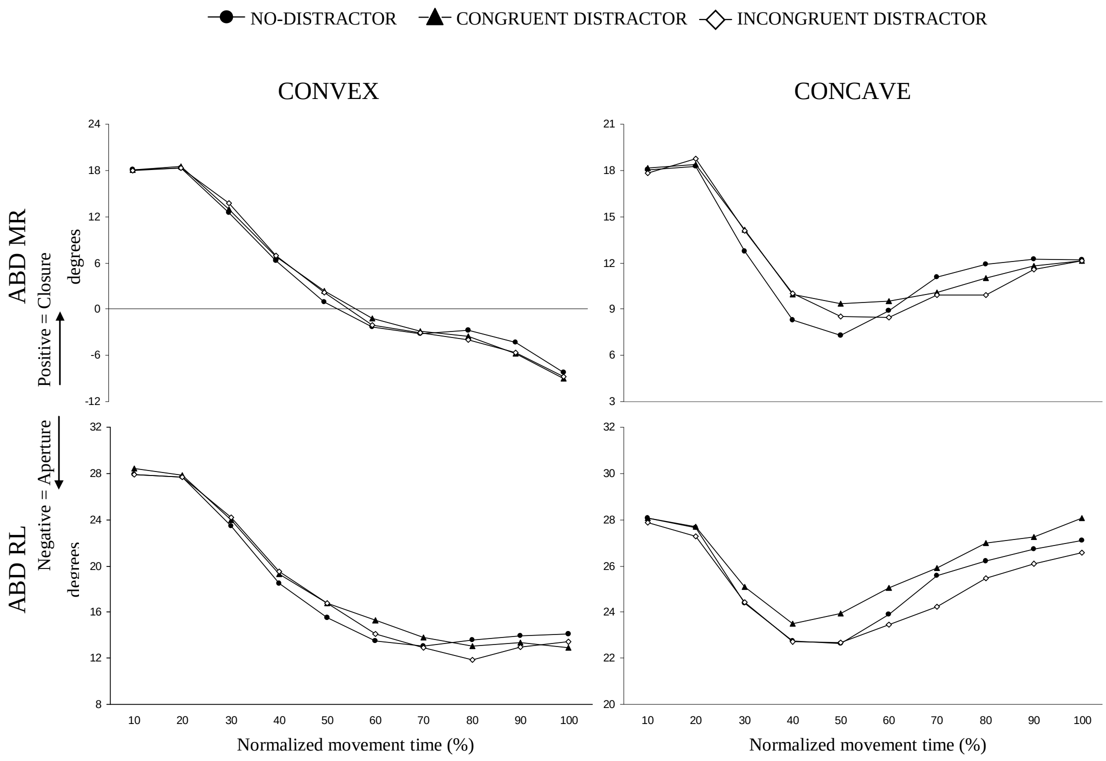

Figure 4.6 Time course of abduction angle between fingers during reaching for the convex (left column) and concave (right column) objects in the no-distractor (filled circles), congruent distractor (filled triangles), and incongruent distractor (empty diamonds) conditions. Abduction angles between middle and ring fingers (top panels) and between ring and little fingers (bottom panels) are represented. Data are averaged across participants and trials.

4.4 Discussion

The main goal of the present experiment was to observe whether hand shaping to a target of a particular shape was affected by the presence of a distractor object of a similar or a different shape. Our results indicate that the presence of the distractor object produced a significant increase in reach duration for the incongruent-distractor condition and, although not fully significant, also the presence of the congruent distractor elicited a lengthening of reach duration. Furthermore, the presence of the distractor object significantly affected kinematic parameterization of the thumb. Both angular excursion (i.e., *pip* joint) and abduction-adduction angle showed an alteration of the stereotypical aperture-closure pattern found for the no-distractor condition. With respect to the pattern of fingers' angular excursion none of the joints sensitive to object shape, as identified for the no-distractor condition, were affected by the presence of the distractor. Conversely, the fingers' abduction angles which were related to the 'convex' or the 'concave' objects when grasped in isolation, were affected by the presence of the distractor independently from its shape.

This experiment has demonstrated that distractors can produce measurable interference effects in tasks requiring participants to reach out and pick up an object. As previously demonstrated the presence of the distractor increased the duration of the reach (e.g., Castiello, 1996; Tipper et al., 1997; Meegan & Tipper, 1998) indicating that the planning of reach duration has been altered by the presence of the distractor.

Of perhaps more interest, we have also observed that the presence of the distractor does not affect hand shaping at the level of 'shape dependent' fingers' joints, but in terms of the fingers' abduction angles. In particular, these angles were similar for each of the distractor type conditions at the very beginning of the movement, but became larger for the no-distractor than for the congruent and the incongruent distractor conditions from 30 up to 70% of reach duration. Further, from 70% up to 90% of reach duration these angles became smaller for the no-distractor than for the congruent and the incongruent conditions. This would indicate that up to 30% target shape does not affect hand shape (as happens when no distractors are present), suggesting that hand shape is not selective for target shape and/or too noisy up to that point. Then selection of the distractor becomes necessary given that distractor shape is acknowledged and 'shape' interference has to be solved. This 'acknowledgement' phase starts from 30 up to 70%, a temporal window which is crucial for hand preshaping leading to maximum hand aperture. The fact that from 70% to the end of reaching the abduction angles' pattern returned at the same extent as found for the no-distractor condition signifies that the distractor-related movement plan has been possibly completed and totally filtered out by that moment. These findings give an estimate of the time period within which identifiable changes in kinematic patterning consequent to the presence of the distractor are noticed.

It is known that when humans manipulate irregularly shaped objects, they typically strive to select grasp points that result in a grasp axis that is normal to local surface curvatures at contact points. This suggests the use of a broader strategy to cope with such torsional loads to local surface curvatures at contact points (see Blake, 1992; Goodale, Meenan, Buelthoff, Nicolle, Murphy, & Racicot, 1994). Consequently it might be hypothesized that the presence of a distractor object produced a disturbance which in principle could have threaten grasp stability. In other words, by modulating the points in which the digits were placed, the applied forces would be more effective when the object had to be lifted. This modulation may bring to an amplification of the abduction angles. Furthermore, work by Jenmalm, Goodwin and Johansson (1998) seems to suggest that grip forces as to obtain grasp stability varies depending on surface curvature. In particular, the minimum grip forces required to prevent frictional slips were influenced by surface curvature, being higher for markedly convex and concave surfaces as those utilized in the present study. Therefore, the modulation of fingers' abduction angle along the object surface may be functional if grasp stability is considered in this wider context.

The thumb, in contrast to the other fingers, appears to be sensitive to the presence of the distractor at the level of single joints. This might be explained in terms of the role played by the thumb, an element of grasp, for the visual guidance of reaching. During normal reaching, as the object is approached, the thumb takes a relatively straight line of approach with most of the changes in grasp aperture resulting from the other fingers (Wing & Fraser, 1983; Wing, Turton, & Fraser, 1986). Therefore the thumb sensitivity to the presence of the distractor might be dictated by the necessity to maintain a reference point for the conduction of reaching. In this respect it is worth noting that the target and the distractor objects in this study were presented in different locations. Thus, it might be hypothesized that both of target and distractor objects triggered the planning of movements toward their respective locations. The parallel computation for the two different locations and the consequential interference then would be most evident at the level of the digit which acts as a point of reference for the target position, that is, the thumb.

Further, the specific effect of a distractor present (versus no distractor) on thumb flexion may suggest a possible obstacle explanation (Tresilian, 1998; Biegstraaten, Smeets, & Brenner, 2003). It might be hypothesized that participants were constrained in thumb extension by the presence of the distractor. In this sense bumping into the distractor would indeed be a real concern. The longer movement duration for congruent and incongruent distractor conditions, consistent with a more careful approach of the object, together with the specific effect of a distractor present (versus no distractor) on thumb flexion seem to support the obstacle explanation. However, given the distance between target and distractor (see Fig. 4.1b) and the lack of distractor location effects (which should have emerged for the thumb when the distractor was located to the left of the target) it might be unlikely that the physical presence of the distractor would cause a problem. The obstacle hypothesis, however, may become plausible when looking at the lack of difference between the congruent and incongruent distractor conditions for fingers' shaping regarding target's shape. In this respect, it can be hypothesized that the distractor is processed as an unspecific obstacle independently from its shape.

At the outset we hypothesized that how the hand responds to the presence of the distractor might be an index of the type of analysis performed on the distractor object. We suggested that if the analysis of the distractor would be concerned with the object general volumetric properties then the maximum hand aperture should be chiefly affected. Alternatively if the analysis of the distractor would be concerned in terms of a more holistic 'shape' type of processing then individual fingers' joint should be affected. Our findings suggest that the selection mechanisms mediating action seem to proceed using a more analytical type of processing considering object volume as the relevant dimension while partially ignoring a potential 'holistic' process which would imply the coding of the distractor more fine-grained perceptual features. Support to this hypothesis comes from a recent study by Ganel and Goodale (2003) which demonstrated that in situations in which the elementary dimensions of an object's shape are perceived in a holistic manner, the same dimensions are treated analytically when a visually guided action is directed at the same object. The proposal here is that unlike visual perception, the visual mechanisms mediating action are able to process the most relevant dimension while ignoring irrelevant dimensions. We extend this notion to the implicit processing of objects which are potential target for action. That is, in order to minimize interference effects when distractor objects are presented the general volumetric properties, but not the specific perceptual features of the distractor object are considered.

In conclusion, a series of studies has demonstrated that hand shaping may be sensitive to the presence of distractor objects (for a review see Castiello, 1999). However the majority of these studies focused only on the distance between thumb and index finger paying no attention to the configuration assumed by individual fingers and abduction angles between the other fingers. In this respect the present results extend this literature by looking at individual finger joints and at a more complete description of fingers' abduction angles. Looking at these measures adds a level of complexity to previous descriptions of interference effects in grasping demonstrating that task-irrelevant objects affect the expression of hand prehension at a level of coordination which involves all digits and goes above the thumb-index distance.

5. Effect of end-goal accuracy on hand shaping[4]

Abstract

The aim of the present study was to determine whether hand shaping was affected by planning of an action subsequent to object contact. Participants were requested to reach and grasp a convex object between the thumb and the fingers of the right hand and to perform one of the following actions: 1) lift up the object; 2) insert the object into a niche of a similar shape and size as the object, or 3) insert the object into a rectangular niche much larger than the object. Although all experimental conditions required grasping the same object, we found different covariation patterns among finger joint angles across conditions. Gradual preshaping of the hand occurred only when planning object lift or when the end-goal required object placement into the tight niche. In contrast, for the larger niche, gradual preshaping was not evident for the ring and the little finger. Further, reaching movements were faster for movements ending with the larger niche than for the other conditions. The present results suggest that hand shaping takes into account end-goal in addition to object geometry. We discuss these findings in the context of forward internal models that allow the prediction of the sensorimotor consequences of motor commands in advance to their execution.

---

[4] *Published*: Ansuini, C., Santello, M., Massaccesi, S., & Castiello, U. (2006). Effect of end-goal on hand shaping. *Journal of Neurophysiology, 95,* 2456-2465.

5.1 Introduction

A major theme in motor control is whether contextual factors have an effect on motor behaviour. Evidence for such context effects comes from studies in which ongoing movements are influenced by manipulation of forthcoming task demands. For example, coarticulation effects occur during speech production in which articulation of a phoneme is affected by the identity of upcoming phonemes (Liberman, 1970). Context effects have also been reported in a variety of manual tasks including typing (Rumelhart & Norman, 1982), handwriting (Van Galen, 1984), manual aiming (Klapp & Greim, 1979), finger spelling (Jerde, Soechting, & Flanders, 2003 a,b), and prehension (e.g., Cole & Abbs 1986; Gentilucci, Negrotti, & Gangitano, 1997; Marteniuk, Leavitt, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Quaney, Nudo, & Cole, 2005; Rosenbaum & Jorgensen 1992; Soechting, 1984; Stelmach, Castiello, & Jeannerod, 1994). In general, these context effects indicate that individual movements are often not planned in isolation, but rather as part of larger action sequences.

Here we shall focus on context effects on prehension in relation to the end-goal of an upcoming action sequence. In a previous study, Marteniuk and colleagues (1987) asked participants to reach for an object and to either fit it into a similarly sized opening or throw it away. Although the initial task requirements of reaching for the object were identical across the two conditions, kinematic analyses revealed substantial differences. Compared with reaching movements in the “throw condition”, reaching movements performed in the “fit condition" revealed lower peak velocities and longer deceleration periods. Similarly, people pick up a dowel with the thumb pointing to one end or the other depending on how they will orient the dowel after moving it to a new location (Rosenbaum & Jorgensen, 1992; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992).

The above evidence suggests that planning plays a role in grasping objects, but also that the execution of prehension, like a variety of other motor behaviours, is sensitive to the context in which it is implemented. Surprisingly, there has been little research on the question of where actors place their hands on objects and how hands approach objects depending on where and for what purpose the objects will be moved. An answer to the first question has been provided by Cohen and Rosenbaum (2004). They asked participants to take hold of a vertical cylinder to move it to a new position. They found that grasp heights on the cylinder were inversely related to the height of the target position. This demonstrates that where people grasp objects give insight into the planning of movement.

The current research focuses on whether and how the hand approaches an object depends on the manipulative action following object contact and grasping. In particular, we examined whether when a plan is generated the actor may rely on internal models to determine which movement should be performed in order to achieve desired perceptual consequences (e.g., Kawato, 1999; Miall & Wolpert 1996). Despite the growing body of evidence for internal models underlying grasping (Quaney et al., 2005; Salimi, Hollender, Frazier, & Gordon, 2000) it is unclear how and whether the occurrence of these ‘anticipatory’ effects on hand shaping would reflect differences in cognitive planning of the subsequent action rather than merely the planning of object grasping at the end of the reach.

We addressed this question by asking participants to perform three tasks after reaching and grasping an object: (1) lift it up; (2) grasp the same object and place it carefully into a tight fitting niche or (3) place it in a large niche. We adopted the approach used by Santello and Soechting (1998) to quantify hand shaping during reach-to-grasp through the analysis of angular excursion of the joints of the digits. Their study revealed that the correlation between hand posture during reaching and hand posture at contact increased gradually and monotonically (i.e., hand shaping phenomenon, see Chapter 1).

The present study was designed to assess the extent to which the above phenomenon of gradual hand shaping during reaching is independent of object manipulation following contact. If context has no influence on hand shaping, we should find similar patterns of motion of individual digits during reaching to the *same* object regardless of the action following object contact. Conversely, if context has some influence on the phenomenon of hand shaping, planning different object manipulations should affect the gradual moulding of the hand.

Our main results are that the subsequent placement task had an effect on the motion of individual fingers during the reach towards the same object and on the reach duration. In particular, participants gradually shaped their hands only when planning object lift or when the end-goal required a great level of accuracy, i.e., object placement into the tight niche. Conversely, when the end-goal did not require accurate manipulation, i.e., object placement into the large box, hand posture used to grasp the object was attained early in the reach and did not change significantly during the reach. Last, reaches followed by object placement into the large niche were faster than reaches for the other conditions.

5.2 Methods

5.2.1 Participants

Ten participants (5 females and 5 males, ages 19-33) took part in the experiment.

5.2.2 Stimuli and apparatus

There were three types of grasping task. For the one object lift task we used a convex wooden object (see Fig. 5.1a). The object weighed approximately 100 g and was 12 cm high, 2.4 cm deep and 8 cm wide at the point of maximum convexity. The object was presented at 30 cm from the start location of the hand (Fig. 5.1b) and positioned such that participants could comfortably place their fingers and thumb on the convex sides of the object. The same object as for the object lift task was used for the two placement tasks (object placement following grasping; see below), and we used either a convex or a rectangular niche (Fig. 5.1a). The convex niche had the same shape as the object and was slightly larger than the object, i.e., 14 cm in height, 4 cm in depth, and 12 cm wide at the point of maximum convexity

(Fig. 5.1a). The size of the rectangular niche was much larger than the size of the object, i.e., 21 cm high, 4 cm deep, and 15.5 cm wide. (Fig. 5.1a). The two niches were positioned 6 cm from the object and at a small angle (~3°) relative to it (Fig. 5.1b).

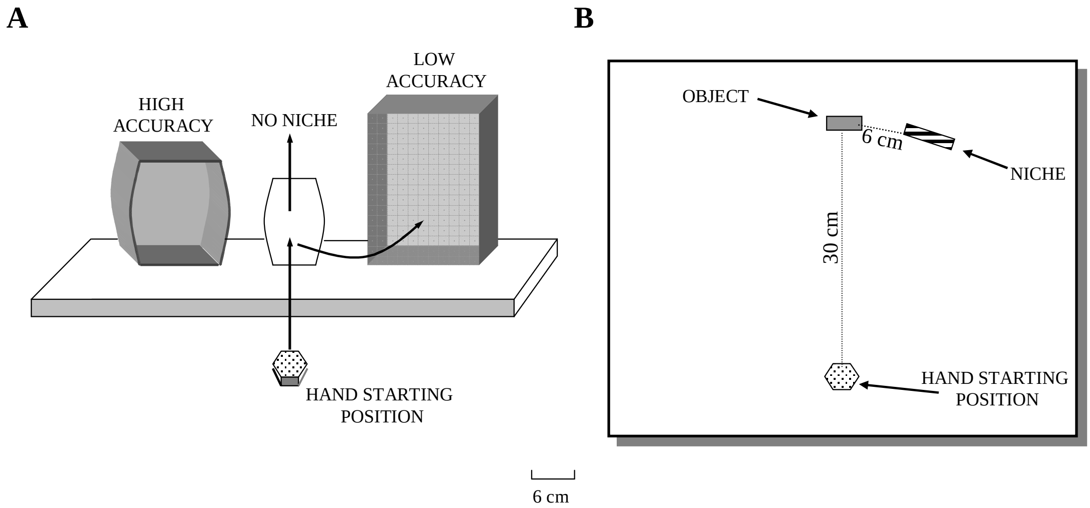

Figure 5.1 Panels A and B show the workspace (front and top view, respectively) and the three experimental conditions [no-niche is equivalent only to the object lift action (arrow direction)]. Although panel A shows both types of niches on both sides of the object, note that only one niche was presented for each block of trials.

5.2.3 Procedures

Participants were requested to perform the reach-to-grasp movement under three experimental conditions that varied depending on whether participants were asked to either lift the object (#1) or place it into a niche (#2 and #3), as well as on the high or low accuracy requirements of the placement task (#2 and #3, respectively):

1. No-niche. Reach to and grasp the object between the thumb and the four fingers of the right hand, followed by object lift and hold (Fig. 5.1a).

2. High accuracy. Reach to and grasp the object between the thumb and the four fingers of the right hand, followed by insertion of the object into the tight convex niche (Fig. 5.1a). The niche could be located to the right or to the left of the object.

3. Low accuracy. Reach to and grasp the object between the thumb and the four fingers of the right hand, followed by insertion of the object into the large rectangular niche (Fig. 5.1a). The niche could be located to the right or to the left of the object.

Each participant performed a total of 50 trials. Each experimental condition (no-niche, low accuracy/right, low accuracy/left, high accuracy/right, high accuracy/left) was presented in blocks of 10 trials. Order of blocks was counterbalanced between participants.

5.2.4 Data analysis

Due to technical problems, the data from one participant were excluded. The preliminary analysis performed on the remaining data, as to compare trials in which the niche was presented to the right or to the left, revealed no statistical difference. Consequently, trials for the left and right niche positions were collapsed. We carried out five repeated measures multivariate analyses of variance (MANOVAs) with experimental condition (no-niche, high accuracy, low accuracy) and time (from 10% to 100% of the reach, at 10% intervals) as within-subjects factors. The MANOVAs' model consisted of two joints (i.e., *mcp* and *pip*) for each finger separately to assess the modulation of their angular excursion in time as a function of experimental condition. We also performed linear regression analysis (Pearson's coefficient) between hand posture at different epochs of the reach and hand posture at contact to assess (1) at which time period(s) hand posture during the movement (from 10 to 90% of the reach) correlated significantly with hand posture at object contact (100% of the reach); and (2), whether the pattern of linear correlation (if any) changed across experimental conditions. Finally, a one-way ANOVA was performed to test for differences in the absolute duration of reaching movements as a function of experimental condition. Experimental condition (no-niche, high accuracy and low accuracy) was the within-subjects factor.

5.3 Results

This section is organised in four parts. In the first part, we present a qualitative description of how hand shaping occurred throughout the reach and across experimental conditions. In particular, we show how the patterns of motion of individual and pairs of digits were affected by the object placement task and its accuracy demands. In the second part, we describe the results of linear regression analysis to assess hand shaping during the reach and at object contact. In the third part we describe the MANOVA results to quantify statistically the effects of experimental condition on hand shaping. Finally, in the fourth part, we describe the results of the ANOVA on the effects of experimental condition on reach duration.

5.3.1 Qualitative description of hand shaping during reaching

Figure 5.2a-c shows representative kinematic data from one trial for each of the three experimental conditions (a-c). The traces depict the time course of motion at the *mcp* joints of each finger.

Figure 5.2 shows that for the no-niche and the high accuracy conditions (Figs. 5.2a and 5.2b, respectively) the pattern of angular excursion at the *mcp* joints of the four fingers was similar and differed from that obtained for the low accuracy condition (Fig. 5.2c). For the low accuracy condition, both the index and the middle fingers show a similar pattern of angular excursion. Similarly, both the ring and little fingers show a similar pattern of angular excursion, which differed from that obtained for the index and middle fingers.

Hand shaping to object shape occurs through pattern of covariations in the angular excursions of the joints (e.g., Santello et al., 1998; Winges et al., 2003). In the present study, we used the same object shape for all experimental conditions. Hence, if the task following grasping or its accuracy requirements do not affect hand shaping, the covariation patterns among finger joints should have been the same across all experimental conditions.

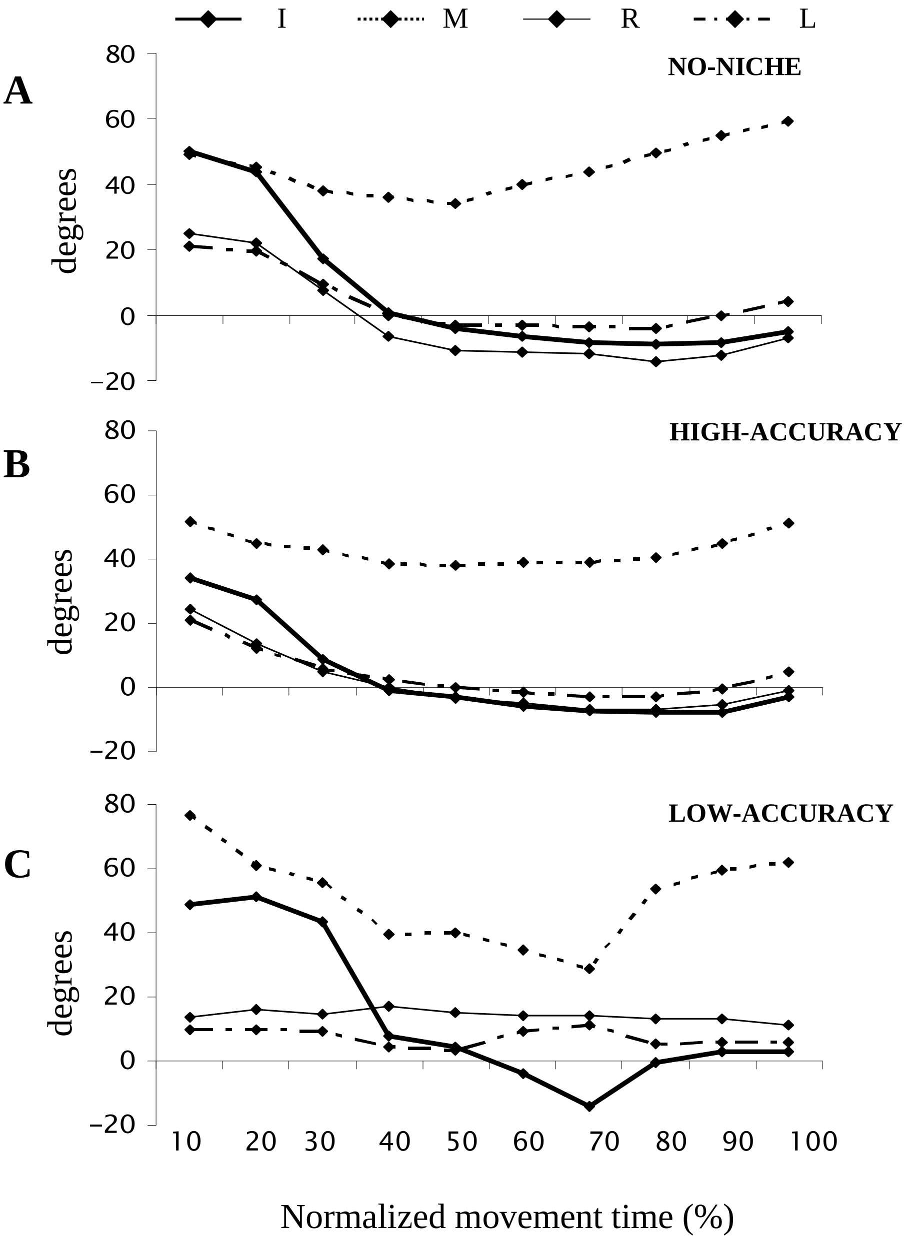

Figure 5.2 Each trace denotes angular excursion of *mcp* joints of the index (I), middle (M), ring R and little (L) finger (participant no. 7) during one trial (#1) performed in the no-niche, high accuracy, and low accuracy conditions (Panels A, B and C, respectively).

However, as shown in Figures 5.3, 5.4, and 5.5, we found that the requirements of the subsequent task elicited distinct patterns of angular covariation (data shown are from one trial of one participant).

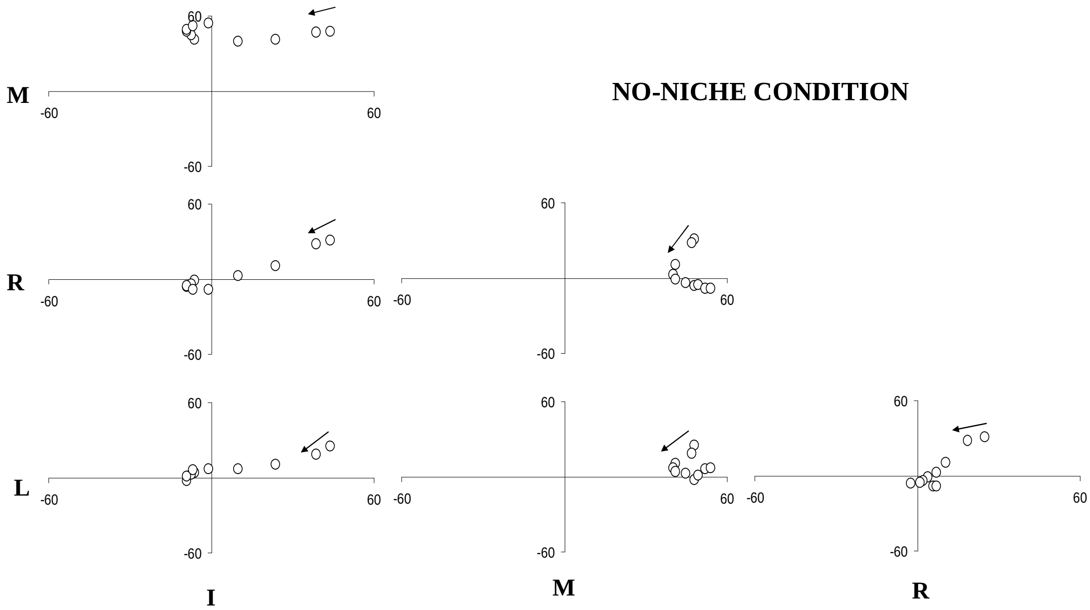

Figure 5.3 Covariations in angular excursion at the *mcp* joints among digit pairs are shown (I, M, R, and L denote index, middle, ring, and little fingers, respectively). The arrows indicate the direction of the covariation patterns from the beginning of the movement. The origin of the axes is 0°. Data are from a single trial (no. 3) from one participant (no. 1).

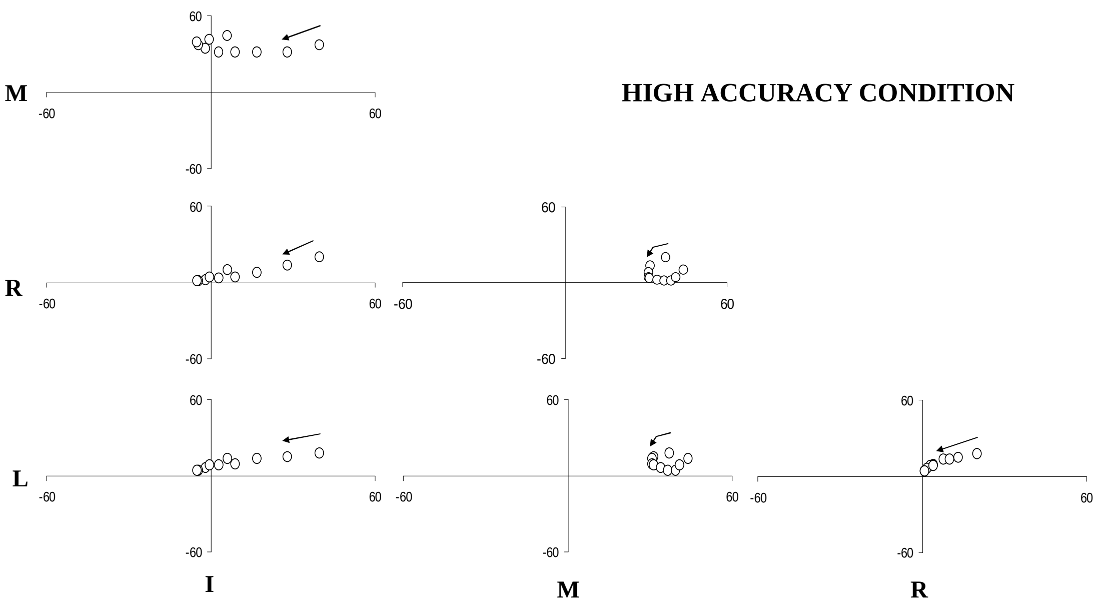

Figure 5.4 Same notations as in Figure 5.3.

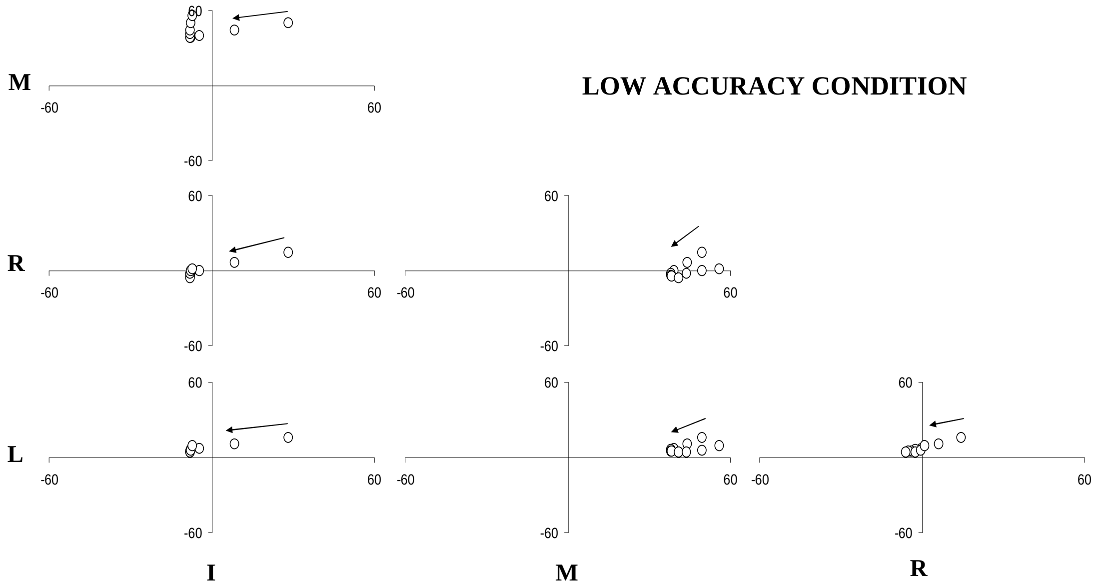

Figure 5.5 Same notations as in Figure 5.3.

For example, in the low accuracy condition, the finger combinations involving the ring finger were characterized by covariation patterns that were different from either the no-niche or the high accuracy conditions. The quantification of the effects of experimental condition on joint kinematics is presented below.

5.3.2 Correlation analysis

We found significant linear correlations between the posture of the hand during the reach and the posture of the hand at contact with the object for all three niche conditions. The level of correlation for the *pip* joint of the thumb, index and ring fingers was significant after 70% of movement duration (Fig. 5.6; first, second and fourth panel from the top right column, respectively).

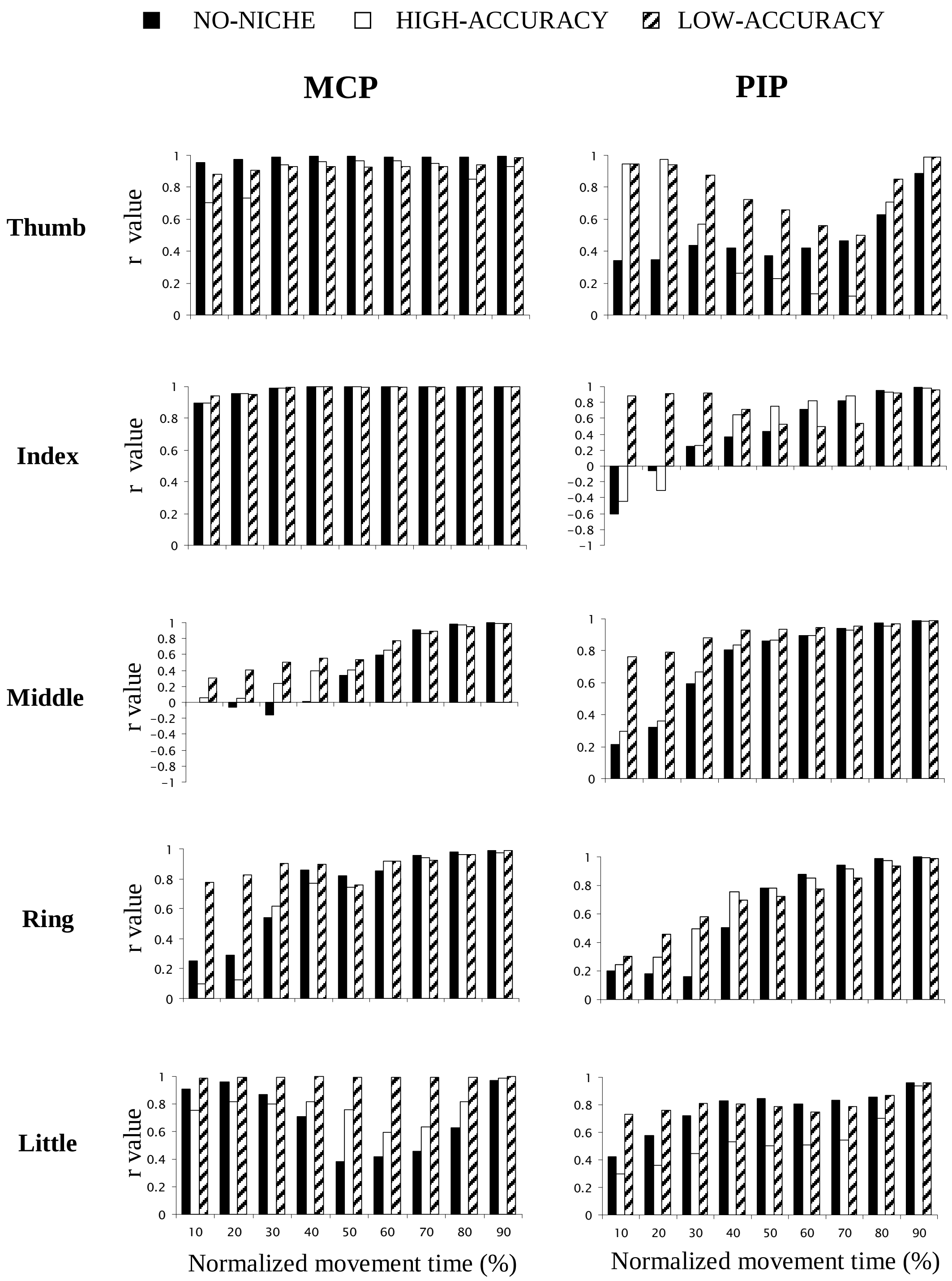

Figure 5.6 Each panel shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at contact. Data on the *left* and *right* columns are metacarpal (MCP) and proximal interpahlangeal (PIP) joint correlation coefficients, respectively. An r value > 0.797 is significant at $P < 0.01$.

A similar pattern was also found for the *mcp* of the middle finger (Fig. 5.6; third panel from the top left column). Similarly, for all conditions, the *mcp* of both the thumb and index finger showed a significant correlation from the very beginning of the movement that was maintained up to object contact (Fig. 5.6; first and second panels from the top left column). However, the time course of correlation during the reach also varied depending on the type of niche used for object placement. For example, in the *mcp* joint for the ring and the little finger (Fig. 5.6; fourth and fifth panels from the top left column) and the *pip* joint for the middle and little finger (Fig. 5.6; third and fifth panels from the top right column), the high level of correlation from the very beginning to the end of the movement was only found for the low accuracy condition.

5.3.3 Multivariate analysis of variance

As expected, there was a gradual moulding of the digits during the approach phase to the object. This behaviour was confirmed by MANOVA revealing a significant main effect of the factor 'Time' for all digits at both *mcp* and *pip* joints (see Appendix G). Although all fingers showed a specific pattern of angular excursion, for the no-niche and the high accuracy conditions these patterns remained similar. In contrast, for the low accuracy condition, ring and little fingers (Fig. 5.7; top and bottom raw, respectively) were characterized by a kinematic pattern that was different from that observed for the other two conditions. To date, the interaction between 'Time' x 'Experimental condition' was significant only for these two fingers (see Appendix G). In the low accuracy condition, the *mcp* and *pip* joints of the little finger were more extended within the first 30% of reach duration and more flexed during the remainder of the reach (≤80-90% of reach duration) relative to the other two conditions. For the same condition a similar pattern was also found for the ring finger (Fig. 5.7). However, the *mcp* joint of the little finger was the joint mostly affected by our experimental conditions (Fig. 5.7).

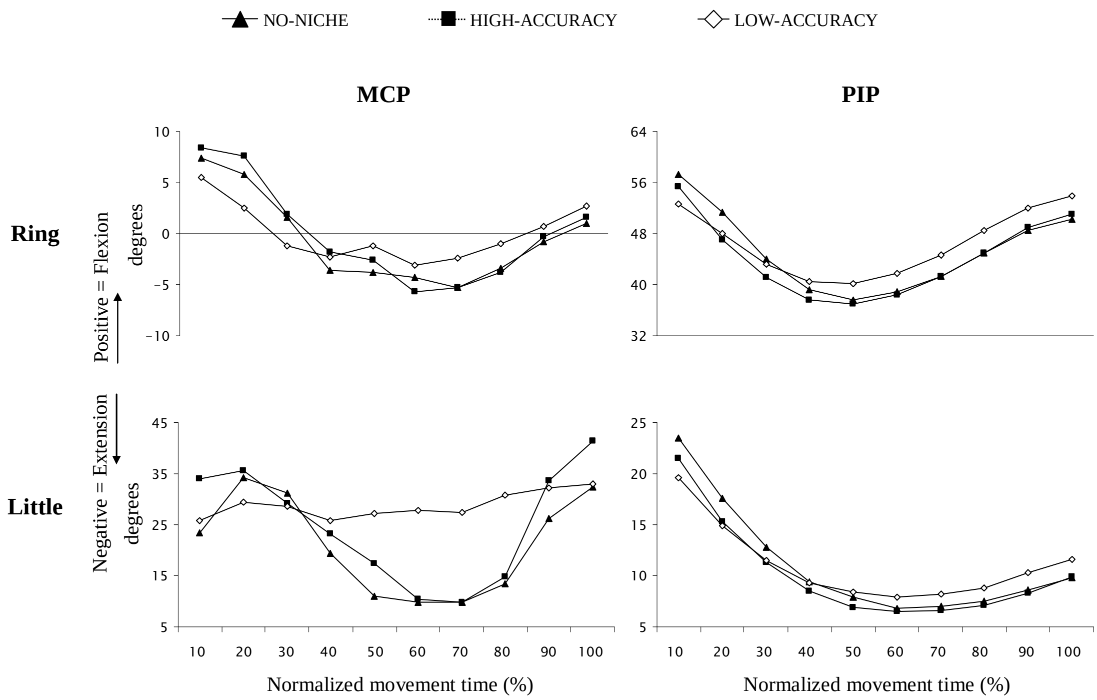

Figure 5.7. Angular excursion averaged across trials and participants for the metacarpal (MCP) and proximal interphalangeal (PIP) joint for the ring (top) and the little (bottom) fingers, respectively.

Both *mcp* and *pip* joints of index and middle fingers were not significantly affected by the experimental condition. Note that despite these across-condition differences in the time course of joint rotations, the hand configurations at object contact were very similar (see 100% on the *x*-axis; Figure 5.7). This evidence is supported by the lack of statistical effects when comparing both *mcp* and *pip* joints for each finger at the 100% interval for the three experimental conditions. Therefore, differences in hand shaping as a function of planned object manipulation did not result from planning different hand postures at contact with the object.

5.3.4 Reach duration

The duration of reaches was significantly affected by experimental condition ([$F_{(2,178)} = 12.98$, $P < 0.0001$]). Multiple comparisons revealed that movement duration was longer for the high accuracy than for the low accuracy niche condition (1129 vs. 918 ms; $P < 0.0001$). Furthermore, reach duration for the no-niche condition was longer than for the low accuracy niche condition (1064 vs. 918 ms; $P < 0.0001$).

To summarize, the type of task that followed object grasping affected preshaping of the hand during the reach, as revealed by effects on the joint angular covariation patterns and the time course of angular excursion of specific digits, i.e., ring and little fingers. Reach duration was also affected by experimental condition, as participants responded to the low accuracy condition with faster reaches than those to either grasp and lift or grasp and place the object into the tight niche.

5.4 Discussion

The aim of the present study was to investigate the effect of a subsequent task on finger posture during the execution of a reach-to-grasp movement. Our data revealed that the task to be executed following object contact elicited different patterns of coordination between the digits prior to object contact, thus leading to distinct patterns of hand shaping. The speed at which participants reached for the object was also affected by the type of experimental condition, with lowest accuracy constraints being characterized by the shortest reach duration. The effect of planned object manipulation was particularly clear when comparing object placement to be performed under high versus low accuracy constraints. Therefore, it appears that the temporal evolution of hand posture reflects how participants plan to manipulate the object following grasping.

5.4.1 Effects of planned object manipulation on hand shaping

The novel result of the present study is that we found differences in hand shaping depending on the accuracy demands imposed by the task following object contact, i.e., by the type of niche used for object placement. Note that the object to be grasped was the same for all experimental conditions, therefore differences in hand shaping cannot be ascribed to object geometry or to planning of different hand postures on contact with the object (final hand postures were not significantly different across experimental conditions). Therefore the present findings indicate that hand shaping was affected by planning the action following contact with the object. Specifically, it was the low accuracy niche that affected hand pre-shaping during the reach. When this type of niche was presented, participants configured the hand with respect to hand shape at object contact from the very beginning of the movement. In contrast, participants shaped their hand more gradually during the reach for the no-niche and high accuracy conditions.

A possible explanation for this effect is that planning of final hand configuration was affected by the interference between the shape of the low accuracy rectangular niche and the convex object to be grasped. As a result, participants may have adopted the strategy of an early shaping of the hand to bypass the incongruent shape information provided by the nearby low accuracy niche. In contrast, when the niche had the same shape as the object (high accuracy niche), the lack of potential conflict between the shape of the niche and the shape of the target object allowed for a gradual hand shaping similar to that found for the no-niche condition. This interpretation is supported by many studies showing that different objects in the visual field might compete in terms of their structure and dimension as well as in terms of the action they afford (for review see Castiello, 1999). Within this theoretical framework, grasping an object with the goal of putting it in a niche that has a different shape than the object itself might elicit the activation of a competing grasping pattern, with this interference affecting the modulation of hand shape during the reach.

5.4.2 Functional role of hand shaping for object grasping and manipulation

The above effects of object manipulation of hand shaping were particularly clear at specific digits. Specifically, motion of the ring and little fingers in the low accuracy condition was not characterized by the typical extension/flexion pattern described by many studies (e.g., Santello & Soechting 1998; Santello et al., 2002; Mason, Gomez, & Ebner, 2001; Winges et al., 2003) and found also in our no-niche and high accuracy conditions. In addition to a possible interference effect between the shapes of the object and the niche (see above), an alternative interpretation is that these digit-specific effects might reflect the functional role played by given digits during object transport following grasping.

Object lift and accurate placement of the object into a tight niche require accurate force coordination among all digits to prevent object slip and allow fine control of object position and orientation. In contrast, object placement into a large box might not require the same degree of accurate force coordination among the digits, as the object can be inserted without paying too much attention to its orientation relative to the shape and size of the niche. It follows that, when accuracy constraints are low, some digits might not be fully engaged in grasping the object. The lack of gradual extension and flexion of the ring and little fingers might result from the fact that accurate placement of ring and little fingers may not need to be specified as precisely as those for other digits - i.e., thumb, index and middle fingers. Note, however, that this interpretation is based on two assumptions: (1) that forces exerted by the ring and little fingers were different in the high vs. low accuracy conditions; and (2) that the functional role of hand shaping is to enable accurate placement of fingertips on the object. Further work is needed to determine the functional role of hand shaping in relation to accurate placement of contact points and force control.

It remains to be explained why a similar pattern was found for the no-niche and the high accuracy conditions. Tentatively we suggest that in both the no-niche and the high accuracy conditions gradual preshaping is related to the need for fine control of object position and orientation, both requirements being important for object lift and object placement in the tight niche. In contrast, the low accuracy condition might not impose the same degree-of-accuracy requirement in finger placement on the object. In this case, the lower accuracy demands of placing the object in a large niche might release the constraints of anticipatory adjustments of hand shape in preparation for the end-goal. Another possible explanation for the similarities between no-niche and high accuracy conditions relies on the observation (post-hoc) that the no-niche condition might also impose significant accuracy requirements. Specifically, in the no-niche condition, participants were instructed to lift the object and replace it on to the same area from which it was lifted (though no specific instructions in terms of accuracy were given to the participants). As the area encompassing the pressure switch was identical to the base area of the object, it might well be that precision constraints implicitly arose for the no-niche condition.

5.4.3 Effect of object manipulation on the coordination between hand transport and shaping

Our reach-to-grasp task consisted of two synergistic movements: transporting the hand to the object and modulating hand shape. We found that planned object manipulation affected not only the fine regulation of finger motion but also the reach component. Specifically, we found that participants showed slower movements for the high accuracy than for the no-niche and the low accuracy condition. The shorter movement for the low accuracy than for the no-niche condition confirms the observations made by Gentilucci and colleagues (1997), who found shorter movement durations when participants grasped and placed objects onto a target versus when objects were merely grasped and lifted. Furthermore, the longest movement duration, found for the high accuracy conditions seems to suggest that this effect was modulated by the accuracy demands of the subsequent task. In general, our results seem to be consistent with the notion that when two motor acts have to be performed sequentially, planning of the subsequent action can influence the execution of the first action.

Note that object placement for the high accuracy condition also affected reach duration such that participants approached the object with slower reaches compared to those in the low accuracy condition. We would like to point out that these slower reaches were also accompanied by a more gradual moulding of the hand to object shape (see above). As the whole reach-to-grasp movement was affected in a similar fashion by the accuracy demands of object manipulation, we conclude that both components of the movement are planned as a unit. Furthermore, we conclude that slower reaches might allow a more precise modulation of hand posture that takes into account not only the geometry of the object (i.e., the grasping component), but also the subsequent task.

5.4.4 Planning sequential manipulative actions

Overall, our findings indicate that reach-to-grasp movements and object manipulation are not planned in isolation, as different patterns of hand shaping and movement duration were found when participants planned different actions after contact with the object. Such modulation of motor commands as a function of anticipated interaction with the object suggests the use of a forward internal model (e.g., Kawato, 1999; Miall & Wolpert, 1996). Consistent with the forward model hypothesis, the degree of flexion for specific fingers and the duration of the reach-to-grasp movement differed significantly between types of niche, despite the fact that reaches were performed under identical circumstances.

When the task is to reach for and transport an object to a new location, a forward model of the arm's dynamics would use information about the current state of the arm to predict the motor commands necessary to update the 'new' state at later stages of the movement. This new state would consist of hand postures throughout the reach necessary to perform the desired end-goal, i.e., hand configuration at contact with the object or during object manipulation. Thus a forward sensory model could be used to predict the sensory consequences associated with the planned movement. During the actual execution of the movement, feedback mechanisms might also be incorporated to monitor progress toward the end-goal state by comparing predicted and actual sensory information and making on-line adjustments to the motor command as needed.

The fact that a more accurate subsequent movement affects hand shaping suggests that the context effects were related to the intention to perform a subsequent action that involves precise requirements. Thus in conditions where the precise task demands are more explicit at the beginning of the trial, predictions arising from this model allow participants to represent the entire movement sequence in advance to its execution. Specifically, the goal of fitting the object is specified by the requirement to place the object through a niche of specific dimensions at a known location in the workspace. Consequently the movements required to complete the action can be accurately predicted by a forward model soon after the start of the trial and planned in unison as coordinated components of the larger action sequence.

A forward model may account for the patterns of task-specific covariation patterns in the motion of the digits that emerge as the hand approaches the object. For example, motion of the ring and little fingers are 'decoupled' from motion of other digits after 30% of reach duration, but only for the low accuracy condition. Thus it might well be that the current state of the arm is influenced by predicting the future state of the arm, i.e., optimal configuration of the hand to perform the planned subsequent task. This new information determines the implementation of a novel optimal posture that minimizes the use of those fingers that are not functionally important or that might even interfere with accurate object manipulation. It is reasonable to assume that for our task, the index and middle finger, together with the thumb, might be the most relevant digits for dexterous hand-object interaction.

In this connection, the present results may fit with the idea that multiple effector and object internal representations may be used during the anticipatory control of grasping movements (Quaney et al., 2005; Salimi et al., 2000; see also Wolpert, Goodbody, & Husain, 1998).

In effector terms, Salimi and colleagues (2000), based on their examination of anticipatory control of fingertips forces during grasping based on the center of mass (CM) of a manipulated object, proposed two levels of representation: one concerned with the object's overall weight and texture, and one concerned with object's weight distribution or texture at each digit.

In object-based terms, Quaney and colleagues (2005) examined whether object information during one prehension task is used to produce fingertip forces for handling the same object in a different prehension task. They demonstrated that the object representation that scaled lift force was not available to scale grip force. All in all, these findings suggest that multiple internal representations may be used during anticipatory control of grasping, which include object features and the forces used during manipulatory experiences. Our results add to these notions, suggesting that possible effector and/or object representations are modulated by the perceptual consequence of a motor plan.

6. An object for an action, the same object for other actions: effects on hand shaping[5]

Abstract

Objects can be grasped in several ways due to their physical properties, the context surrounding the object, and the goal of the grasping agent. The aim of the present study was to investigate whether the prior-to-contact grasping kinematics of the same object varies as a result of different goals of the person grasping it. Participants were requested to reach towards and grasp a bottle filled with water, and then complete one of the following tasks: 1) grasp it without performing any subsequent action; 2) lift and throw it; 3) pour the water into a container; 4) place it accurately on a target area; 5) pass it to another person. The results showed that the presence and the nature of the task to be performed following grasping affect the positioning of the fingers during the reaching phase. We contend that a one-to-one association between a sensory stimulus and a motor response does not capture all the aspects involved in grasping. The theoretical approach within which we frame our discussion considers internal models of anticipatory control which may provide a suitable explanation of our results.

[5] *Published*: Ansuini, C., Giosa, L., Turella, L., Altoè, G., & Castiello, U. (2007). An object for an action, the same object for other actions: effects on hand shaping. *Experimental Brain Research,* Epub ahead of print.

6.1 Introduction

While Napier's model (1956) highlighted the importance of action goals in determining different prehension patterns (see Chapter 1), there has been little research on the role played by intention on how actors shape their hands while reaching towards an object.

For instance, Eastough and Edwards (2007) showed that knowledge of the weight of a to-be-grasped object can affect prior-to-contact grasp action kinematics and the placement of the fingers upon the object. Heavy, as compared to light, objects caused increased PGA and a final finger and thumb placement on the object that more closely passed through the object's centre of mass. The influence of different consecutive movements on initial reaching and prehension movement was also examined by Armbrüster and Spijkers (2006). They considered four after-grasp movements differing in direction and accuracy requirements: lifting, raising, throwing, and placing. Their results showed that movement parameter values were affected by the type of subsequent movement. Specifically, peak aperture was larger and peak deceleration was higher when the grasp was followed by either a throwing or a placing movement than by the lift and raise conditions. These findings suggest that the reason why an object is grasped has an effect on initial prehension kinematics. As reported in Chapter 5, we added a level of complexity to this analysis by not only investigating the grasp component at the level of two-digit kinematics (i.e., index finger and thumb) but also by considering whether the angular excursion of individual fingers varied depending on the accuracy requirements of the action that follows the grasping of the object (Ansuini, Santello, Massaccesi, & Castiello, 2006). By asking participants to grasp the same object and either lift it and fit it into a tight or a large niche, it was shown that the degree of end-goal accuracy did affect hand shaping during the approach phase (Ansuini et al., 2006).

Altogether, the above mentioned results strongly suggest that human hand movements are associated with the action end-goal. However, in order to shed more definite light on this issue, a paradigm is needed that addresses two questions which so far have remained untested. First, whether hand shaping varies depending on the presence or absence of an action beyond grasping. The second, and interconnected question, is whether what occurs beyond grasping elicits specific patterns of hand shaping. Findings from previous studies do not answer these questions because subsequent action and end-goals were only varied along one dimension (e.g., accuracy) within the same class of tasks.

We addressed these questions by asking participants to perform five tasks involving the same object: grasp it; grasp and throw it into a container; grasp and place it accurately on a base matching its diameter; grasp and pour the water inside the object into a container; and grasp and put it into the hand of an another person. The rationale for choosing these particular tasks was the following: the grasp condition served as a baseline to identify the 'beyond grasp' effect. The passing and placing actions were accurate conditions which differed in terms of the after-grasp movement direction. The throwing action represented an example of a low-accuracy condition. Finally, the pouring action was considered as it implies a wrist rotation which added a level of complexity in terms of planning.

The effect of the a-specific presence of an action beyond grasping will be revealed by the comparison between hand shaping for the grasping task and the tasks involving a subsequent action. Any specific 'beyond grasping' effects will be revealed by comparing hand shaping across tasks including subsequent actions.

6.2 METHODS

6.2.1 Participants

Twenty participants (10 females and 10 males, ages 20-30) took part in the experiment.

6.2.2 Stimulus and apparatus

The target object was a plastic bottle filled with 350 ml of water and located at 30 cm from the hand starting position (Figure 6.1). The target object was placed on a pressure switch embedded within the table surface and located at 35° to left of the hand starting position (see Fig. 6.1).

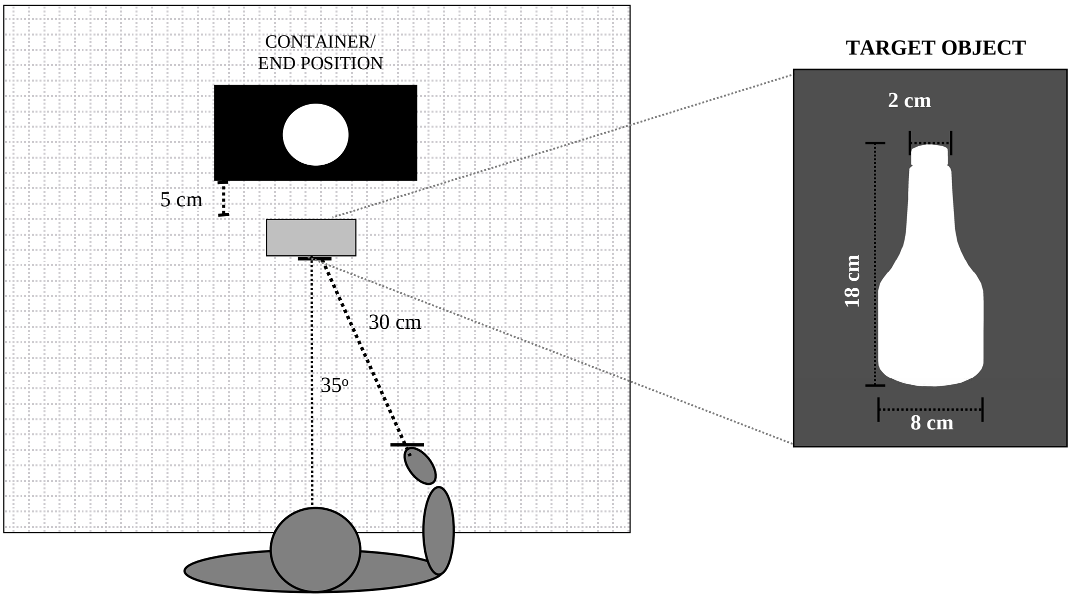

Figure 6.1 Top view of the experimental setup (not to scale) and the object used as a target.

6.2.3 Procedures

Participants naturally reached towards and grasped the target object. This task had to be performed under five different experimental conditions:

1. 'Grasp' condition. Participants were requested to reach towards and grasp the target object. No further action was requested.

2. 'Throw' condition. Participants were requested to reach towards, grasp the target object, lift it and throw it into a cardboard container (depth = 19 cm; width = 30 cm; height = 9

cm). The container was located on a 23 cm high platform (depth = 21 cm; width = 33 cm). This platform was placed 5 cm behind the base of the object (see Fig. 6.1).

3. ‘Place’ condition. Participants were requested to reach towards, grasp the target object, lift it, and place it precisely within a drawn circle perfectly matching the diameter of the base of the bottle. The circle was drawn at the centre of the top of the container (Fig. 6.1). The container was the same used for the ‘throw’ condition.

4. ‘Pour’ condition. Participants were requested to reach towards, grasp the target object, lift it and pour the water into a plastic container. The object was re-filled after each trial as to maintain the same weight for all conditions.

5. ‘Pass’ condition. Participants were requested to reach towards, grasp the target object, lift it and pass it to the experimenter.

The centroid of the location at which we located the cardboard container (condition #2), the circle (condition #3), the plastic container (condition #4), and the experimenter’s hand (condition #5) was kept constant across conditions. A block of 50 experimental trials, which included 10 trials for each of the five experimental conditions, was administered. Trials of different types were randomized within the block. Before the start of each trial, participants were informed about the action to be performed and a block of ten practice trials (two examples for each type of experimental condition) was administered. To avoid fatigue and lack of concentration/attention, participants were given a pause every 10 trials.

For all conditions, except that for the 'grasp' condition, reach duration was calculated as the time interval from the release of the starting switch and the time at which the switch underneath the target object was released (see Chapter 2). For the 'grasp' condition, which did not imply a subsequent action, reach duration was determined off-line as the time at which at least ten over the fourteen recorded sensors remained stationary for at least five temporal samples.

6.2.4 Data analysis

To test for possible differences in reach duration as a function of experimental condition an analysis of variance (ANOVA) with 'Functional Goal' ('grasp', 'throw', 'place', 'pour', 'pass') as within-subjects factor was performed. To assess how and to what extent the angular excursion at the analyzed joints for each digit differed across experimental conditions, relative values for the dependent measures of interest were entered into ten repeated measures ANOVAs, one for each of the two joints (i.e., *mcp* and *pip*) for each digit separately. The within-subjects factors were 'Functional Goal' ('grasp', 'throw', 'place', 'pour', 'pass') and 'Time' (from 10% to 100% of the reach, at

10% intervals). Similar analyses were conducted to ascertain the effect of the experimental condition on each of the considered abduction angles (i.e., thumb-index, index-middle, middle-ring, and ring-little fingers).

6.3 RESULTS

6.3.1 Reach duration

As depicted in Figure 6.2, reach duration was significantly affected by both the presence and the type of action following grasping (i.e., main effect of 'Functional Goal', [$F_{(4,76)} = 163.374$, $P < 0.0001$]).

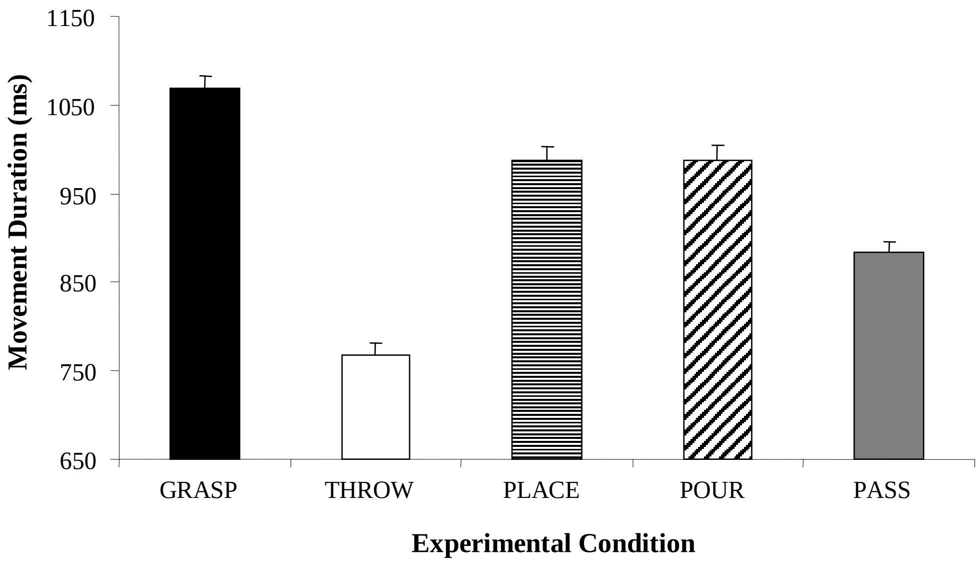

Figure 6.2 Reach duration in milliseconds (ms) for the five experimental conditions. Bars represent standard error of the means.

In first instance, when a subsequent action was not requested (i.e., 'grasp' condition) reach duration was longer than for all the other conditions (1068 ms; $P_s < 0.05$; see Fig. 6.2). In second instance, except for the comparison between the 'pour' and the 'place' conditions, significant differences were found when comparing reach duration across the other conditions ($P < 0.05$; Fig. 6.2). As depicted in Figure 6.2, the shortest reach duration was associated with the 'throw' condition (768 ms). The 'pass', the 'place', and the 'pour' conditions were significantly longer than the 'throw' condition (883, 988, and 988 ms, respectively; $P_s < 0.05$). However, similar values were found for the 'place' and the 'pour' conditions ($P > 0.05$).

6.3.2 Angular excursion at individual fingers' joints

The ANOVAs performed on the angular excursion at individual fingers' joint revealed a significant interaction 'Experimental Condition' by 'Time' for both *mcp* and *pip* joints of all digits (see Appendix H). Indeed, the posture assumed by individual fingers' joint during reaching was significantly affected by both the presence and the type of subsequent actions. In particular, an effect due to the presence of a subsequent action was evident from 20% up to 50% of reach duration for both *mcp* and *pip* joints for all digits (see Figure 6.3). As depicted in Figure 6.3, both *mcp* and *pip* joints for all digits were more extended for the 'grasp' than for the other conditions. However, after 50% of reach duration, an inversion of this pattern was particularly evident for both *mcp* and *pip* joints of the thumb and the index finger and for the *mcp* joint for both the middle and the ring fingers (see Fig. 6.3). At these joints a greater flexion was found for the ‘grasp’ than for all remaining conditions.

Differences depending on the type of subsequent actions were evident when comparing the ‘pour’ condition with the ‘place’, the ‘pass’ and the ‘throw’ conditions. As shown in Figure 6.3, it is only after 60% of reach duration that the *pip* joint for both the middle and the ring fingers were more extended for the ‘pour’ than for the ‘place’, the ‘pass’, and the ‘throw’ conditions. During the first half of the movement the angular excursion of these joints did not significantly differ for the ‘pour’, the ‘place’, the ‘throw’, and the ‘pass’ conditions (see Fig. 6.3).

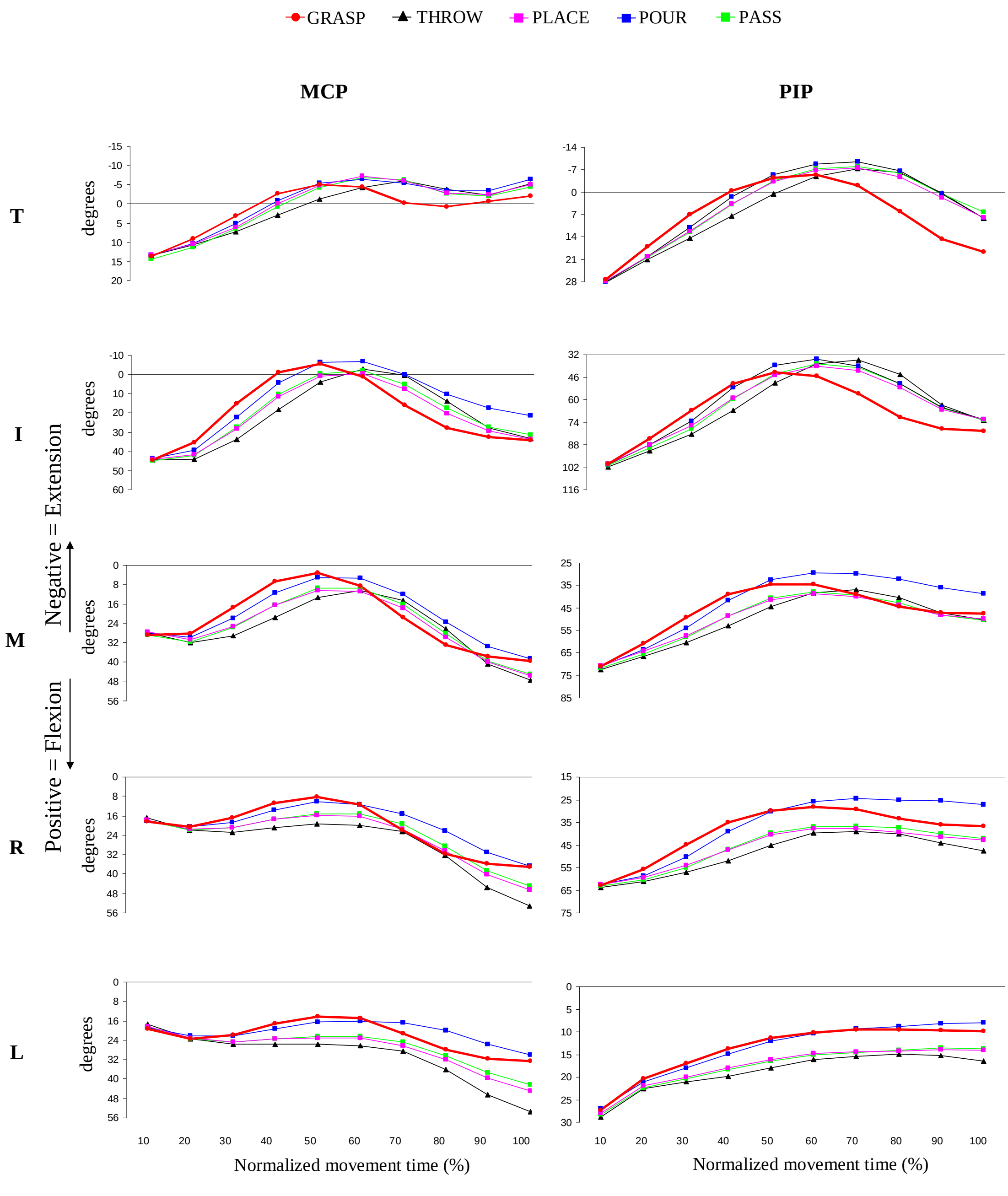

Figure 6.3 Each trace depicts angular excursion of both metacarpal (MCP) and proximal interphalangeal (PIP) joint (left and right columns, respectively) of thumb (T), index (I), middle (M), ring (R), and little (L) fingers for all experimental conditions. Data are averaged across trials and participants.

6.3.3 Abduction angles of adjacent digit pairs

The ANOVAs performed on the abduction angles for adjacent digit pairs revealed that the interaction 'Experimental Condition' by 'Time' was significant for the thumb-index, index-middle, middle-ring, and ring-little digits' abduction angles (see Appendix I). For these measures an effect of the presence/absence of a subsequent action was evident on the abduction angle between the thumb and the index finger. Specifically, from the beginning (i.e., 20%) up to the end of reach duration, the abduction angle between these two digits was larger for the 'grasp' than for the other conditions (see Figure 6.4a).

A specific effect concerned with the type of subsequent action was evident for the index-middle and middle-ring fingers' abduction angles. In particular, from 50% up to the end of reach duration (i.e., 90-100%), these angles were larger for the 'throw' than for the other conditions (see Fig. 6.4b-c). On the contrary, these angles showed no differences across conditions from the beginning up to 40% of the reach duration (see Fig. 6.4b-c). Finally, no significant differences were found for the ring-little fingers' abduction angle depending on experimental conditions (see Fig. 6.4d).

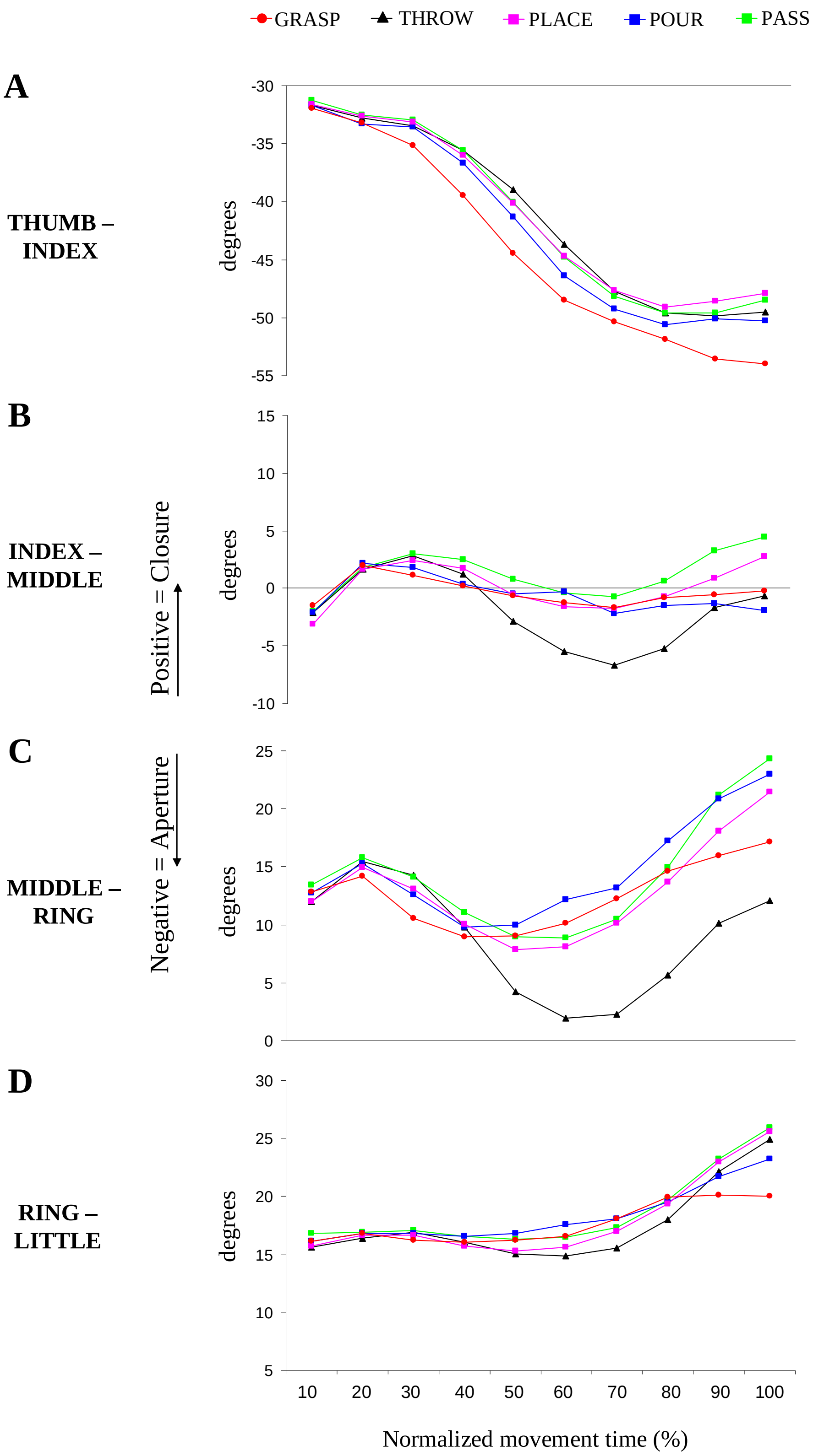

Figure 6.4 The time course of angular distance between thumb-index (Panel A), index-middle (Panel B), middle-ring (Panel C), and ring-little fingers (Panel D), respectively for each experimental condition. Data are averaged across trials and participants.

6.4 Discussion

We set out to investigate whether grasping kinematics is sensitive to both the presence and the type of action following a reach-to-grasp movement towards the same object. Results indicate that temporal and angular aspects of performance are strongly modulated by the purposive component driving the action. These findings extend current grasping literature in two important ways. First, in contrast to previous research which has mainly focused on grasping *per se* – a quite atypical behaviour, given that grasping is normally followed by some other actions – we designed a series of tasks which allow to specifically investigate the effects of end-goal on the planning and execution of reach-to-grasp movements along different dimensions. Second, rather than limiting our analysis to thumb-index finger separation, which may provide a limited amount of information, we considered kinematics at the level of individual finger joints (see Chapter 1).

6.4.1 The effect due to the presence of an action following grasping

When there was no action beyond grasping, reach duration was longer than when the closing of the fingers upon the object represented the starting point for a subsequent action. This result is in agreement with previous evidence suggesting that when the goal of a reach-to-grasp movement encapsulates a subsequent action, the duration of the 'first' movement is shorter than when no subsequent action is requested (e.g., Gentilucci et al., 1997). A possible explanation for this effect might be found in the relationship between the time course of the deceleration phase and the online integration of sensory feedback. For instance, it has been shown that when an actor intends to grasp an object and no transportation movements are requested thereafter, reach duration is longer with respect to the condition in which transportation movements are requested (Johnson-Frey, McCarty, & Keen, 2004). Therefore it might well be that reach duration is longer for the 'grasp' condition because the movement necessary to achieve the intended goal (i.e., grasping) is not specified by the dynamic constraints of the task, causing participant to rely more heavily on sensory feedback.

With respect to hand posture during reaching, the beginning of opening and closing phases was earlier for the 'grasp' condition than for the other conditions. This time shift may signify that the end-point is taken into account: when no subsequent action is requested the end-point location is nearer than when a subsequent action has to be performed. In this respect, many reach-to-grasp studies have consistently reported that parameters concerned with the grasp component are sensitive to object distance (e.g., Gentilucci et al., 1991; Jakobson & Goodale, 1991). For instance, the time of PGA is brought forward for farther objects (Jakobson & Goodale, 1991). Although in the present study object distance was not varied, it might be hypothesized that when planning kinematic parameterization, it is the end-point 'distance' rather than the object distance which may be taken into account.

An effect on the thumb-index finger abduction angle was also revealed. This angle was greater for the 'grasp' than for the other conditions. The absence of a subsequent action implies that no or little force production is needed as to counteract the tangential pull of gravity during the lifting of an object. Since the thumb and index finger have a larger force production capability than the other digits (Kinoshita, Kawai, & Ikuta, 1995), these two digits and their contact points on the object might have been functionally less important (and therefore planned more liberally) when no subsequent action was requested. Support for this hypothesis comes from recent findings indicating that the spatial distribution of digit contact points on the to-be-grasped object is modulated according to the force requirements being implicit in the manipulation following object grasp (Lukos, Ansuini, & Santello, 2007).

An alternative account which may explain the differences in kinematics for the conditions involving a subsequent action with respect to the 'grasp' condition is concerned with the direction of gaze during these trials. Human gaze behaviour has been studied in various dynamic activities, including natural manipulation (Land, Mennie, & Rusted, 1999; Smeets, Hayhoe, & Ballard, 1996; Johansson, Westling, Backstrom, & Flanagan, 2001). For instance, Johansson and colleagues (2001) investigated where participants direct their gaze in a natural manipulation task in which they grasped and moved a bar to a target and then returned the bar to the support surface. Participants directed gaze almost exclusively toward objects involved in the task. Furthermore, participants fixated certain landmarks associated with these objects. Importantly, it appeared that gaze marked key positions to which the fingertips on grasped objects were subsequently directed (actual and potential contact points). Thus, the salience of potential gaze targets was largely determined by the demands of the sensorimotor task. Although we were unable to monitor gaze direction during the present tasks, it might well be that for the 'grasp' condition gaze worked less selectively in anchoring thumb and index finger contact points whose determination would have been more important for the conditions which imply object transportation.

6.4.2 The effect of the type of action following grasping

What is to occur beyond the grasping of an object did have a specific effect on reach duration. In particular, the progressive shortening of reach duration for the 'pour', 'place', 'pass', and 'throw' conditions, respectively, may reflect the degree of accuracy associated with the action goal. In this respect, it is well-known that reach duration increases when accuracy increases (Fitts, 1954; Bootsma et al., 1994). Although this effect has been classically demonstrated by varying object size, it has also been noticed by varying the accuracy constraints related to the action end-goal. This explanation is consistent with previous findings showing that reach duration was longer when the same object, once grasped, had to be fit in a similar sized opening rather than thrown within a larger container (Marteniuk et al., 1987).

When considering fingers' angular excursion, both the middle and the ring fingers were more extended when the bottle was grasped for pouring than to accomplish the other goals considered here. This result might reflect the need to balance the counterclockwise external torque dictated by the wrist rotation component embedded in the pouring action. To do so, some digits will generate antagonist moments (i.e., assisting the external torque) and some others will generate agonist moments (i.e., resisting to the external torque) (Gao, Latash, & Zatsiorsky, 2006). According to the definition provided by Zatsiorsky, Gao and Latash (2003), the agonist moment would be supplied by the "peripheral" fingers (i.e., index and little fingers) and the antagonist moments by the "central" fingers (i.e., middle and ring fingers). In this perspective the bigger extension of the middle and the ring fingers (i.e., "central finger" fingers) found in the present study might represent the kinematic anticipation of this forward dynamic need.

Finally both the index-middle and the middle-ring abduction angles were larger for the 'throw' than for the other conditions. For the throwing action, bigger distances for index-middle and middle-ring abduction angles might be either an index of low accuracy or the need to exert more force as throwing may require. Altogether, these findings indicate that the CNS stipulates sensorimotor programs that specify both the required fingertip actions and the expected sensorimotor consequences associated with different end-goals. The development of such differential sensorimotor programs dependent upon end-goals supports predictive, anticipatory motor control mechanisms in manipulation as outlined below.

6.4.3 Anticipatory control of motor sequences

The ability to predict the consequences of our own actions relies on the use of internal models. Internal models are neural mechanisms that can mimic the input/output characteristics, or their inverse, of the motor apparatus (Kawato, 1999). Internal models by which the CNS represents the causal relationship between actions and their consequences (i.e., motor-to-sensory transformation) are called forward models. Internal models by which the CNS implements the transformation from the desired consequences to actions (i.e., sensory-to-motor transformation) are called inverse models (Wolpert & Ghahramani, 2000). As the inverse internal models can provide the motor command to achieve some desired state transition, they are well suited to act as controllers (Wolpert & Kawato, 1998). Within this theoretical framework, a modular structure has been proposed in which multiple inverse models exist to control the system and each one is paired with a corresponding forward model. Each paired forward and inverse model forms a module together with a responsibility predictor (RP). The RP allows the system to switch between modules prior to generation of a motor command and evaluation of its consequences. The RP switches between modules on the basis of contextual information that could be (among other things) a sequence of movement elements (Kawato, 1999). The RP concept might be useful in explaining the present results. That is, the RP may provide an a priori probability for the selection of a unique module which corresponds to the goal of the actions used here or to two modules, one for the reach-to-grasp action and one for the subsequent action. Although both proposals may provide a suitable explanation for the present results, we are tempted to suggest that the 'two modules' hypothesis may fit the present data better. This is because it might well be that multiple internal models can be mixed in an adaptive way when necessary and when dealing with an environment in which both transformation are present (Ghahramani & Wolpert, 1997; Flanagan, Nakano, Imamizu, Osu, Yoshioka, & Kawato, 1999). To translate this theoretical framework within the context of our experiment it might well be that the CNS may combine internal models relative to the sensorimotor transformations characterizing the two steps of the action (i.e., reach-to-grasp and the task following it) considered here – one concerned with the reach-to-grasp movement, the other concerned with the subsequent action. Importantly such an ability of the motor system to integrate different modules would make it able to generate a vast repertoire of motor behaviours by mixing the outputs from the different modules such that the final output reflects the relative and weighted contribution of each one for the attainment of the overarching goals guiding action.

7. Breaking the flow of action[6]

Abstract

The present study aimed at investigating whether the execution of a motor act changed when its temporal structure is altered. Participants were requested to reach and grasp an object and pour its content. This task was performed under two conditions: a 'continuous pouring' condition, in which participants were instructed to execute the action fluently. An 'interrupted pouring' condition in which participants were instructed to reach and grasp the object, wait for an acoustic signal and then complete the pouring action. A control condition in which participants were requested to reach and grasp the object without performing any subsequent action was also administered. Instructions regarding the type of action to be performed were given at the beginning of each trial. The measures relevant to test the specific experimental hypothesis were reach duration and the thumb-index finger abduction angle. Results show that both these measures varied depending on temporal relationship between the two sub-movements composing the action (i.e., reach-to-grasp the object and lift-to-pour its content). These results are interpreted in light of current theories suggesting that the CNS might use time-locked strategies when a skilful movement has to be planned and executed.

[6] *Under review*: Ansuini, C., Grigis, K., & Castiello, U. Breaking the flow of action. *Cognition*.

7. 1 Introduction

In everyday life we often use objects in tasks involving a motor sequence. The act of reaching towards and grasp a bottle might represent the first phase of a motor sequence which can end in different ways. For instance, the bottle can be grasped with the intent to pour its content as well as to bring it to the mouth for drinking. In this respect, it has been shown that the overarching (end-) goal of the action determines the global organization of the motor sequence. In other words, a reach to grasp movement towards the very same object might be performed in different manners depending on the use one wants to make of it (Ansuini, Giosa, Turella, Altoè, & Castiello, 2007; Armbrüster & Spijkers, 2006) (see Chapters 5 and 6).

The existence of such differential sensorimotor programs depending upon end-goals supports the notion of anticipatory motor control mechanisms. In particular, it has been hypothesized that the motor control system makes use of internal model as to anticipate the consequences of our own actions (see Chapter 6 'Discussion' section). According to the 'internal model' approach, the brain contains multiple internal models that can be conceptually regarded as motor primitives, the building blocks used to construct motor behaviours (Wolpert & Kawato, 1998). In this perspective, each single phase of a motor sequence is learned by a separate module in the brain and that the CNS would combine internal models of previously learned sensorimotor transformations when dealing with an environment in which these transformations are present (Kawato, 1999; Blakemore, Wolpert, & Frith, 1998).

Here we test whether the motor system ability to combine different steps of a coordinated action is affected by imposed delays in between steps. To this end, we ask participants to perform the very same action upon the very same object under three different experimental conditions characterized by a diverse temporal structure. A 'continuous pouring' condition, in which participants were requested to reach and grasp an object and pour its content within a container. An 'interrupted pouring' condition, in which participants were requested to reach and grasp the object, and then wait for an acoustic signal as to complete the action. A 'control' condition in which participants were requested to reach and grasp the object, but not to perform any subsequent action. The comparison between the 'continuous pouring' and the 'interrupted pouring' conditions should reveal whether interrupting the flow of action prevents the motor system from 'combining' the sensorimotor transformation necessary to achieve the overarching functional end-goal. The comparison between the 'interrupted pouring' and the 'control' conditions would allow to determine (i) whether they elicit a similar motor response independently from the presence or absence of a subsequent action step and (ii) whether knowledge by the participants that for the 'interrupted pouring' condition maintaining the hand stationary on the object is a temporary event, would lead to a kinematic pattern which differ from the 'control' condition. Remember that both the 'interrupted pouring' and the 'control' condition require to participants to maintain the hand stationary upon the object (though for different periods of time).

7.2 Methods

7.2.1 Participants

Eight right handed participants (5 females and 3 males, ages 19-26) took part in the experiment.

7.2.2 Stimuli and apparatus

The target was a copper amphora filled with 350 ml of water (see Figure 1a) located on a 7 cm high plastic support (Figure 7.1a) at a 30 cm distance from the initial hand position (Figure 7.1a). Hand posture was measured as for the other experiments by means of the CyberGlove (for details see Chapter 2) except that metal wires were inserted into the volar surface of the device. The wires covered the length of the five digits, and both the thenar and the hypothenar eminence of the hand.

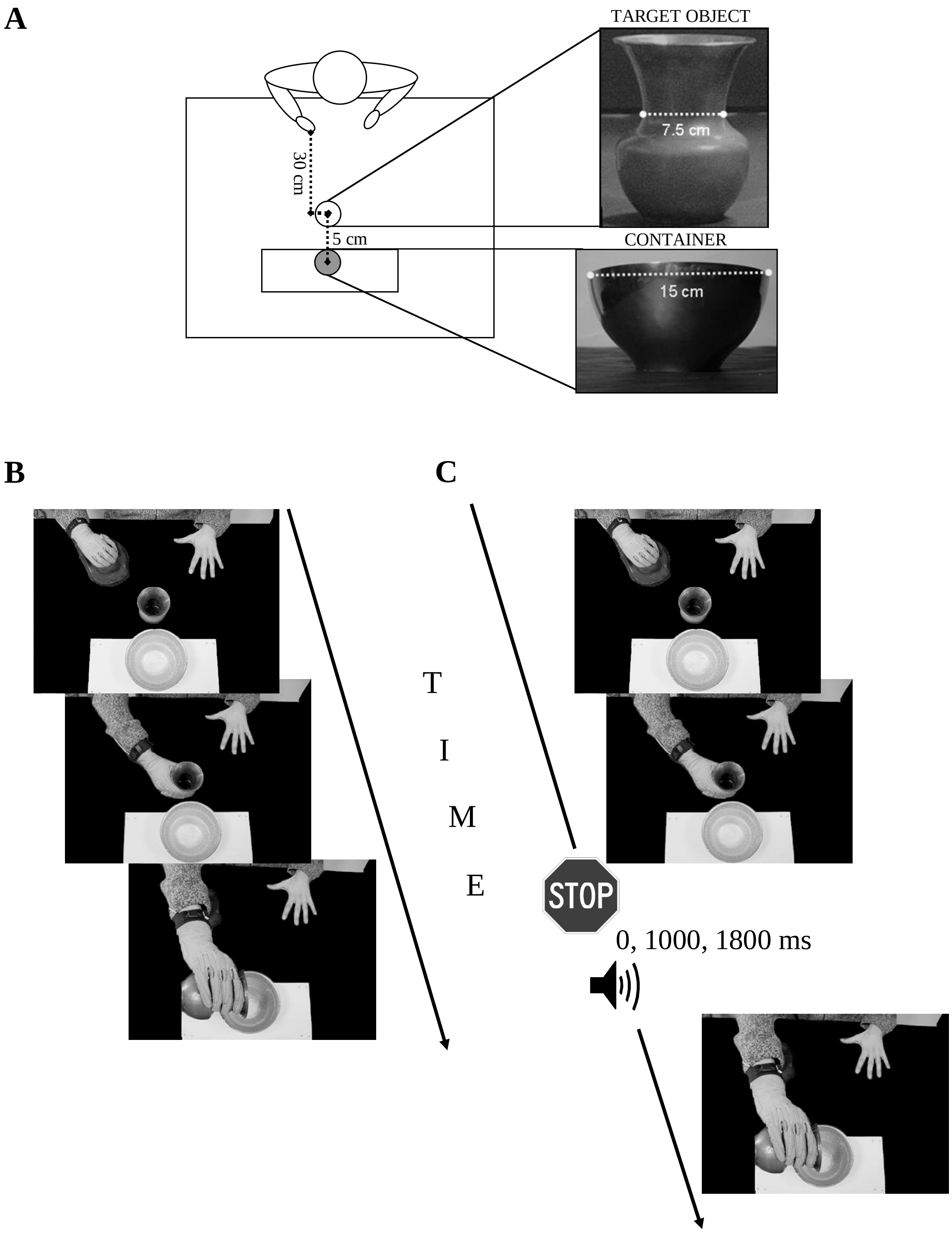

Figure 7.1 Panel A shows the top view of the experimental setup (not to scale), the target object and the container in which the object's content was poured. Panels B and C show a schematic representation of the sequence of events for the 'continuous pouring' and the 'interrupted pouring' conditions, respectively.

Participant naturally reached towards and grasped the target object opposing the thumb to the four fingers after hearing an auditory signal (Hz = 880; duration = 200 ms) (see Chapter 2). This signal was termed 'start' signal. When the metal wires mounted on the CyberGlove entered in contact with the target another sound (Hz = 400; duration = 200 ms), termed 'grasp' sound, was delivered at specific time delays: (i) at target contact (0 ms); (ii) 1000 ms after the hand entered in contact with the target; and (iii) 1800 ms after the hand entered in contact with the target. In some circumstances, the delivery of the 'grasp' sound signified that an action subsequent to grasping had to be performed as explained in the following section.

7.2.3 Procedures

Participants undergo three experimental conditions:

1. 'Control'. In this condition participants were requested to perform a reach to grasp action towards the target and they were explicitly told not to perform any subsequent action. The 'grasp' sound was only presented at target contact (0 ms).

2. 'Continuous pouring'. In this condition participants were requested to perform a reach to grasp action towards the target and then pour its content within a plastic container (see Figure 7.1b). The 'grasp' sound was presented only at target contact (0 ms). Participants were explicitly told to

perform the action fluently without taking any notice of the 'grasp' sound.

3. 'Interrupted pouring'. In this condition participants were requested to perform a reach to grasp action towards the target and explicitly instructed to wait for the 'grasp' sound as to complete the pouring action. The 'grasp' sound could be delivered at target contact (0 ms), or after 1000 or 1800 ms after target contact (see Figure 7.1c).

Participants performed a total of 50 trials, 10 trials for the 'control' condition, 10 trials for the 'continuous pouring' condition, and 30 trials for the 'interrupted pouring' condition (10 trials for each grasp sound time delay, i.e., 0, 1000, 1800 ms).

7.2.4 Data analysis

The dependent measures which were thought to be specifically relevant as to test the experimental hypotheses were reach duration and the thumb/index finger abduction angle. Reach duration was chosen because it is a measure which is sensitive to the presence or absence of a subsequent action following grasp (Ansuini et al., 2007; Gentilucci et al., 1997; Johnson-Frey et al., 2004). Therefore, the explicit requirement to interrupt the flow of action should be evident on this measure. Reach duration was calculated as the time interval between the release of the starting switch and the time at which the fingers contacted the object. Abduction angle reflects the distance between the thumb and index finger along reach duration. As for reach duration, this measure appears to be sensitive to situations in which grasping an object is the intermediate step of an action (Ansuini et al., 2007). An increase in such values indicated relatively greater abduction.

The main scope of using different time delays for the presentation of the 'grasp' sound during the 'interrupted' condition was to ensure that participants relied on the sound to start the subsequent action and did not start the movement automatically. Therefore, we did not expect any significant difference depending on the extent of the delay. In this respect, preliminary analyses revealed there were no differences in reach duration and in the thumb/index finger abduction angle when comparing trials at each time delay (i.e., 0, 1000, 1800 ms). Consequently, we randomly selected trials (by groups of 3, 3, 4 trials for the control, continuous, and interrupted conditions, respectively) from each time delay and we used this new pool of data for the 'interrupted pouring' condition.

To test for possible differences in reach duration as a function of experimental condition an analysis of variance (ANOVA) with 'Condition' ('control', 'continuous pouring', 'interrupted pouring') as within-subjects factor was performed. To assess how and to what extent the thumb/index finger abduction angle differed across experimental conditions, we performed an ANOVA with 'Condition' ('control', 'continuous pouring', 'interrupted pouring') and 'Time' (from 10% to 100% of the reach, at 10% intervals) as within-subjects factors.

7.3 RESULTS

Despite the distance between the hand starting position and the target was maintained constant, the time taken by the hand to cover this distance differed depending on the type of experimental conditions ([$F_{(2,14)} = 19.603$, $P < .0001$]). Specifically, post-hoc contrasts revealed that reach duration was shorter for the 'continuous pouring' than for the 'interrupted pouring' condition, (1304 versus 1886 ms, respectively) (see Figure 7.2). Furthermore, reach duration was significantly longer for the 'interrupted pouring' than for the 'control' condition (1286 ms) (Figure 7.2).

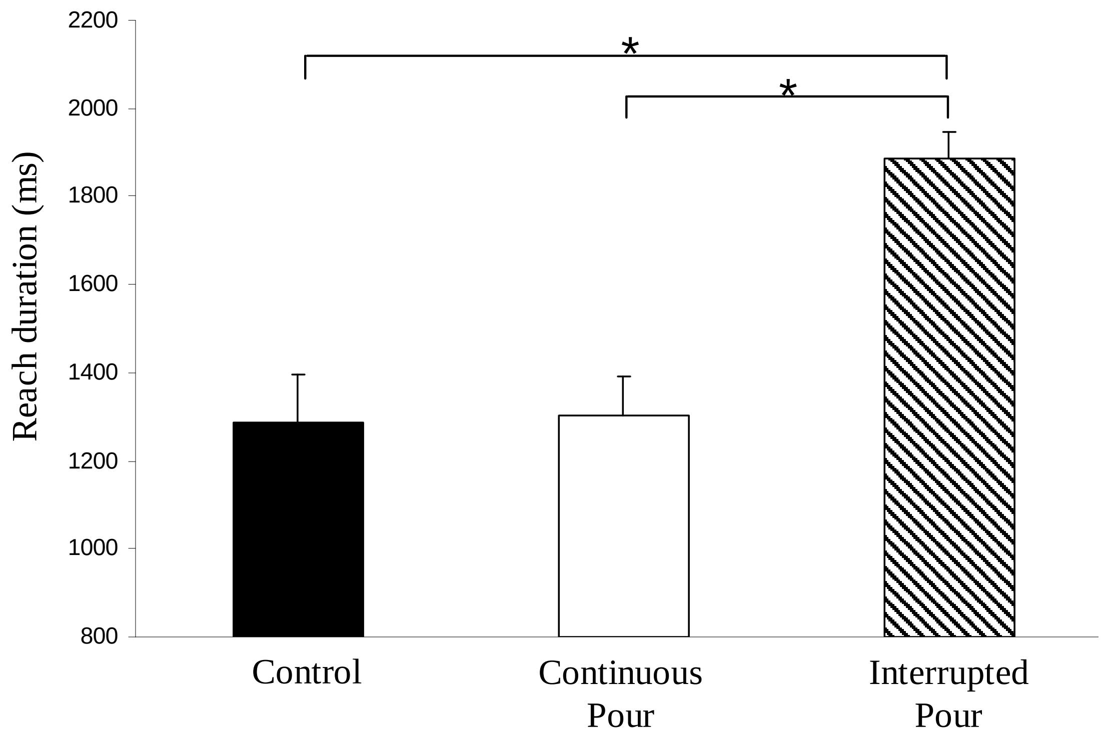

Figure 7.2 Reach duration in milliseconds (ms) for the three experimental conditions. Bars represent standard error of the means.

The analysis performed on the distance between the thumb and the index finger revealed a significant main effect of 'Condition' ([$F_{(2,14)}$ = 7.358, P < .008]). Post-hoc comparisons indicated that the thumb – index distance was smaller for the 'continuous pouring' than for both the 'interrupted pouring' and the 'control' condition (see Figure 7.3). The main effect of 'Time' was also significant ([$F_{(9,63)}$ = 92.773, P <.0001]). All possible post-hoc contrasts which could be performed for this factor were significant. Broadly speaking, the thumb-index abduction angle progressively and significantly increased up to the time the object was grasped (Figure 7.3).

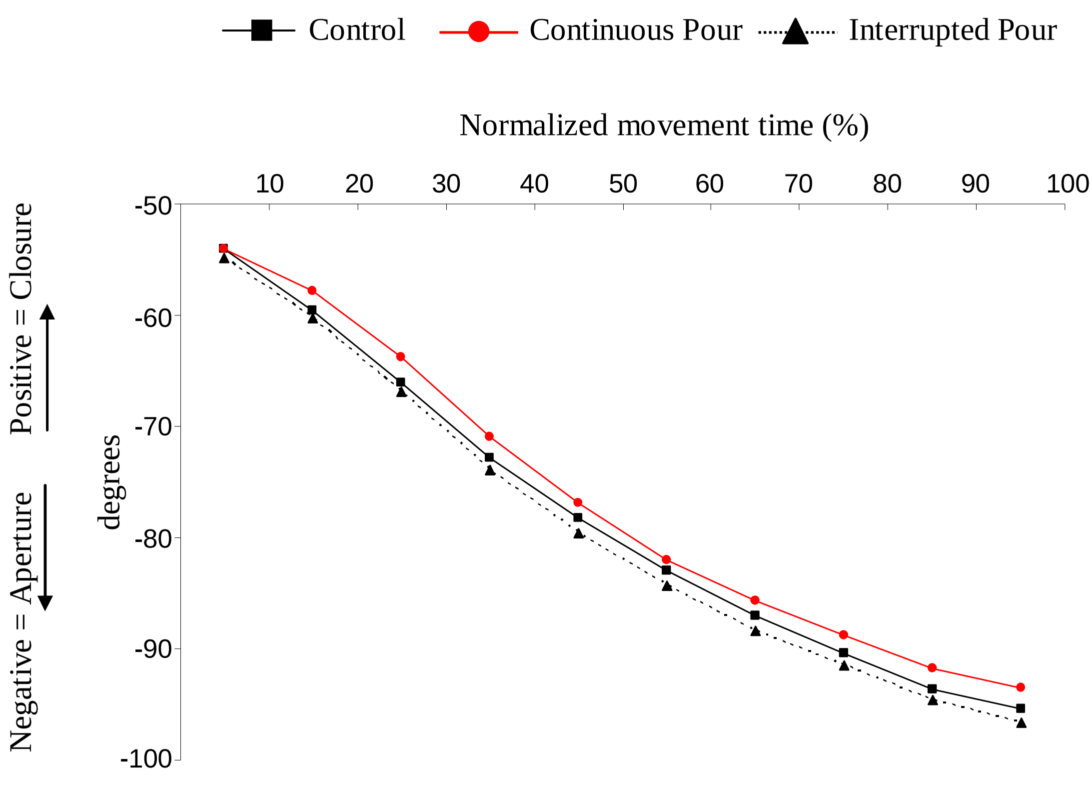

Figure 7.3 Time course of angular distance between the thumb and the index finger for each experimental condition. Data are averaged across trials and participants.

7.4 Discussion

The goal of the present study was to determine whether imposing a temporal break between the two main segments of an action would affect movement kinematics. It was found that when grasping an object with the intent to pour its content within a container, a delay between the first (i.e., grasping) and the second (i.e., lift-to-pour) segment of the action determined kinematic differences in how the hand approached the object with respect to when no delays were introduced. Overall these results indicate that when planning and executing an action requiring the assemblage of two main movement phases, a key factor considered by the CNS is the time interleaving between the implementation of the two phases.

7.4.1 Interrupted versus continuous pouring conditions

We found that when the pouring action was interrupted reach duration and the thumb-index distance increased with respect to when the same movement was performed fluently. Remember that the reach-to-grasp phase for these two conditions was identical in terms of target distance and no constraints on how to grasp the target were given.

These results are in agreement with previous evidence showing that motor actions performed in 'real-time' differ from those performed under 'delayed' circumstances (Hu, Eagleson, & Goodale, 1999; Wing et al., 1986; Goodale et al., 1994). For instance, in a study by Hu and colleagues (1999) participants were asked to reach and grasp an object either as soon as it became visually available (i.e., on-line movement) or after 5-s delay from its viewing (i.e., delayed movement). The results revealed that reach duration was longer and the distance between the thumb and the index finger was greater for the 'delayed' than for the 'real-time' condition. The suggestion was that the type of sensory information guiding the 'delayed' actions derives from a 'perceptual' analysis of the target object rather than from the sensory-motor transformation of its properties, as it might have occurred for 'real-time' movement (Hu et al., 1999). In other words, whereas for the 'delayed' condition participants cognitively estimated the properties of the target object, for the 'real-time' condition they added an additional step concerned with the transformation of the cognitive estimation of the object's properties into appropriate motor commands (i.e., internal models). Therefore it was the absence of such additional step which might have determined the increase in both reach duration and thumb-index distance. In this view, grasping might be controlled by means of two dissociable processes. That is, the use of internal models and the conscious perception of object properties (Danckert, Sharif, Haffender, Schiff, & Goodale, 2002).

The present results may be explained along the same lines. It might well be that whereas the interrupted pouring action was driven by the perceptual properties of the target object per se, the continuous pouring action was driven by the motor representations elicited by these properties. A point worth noting is that our study differed from that by Hu and colleagues (1999) in an important way:

whereas in Hu and colleagues (1999) study the delay preceded the execution of the reach-to-grasp movement, in the present study the delay followed it. Therefore, we hypothesize that the 'break' effect found here reflects the difficulty of using internal predictive models in controlling 'broken' actions. This hypothesis will be elaborated in the following paragraph.

7.4.2 Internal predictive models: when the flow of action is broken

Contemporary thoughts indicate that we are able to anticipate the consequences of our own action and that such an ability relies on the use of internal models (see 'Introduction' section). In the dominant interpretation of this theory, the CNS stores multiple internal models and these models can be mixed when dealing with an environment in which more than one sensory-motor transformation is present (Ghahramani & Wolpert 1997; Flanagan et al., 1999; Davidson & Wolpert, 2004). It is also assumed that the extent to which two or more sensory-motor transformations might be adaptively 'merged' depends on the time relationship amongst them; reaching the highest probability when they are presented at the same time or in a strict succession within the same environment. To translate this theoretical framework within the context of our experiment, it might well be that the CNS may combine the internal models of the sensory-motor transformations relative to the sub-movements composing the pouring action (i.e., reaching, grasping, lifting, and so on) into one internal model, i.e., the 'pouring' internal model. However, according to the 'internal model' theory, such merging should be differently managed or prevented depending on whether the pouring action is performed under interrupted rather than continuous circumstances, respectively. Our results are in line with these predictions. As explained above, the lengthening in reach duration and the increase of the distance between thumb and index finger for the 'interrupted pouring' condition suggest that the motor system was using perceptual information about the target properties rather than the motor transformation elicited by these properties (as may have happened when dealing with the 'continuous pouring' condition). A possible explanation for this differential processing concerns the role played by error signal derived from sensory feedback related to the attainment of the first motor act (i.e., reach-to-grasp movement). In this respect, it has been shown that when digits initially contact an object, ensembles of tactile afferents provide early information about both the frictional status of the contact (Johansson & Westling, 1987) and the direction of fingertip forces (Birznieks, Jenmalm, Goodwin, & Johansson, 2001). At that time, the proprioceptive feedback furnishes information regarding the body state, as for instance wrist acceleration or position of the fingers on the object. All these 'actual' sensorial information are matched with the predicted sensory feedback and if differences are detected an error signal would be generated (Wolpert & Kawato, 1998). This 'error' mechanism is fundamental for updating the motor plan initially selected on the basis of the forward model and for providing initial state information for the subsequent phase (Flanagan, Bowman, & Johansson, 2006). However, when the transition between the first and the second movement phases is interrupted, the use of such monitoring-correction mechanism is altered. Using the error signal derived by the grasping attainment for evaluating the sensorial background for the successive lifting phase may cause an error because the sensorial information might change during the interruption. For instance, such change may occur at the level of the grip forces which are necessary for lifting the object and that heavily depend on hand acceleration (i.e., the greater the acceleration, the greater is the pre-planned force when lifting the object) (Johansson & Westling, 1987). Consider the present 'interrupted pouring' condition: if the motor system would use the information derived from hand acceleration at the moment the hand makes contact with the object (and the error signal derived from it) for pre-planning the forces suitable for lifting that object, then this may result in an erroneous force application because during the interruption the acceleration of the hand might change. In other words, the predicted sensory feedback for the first movement phase is time-locked with the state that it allows to estimate (that relative to the second phase). When this time-lock procedure is broken (as for the 'interrupted pouring' condition), merging the sensory-motor transformations related to grasping and lifting into one 'pouring' internal model would not be adaptive. The consequence would be an inappropriate task performance.

Therefore, for the 'interrupted pouring' condition, the CNS might plan and control the reach-to-grasp movement without considering the subsequent movement phase (e.g., object lifting). And, as hypothesized above (see 'Interrupted versus continuous pouring condition' section), it may be guided by a perceptual rather than a sensory-motor analysis of the target object. Support for this contention comes from the results obtained for the 'control' condition. Indeed, if the reach-to-grasp movement phase for the 'interrupted pouring' condition would have been planned giving no consideration to a potential subsequent action, then kinematics should be the same as for the 'control' condition which does not consider any subsequent movement. As discussed in the following section, the comparison between the 'interrupted pouring' and the 'control' condition seems to confirm our hypothesis.

7.4.3 Interrupted versus control condition

When comparing the 'interrupted pouring' and the 'control' condition the thumb-index finger distance did not differ. In contrast, the comparison between these two conditions led to significant differences in reach duration. In particular, reach duration was longer for the 'interrupted pouring' than for the 'control' condition. The very fact that the kinematics for the grasp component (i.e., thumb – index finger distance) was the same for both conditions seems to confirm that in both circumstances the CNS planned and controlled the prehensile movement as if no actions had to be performed after object's grasping.

However, it remains to be explained why a difference emerged in terms of reach duration. In our view, the lengthening in reach duration found for the 'interrupted pouring' condition might reflect the occurring of an active inhibiting process. For the 'interrupted pouring' condition, participants knew that, at some stage, they will be requested to pour the content of the target once grasped. Therefore, it is reasonable to assume that the CNS might select a given model-movement and set the time at which the schema for this model should be delivered, i.e., the appropriate model at the appropriate moment. By following this line of reasoning, an active inhibiting process might guarantee that the model next in line would not be delivered too early (i.e., before the sound), thus compromising task performance.

8. General conclusions

During our daily activities we reach towards and grasp objects effortlessly. However, for the CNS planning and executing a reach-to-grasp movement is an extremely complex task. Such complexity is dictated by various factors including the biomechanical characteristics of the hand, the properties of the to-be-grasped objects, the physical environment within which the movement is performed and the intentional component which drives it. All these aspects have to be confronted in order to appropriately plan and successfully control a desired hand action.

The experimental work included in the present thesis aimed at investigating some of these factors by asking participants to reach and grasp an object under different circumstances. The angular excursion at the level of individual digits, adduction-abduction angles, and reach duration were recorded. An overview of this experimentation, its implications for our understanding of the mechanisms underlying prehensile movements and some final considerations are outlined in the following sections.

8.1 Overview of the present research

In the first experiment (Chapter 3) I administered an 'object shape' perturbation in which the to be grasped object (i.e., concave or convex) was either presented from the start to the end of the movement or could unpredictably change as soon as the reaching movement started, (i.e., either from concave to convex or vice versa). The aim of this experiment was twofold. First, to understand how the CNS controls digits' motion during reaching for objects having different shapes. Second, to shed more light on how the CNS copes with a quick reorganization at the level of individual digits' motion. The results showed that when the shape of the to be grasped object did not change during the time course of the action, the fingers – but not the thumb – were differently conformed depending on the shape of the to-be-grasped object. When an 'object shape' perturbation was applied, all fingers responded to the perturbation, but the kinematic response differed depending on the 'direction' of the perturbation (i.e., either over-flexing or over-extending depending on whether the perturbation was from concave to convex or vice versa, respectively). Conversely, the thumb 'reacted' to the perturbation similarly regardless the direction of the perturbation (i.e., over-flexing). Finally, the presence of the perturbation led to a longer reach duration with respect to unperturbed trials.

All in all the results reported in Chapter 3 indicated that when a reach-to-grasp movement towards a specific shaped object is planned and executed, the CNS takes into account the shape of the to-be-grasped object and fingers' motion is moulded accordingly. Further, when object shape is unexpectedly changed the hand reacts showing an harmonic kinematic response. This seems to suggests that the hand response to the perturbation is achieved by controlling all digits as a unit. Within this unit, however, the thumb would play a specific role in action guidance. Naturally, reorganizing all digits in response to the ‘object shape’ perturbation takes time and therefore reach duration was found to be longer for perturbed trials.

Given that fingers’ posture reflects the shape of the to be grasped object, a plausible assumption is that such a posture might be sensitive to the properties embedded in the physical context within which the prehensile movement occurs. The experiment reported in Chapter 4 was designed in order to elucidate this specific issue. In this experiment the to- be-grasped object (i.e., concave or convex) was either presented in isolation or flanked by another object (i.e., distractor). The distractor could be of an identical or a different shape than the target (i.e., concave or convex). The results showed that when the target was presented in isolation, the fingers – but not the thumb – were sensitive to its shape. When the target was presented flanked by a distractor, the adduction angles were affected by the presence of a distractor regardless of its shape. However, the kinematic patterning of the digits was the same as that found for the target when presented in isolation. The only exception was represented by the thumb which, instead, was significantly affected by the presence of the distractor independently from its shape. Finally, the presence of the distractor brought to a lengthening in reach duration.

Altogether the results reported in Chapter 4 indicated that hand posture was sensitive to the properties of task-irrelevant objects. However, the very fact that adduction angles, but not fingers’ angular excursion, were affected by the presence of the distractor seems to suggest that the type of analysis performed on the distractor object was analytic rather than holistic. In other words, when the target was flanked by a distractor the mechanisms of selection for the control of hand action might ‘detect’ the volumetric properties of the distractor (i.e., effect on adduction angles), while partially ignoring fine-grained properties such as shape (i.e., lack of effects on individual fingers’ motion). Further, the distractor effect on thumb kinematics suggested that the presence of both the target and the distractor object determined a parallel planning for their respective locations. In this view the thumb might represent the key-digit for the guidance of the hand towards the target and distractor avoidance. Along these lines the lengthening of reach duration might reflect the extra-time needed to filter out the interfering plan elicited by the distractor.

In the experiment described above the reach-to-grasp movement was differently performed depending on the context within which it occurred. Specifically, the context differed in terms of its tangible properties, i.e., presence-absence of an object nearby the target. However, context can also be characterized by the intentional component driving the action. For instance, a reach-to-grasp movement towards the same object might be differently performed depending on the intentional goal driving the action. In order to investigate this issue I performed two experiments which are reported in Chapters 5 and 6. In these experiments the intentional context was manipulated by varying the goal of the action participants were requested to achieve following object grasping.

In the experiment reported in Chapter 5 the reach-to-grasp movement for the very same object was followed by actions that differed in accuracy requirements (e.g., placement of the target into a large versus a tight niche). The results showed that, although the to-be-grasped object remained the same, the posture assumed by the hand during reaching varied depending on the level of accuracy. In particular, the motion of some fingers (i.e., ring and little finger) for the 'low-accurate' action was not characterized by the gradual modulation which, instead, was found when the succeeding action required high accuracy. Furthermore, reach duration was shorter when a low level of accuracy characterized the subsequent action.

Altogether these results indicated that the accuracy requirements being implicit in the action following grasping are taken into account. When this action does not require a high degree of accuracy the need for establishing firm hand-object contact points and finely modulate digits' forces decreases. The decrease in the number of kinematic computations may account for the shortening of reach duration found for the less accurate action.

How the overarching goal of a reach-to-grasp movement determines how an object is approached was also the theme for the experiment reported in Chapter 6. Here the reach-to-grasp movement for the very same object could either represent the only action to be performed or the first step leading to other actions whose functional nature differed (i.e., pouring, placing, throwing, passing actions). The results for this experiment revealed that when no subsequent action was requested after object grasp the pattern of aperture – closure characterizing hand movement was attained earlier than when object grasp was followed by another action. In addition, the kinematic patterning of the hand appeared to be sensitive to the nature of the functional end-goal. Specifically, some digits (i.e., middle and ring) were more extended when object grasp was followed by the pouring action with respect to when it was followed by one of the other actions. As for the previous experiment, reach duration was shorter when the accuracy requirements for attaining the functional end-goal were lower.

Taken together these results indicated that both the presence and the functional nature of the action following object grasp are considered when planning a reach-to-grasp movement. The general pattern of results indicates an anticipation of the hand opening – closing phases when the reach-to-grasp movement represented the only motor act to be performed. This may signify that participants perceived the end-point location closer than when a subsequent action has to be performed. In the latter case the end-point would be focused on the subsequent action end-point location. This is in line with the well-established result that the time of maximum grip aperture is brought forward for grasping objects located at farther distances (e.g., Jakobson & Goodale, 1991). Further, the difference in hand shaping due to the functional nature of the succeeding action seems to reflect that the ability of the CNS to anticipate the dynamic requirements being implicit in such action. In this view, the middle and the ring finger were more extended during the 'pouring' action because this kinematic solution would facilitate the exertion of forces which are needed by these fingers to successfully perform this action. By following this line of reasoning, it might be concluded that the simpler is the dynamic 'problem' embedded in the action following grasping, the simpler are the kinematic computations implemented to optimize the 'solution' of the upcoming problem. This explanation may also account for the observed shortening of reach duration for movements followed by less accurate functional end-goals.

The findings from the experiments presented in Chapters 5 and 6 suggest that the functional requirements of an action following grasping can be anticipated and implemented during the reaching approach phase. However, an aspect remained unsolved. That is, whether the time intervening between the reach-to-grasp phase and the subsequent phase, leading to the action goal, plays a role in action planning and execution. The experiment reported in Chapter 7 was designed to specifically address this issue. In this experiment the reach-to-grasp movement could represent either the only motor act to be performed or the first step of a pouring action. The crucial manipulation was the length of the delay between the two motor steps. The results showed that, despite the object to be grasped, as well as the action to be performed, were always the same, the thumb-index distance differed depending on whether a delay was introduced between the first reach-to-grasp phase and the second lift-to-pour phase. When the performance of the succeeding action was substantially delayed the thumb-index distance was the same as when no action had to be performed after object grasping. In similar circumstances reach duration was longer than when it was performed in a continuous fashion (i.e., no-delay).

Overall these results indicated that the presence of an interruption between object grasping and the following action led the CNS to plan and control hand movement as if no other actions had to be performed. In other words, the ability of the CNS to anticipate the requirements embedded in the action following object grasp seems to depend on the time at which that action will occur. In this view, the presence of the interruption seems to prevent the integration of the two phases. The lengthening of reach duration found under the 'interrupted' circumstances might be explained as an active inhibiting process established by the CNS in order to avoid the subsequent action being executed too early.

With this in mind the central advance of the present work is twofold. First, from a methodological perspective the used paradigms were fairly ecological in many ways. I used objects which did not require an atypical hand posture in order to be grasped and they were objects typically used in daily living activities (see Chapter 5, 6, and 7). In contrast to the majority of previous literature on this topic (for review see Castiello, 2005), participants were let free to grasp the objects by using all five fingers rather than forcing them to use only the thumb and the index – a quite uncommon type of grasp. In this respect the present experimentation considered kinematic measures which can provide a more comprehensive understanding of the processes underlying prehension. They have the potential to 'catch' aspects of grasping that otherwise would be uncovered if simply looking at two-digits – as in the majority of previous reach-to-grasp studies.

Second, in theoretical terms the present work considered processes of selection for the control of hand actions under a new light. This was done by linking current advances in the methodology for recording hand kinematics and paradigms considering the presence of distractor objects. As a final point, the investigation of the intentional, anticipatory components underlying reach-to-grasp movements particularly depicts the novel aspect of the present work.

8.2 Conclusive remarks

8.2.1 The role of hand shaping

The results of the present thesis indicate that fingers are differently moulded depending on the shape of the to-be-grasped object. This result is line with previous evidence showing that there is a strong relationship between the posture assumed by the hand during reaching towards an object and its shape (Santello & Soechting, 1998; Santello et al., 2002; Winges et al., 2003). However, I also found an indication that object shape is not the only aspect that the CNS takes into account when modulating fingers motion during reaching towards an object. As shown in Chapters 5 and 6, fingers' kinematic patterning differed depending on the accuracy and functional requirements embedded in the action following grasping. This occurred even though the object shape remained invariant. Therefore an invariance at the level of object shape does not necessarily lead to an invariance in fingers' shaping. When the action following grasping changes, fingers' motion changes. This indicates that the processes underlying fingers' motion are concerned with an important property of the CNS: the ability to anticipate future states of the system in motion. Therefore, it can be concluded that the processes underlying the fingers' shaping phenomenon are more 'cognitive' than previously thought. The motion of fingers while reaching towards an object seems to be planned in terms of action goals rather than object geometry. Therefore suitable paradigms for investigating such a phenomenon should consider that in everyday life we often grasp an object to make use of it rather than simply grasping it.

8.2.2 The thumb is 'different'

In Chapters 3 and 4 it was found an indication that the thumb did not modulate with respect to the shape of the to-be-grasped object. In this respect previous studies on hand shaping do not provide any indication regarding the role played by the thumb in establishing the relationship between hand posture and target shape (Santello & Soechting, 1998; Santello et al., 2002; Winges et al., 2003). Kinematics related to this digit was excluded from the analyses (Santello & Soechting, 1998; Santello et al., 2002; Winges et al.,, 2003).

In this respect the present results provide two important pieces of information. For one, whereas the thumb did not 'react' to objects shape, the fingers did (see Chapters 3 and 4). A result which highlights a certain degree of independence among digits. For another, the very fact that when the stability of the reaching path was challenged – as when the shape of target object suddenly changed or the target object was flanked by another object – the thumb 'reacted' (see Chapters 3 and 4). This latter finding is in line with the notion that the thumb acts as a reference point for target location (Wing & Fraser, 1983; Wing et al., 1986).

Overall these observations seem to support the proposal made by Smeets and Brenner (1999) to explain how individual digits are controlled during reach-to-grasp. According to this proposal, the thumb moves independently from the index finger as to obtain a perpendicular approach onto the surface of the to-be-grasped object (Smeets & Brenner, 1999). In Smeets and Brenner' view, such a perpendicular approach would allow for the establishment of more firm contact points at the moment the object is grasped. It is worth noting that stable contact points on the object become crucial when the grasped object has to be lifted and manipulated. The present results fully support this hypothesis showing that when there is no need for object lifting – as for the experiment reported in Chapter 6 – the kinematic patterning of the thumb is different than when lifting is requested. Further, the very fact that - in contrast to fingers' behaviour (see Chapters 5 and 6)- the thumb is not sensitive to the demands of the action following grasping suggests that the CNS adopt a specific strategy for controlling how the thumb should approach the target. Although this hypothesis needs to be confirmed in future research, what clearly emerges from the present results is that the thumb is a 'special' digit. Therefore, models on grasping behaviour as well as possible interpretations of kinematic data should consider such evidence.

8.2.3 The 'time' factor in prehension

Another aspect of the present results is that the processes underlying prehensile behaviour are characterized by the anticipation of the demands dictated by a possible upcoming action (see Chapters 5 and 6). Importantly, such anticipatory processes appears to depend on the temporal structure of the motor sequence within which the reach-to-grasp movement is embedded (see Chapter 7). Hand kinematics is projected in the future, but only when this 'future' is very close. This finding extend both the 'two-digits' (Armbrüster & Spijkers, 2006; Cohen & Rosenbaum, 2004; Marteniuk et al., 1987) and the 'multi-digits' (Ansuini et al., 2006, 2007) literature on prehension movements by disclosing the importance of time-lags when the overarching goal of an action requires multiple motor steps. This is an aspect which has been largely neglected, but which appear to be crucial when a reach-to-grasp movement is planned as part of a motor sequence leading to a specific goal.

It has been hypothesized that the ability to predict the consequences of our own actions relies on the use of internal models (Kawato, 1999). According to this theoretical framework, when a motor sequence has to be performed (e.g., reach-to-grasp a bottle and pour its content), the CNS would be able to mix the outputs from different modules – one for each motor act composing the motor sequence – into one module. Following Kawato's postulation, however, the limiting condition for such an integration would be the time relationship across modules, so that two or more modules can be integrated only if they are linked contiguously. Here I demonstrated that ‘how’ an object is grasped is linked to ‘when’ this object will be used. This result provides further fuel in support of the internal model theory main assumption: temporal contiguity is a pre-requisite for integrating internal models referred to different movements into a unique motor act. This result opens to a number of interesting questions which need to be pursued in future research. For instance forcing participants to speed up the execution of the reach-to-grasp phase would alter the performance of the following action concerned with the attainment of the end-goal? If the CNS consider time intervals amongst different movement phases when planning a prehensile action, then where such representations are stored? And, which are the characteristics of these representations?

8.3 Epilogue

“Scientists see new things when looking at old objects”. This Sir Thomas S. Kuhn’s sentence – from ‘The Structure of Scientific Revolution’ (1962) – well catches the issues at the heart of the present thesis. Although a large body of data on reach-to-grasp movement has been provided, I have attempted to adopt a new perspective focusing on aspects which have so far received little attention. Specifically how action goals drive reach-to-grasp movements and the context within which these actions are usually performed. By investigating the kinematic complexity of hand movements in full details it has been possible to ‘see’ beyond grasping and to gain some understanding of how the CNS integrates and manages highly cognitive problems such as time-lags and intentions for the control of hand actions.

References

Allport, A. (1987). Selection for action: Some behavioral and neurophysiological considerations of attention and action. In: H. Heuer & A. F. Sanders (Eds.), *Perspectives on perception and action* (pp. 395-419). Hillsdale, NJ: Erlbaum.

Ansuini, C, Giosa, L., Turella, L., Altoè, G., & Castiello, U. (2007). An object for an action, the same object for other actions: effect on hand shaping. *Experimental Brain Research*. Published on-line.

Ansuini, C., Santello, M., Massaccesi, S., & Castiello, U. (2006). Effects of end-goal on hand shaping. *Journal of Neurophysiology*, *95*, 2456-2465.

Arbib, M. A., Iberall, T., & Lyons, D. (1985). Coordinated control programs for movements of the hand. *Experimental Brain Research*, *10*, 111-129.

Armbrüster, C., & Spijkers, W. (2006). Movement planning in prehension: do intended actions influence the initial reach and grasp movement? *Motor Control*, *10*, 311-329.

Biegstraaten, M., Smeets, J. B., & Brenner, E. (2003). The influence of obstacles on the speed of grasping. *Experimental Brain Research*, *149*, 530-534.

Bingham, G., Iberall, T., & Arbib, M. A. (1986). Opposition space as a structuring concept for the analysis of skilled hand movements. *Experimental Brain Research Series*, *15*, 159-173.

Birznieks, I., Jenmalm, P., Goodwin, A. W., & Johansson, R. S. (2001). Encoding of direction of fingertip forces by human tactile afferents. *Journal of Neuroscience*, *21*, 8222-8237.

Blake, A. (1992). Computational modelling of hand-eye coordination. *Philosophical Transactions of the Royal Society of London*, *337*, 351-360.

Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, *1*, 635-640.

Bock, O., & Jungling, S. (1999). Reprogramming of grip aperture in a double – step virtual grasping paradigm. *Experimental Brain Research*, *125*, 61-66.

Bonfiglioli, C., & Castiello, U. (1998). Dissociation of covert and overt spatial attention during prehension movements: selective interference effects. *Perception and Psychophysics*, *60*, 1426-1440.

Bootsma, R. J., Marteniuk, R. G., Mackenzie, C. L., & Zaal, F. T. J. M. (1994). The speed-accuracy trade-off in manual prehension: effects of movement amplitude, object size and object width on kinematic characteristics. *Experimental Brain Research*, *98*, 535-41.

Castiello, U. (1996). Grasping a fruit: selection for action. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 582-603.

Castiello, U. (1998). Attentional coding for three-dimensional objects and two-dimensional shapes. Differential interference effects. *Experimental Brain Research*, *123*, 289-297.

Castiello, U. (1999). Mechanism of selection for the control of hand action. *Trends in Cognitive Sciences*, *3*, 264-271

Castiello, U. (2005). The neuroscience of grasping. *Nature Review Neuroscience*, *6*, 726-36.

Castiello, U., Bennett, K. M., & Chambers, H. (1998). Reach to grasp: the response to a simultaneous perturbation of object position and size. *Experimental Brain Research*, *120*, 31-40.

Castiello, U., Bennett, K. M., & Paulignan, ,Y. (1992). Does the type of prehension influence the kinematics of reaching? *Behavioural Brain Research*, *50*, 7-15.

Castiello, U., Bennett, K. M., & Stelmach, G. E. (1993). Reach to grasp: the natural response to perturbation of object size. *Experimental Brain Research*, *94*, 163-178.

Chang, S. W. C., & Abrams, R. A. (2004). Hand movements deviate toward distracters in the absence of response competition. *The Journal of General Psychology*, *131*, 328-344.

Chieffi, S., Fogassi, L., Gallese, V., & Gentilucci, M. (1992). Prehension movements directed towards approaching objects: Influence of stimulus velocity on the transport and the grasp components. *Neuropsychologia*, *30*, 877-897.

Chieffi, S., & Gentilucci, M. (1993). Coordination between the transport and the grasp components during prehension movements. *Experimental Brain Research*, *94*, 471-477.

Cohen, R. G., & Rosenbaum, D. A. (2004). Where grasps are made reveals how grasps are planned: generation and recall of motor plans. *Experimental Brain Research*, *157*, 486-495.

Cole, K. J., & Abbs, J. H. (1986). Coordination of three – joint digit movements for rapid, finger – thumb grasp. *Journal of Neurophysiology*, 55, 1407-1423.

Colebatch, J. G., & Gandevia, S. C. (1989). The distribution of muscular weakness in upper motor neuron lesions affecting the arm. *Brain*, *112*, 749-763.

Danckert, J. A., Sharif, N., Haffender, A. M., Schiff, K. C., & Goodale, M. A. (2002). A temporal analysis of grasping in the Ebbinghaus illusion: planning versus online control. *Experimental Brain Research*, *144*, 275-280.

Davidson, P. R., & Wolpert, D. M. (2004). Scaling down motor memories: de-adaptation after motor learning. *Neuroscience Letters*, *370*, 102-107.

Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Visual Cognition*, 5, 81-107.

Eastough, D., & Edwards, M. G. (2007). Movement kinematics in prehension are affected by grasping objects of different mass. *Experimental Brain Research*, *176*, 193-198.

Fischer, M. H., & Adam, J. (2001). Distractor effect on pointing: the role of spatial layout. *Experimental Brain Research*, *136*, 507-513.

Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of a movement. *Journal of Experimental Psychology*, *47*, 381-91.

Fikes, T. G., Klatsky, R. L., & Lederman, S. J. (1994). Effects of object texture on precontact movement time in human prehension. *Journal of Motor Behavior*, *26*, 325-332.

Flanagan, J. R., Bowman, M. C., & Johansson, R. S. (2006). Control strategies in object manipulation tasks. *Current Opinion in Neurobiology*, *16*, 650-659.

Flanagan, J. R., Nakano, E., Imamizu, H., Osu, R., Yoshioka, T., & Kawato, M. (1999). Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments. *Journal of Neuroscience*, *19*, RC34 (1-5).

Frak, V., Paulignan, Y., & Jeannerod, M. (2001). Orientation of the opposition axis in mentally simulated grasping. *Experimental Brain Research*, *136*, 120-127.

Galea, M. P., Castiello, U., & Dalwood, N. (2001). Thumb invariance during prehension movement: effect of object orientation. *NeuroReport*, *12*, 2185-2187.

Ganel, T., & Goodale, M. A. (2003). Visual control of action but not perception requires analytical processing of object shape. *Nature*, *426*, 664-667.

Gao, F., Latash, M. L., & Zatsiorsky, V. M. (2006). Maintaining rotational equilibrium during object manipulation: linear behavior of a highly non-linear system. *Experimental Brain Research*, 169, 519-531.

Gentilucci, M., Castiello, U., Corradini, M. L., Scarpa, M., Umiltá, C. A., & Rizzolatti, G. (1991). Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia*, *29*, 361-378.

Gentilucci, M., Chieffi, S., Scarpa, M., & Castiello, U. (1992). Temporal coupling between transport and grasp components during prehension movements: Effects of visual perturbation. *Behavioural Brain Research*, *47*, 71-82.

Gentilucci, M., Negrotti, A., & Gangitano, M. (1997) Planning an action. *Experimental Brain Research*, *115*, 116-128.

Ghahramani, Z., & Wolpert, D. M. (1997). Modular decomposition in visuomotor learning. *Nature*, *386*, 392-395.

Goodale, M. A., Meenan, J. P., Buelthoff, H. H., Nicolle, D. A., Murphy, K. J., & Racicot, C. I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, *4*, 604-610.

Howard, L. A., & Tipper, S. P. (1997). Hand deviations away from visual cues: indirect evidence for inhibition. *Experimental Brain Research*, *113*, 144-152.

Hoff, B., & Arbib, M. A. (1993). Simulation of interaction of hand transport and preshape during visually guided reaching to perturbed targets. *Journal of Motor Behavior*, *25*, 175-192.

Hu, Y., Eagleson, R., & Goodale, M. A. (1999). The effects of delay on the kinematics of grasping. *Experimental Brain Research*, *126*, 109-116.

Iberall, T., & Fagg, A. H. (1996). *Neural networks models for selecting hand shapes*. In: Wing A. M., Haggard, P., & Flanagan, J. R. (Eds.) *Hand and Brain* (pp. 243 – 264). San Diego, CA: Academic Press.

Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Experimental Brain Research*, *102*, 519-530.

Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Experimental Brain Research*, *86*, 199-208.

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In: J. Long, & A. Baddeley (Eds.), *Attention and performance IX* (pp. 153-169). Hilsdale, NJ: Lawrence Erlbaum Associates.

Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, *16*, 235-254.

Jeannerod, M. (1986). The formation of finger grip during prehension: A cortically mediated visuomotor pattern. *Behavioural Brain Research*, *19*, 99-116.

Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements*. Oxford: Clarendon Press.

Jenmalm, P., Goodwin, A. W., & Johansson, R. S. (1998). Control of grasp stability when humans lift objects with different surface curvatures. *Journal of Neurophysiology*, *79*, 1643-1652.

Jerde, T. E., Soechting, J. F., & Flanders, M. (2003b). Biological constraints simplify the recognition of hand shapes. *IEEE Transactions on. Bio-medical Engineering*, *50*, 265-269.

Jerde, T. E., Soechting, J. F., & Flanders, M. (2003a). Coarticulation in fluent fingerspelling. *Journal of Neuroscience*, *15*, 2383-2393.

Johansson, R. S., Westling, G., Backstrom, A., & Flanagan, J. R. (2001). Eye-hand coordination in object manipulation. *Journal of Neuroscience*, *21*, 6917-6932.

Johansson, R. S., & Westling, G. (1984). Roles of glabrous skin receptors and sensorimotor memory in automatic control of precision grip when lifting rougher or more slippery objects. *Experimental Brain Research*, 56, 550-564.

Johansson, R. S., & Westling, G. (1987). Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. *Experimental Brain Research*, 66, 141-154.

Johnson-Frey, S. H., McCarty, M. E., & Keen, R. (2004). Reaching beyond spatial perception: effects of intended future actions on visually guided prehension. *Visual Cognition*, *11*, 371-399.

Kapandji, I. A. (1970). *The Physiology of Joints. Upper Limb* (2nd ed.). (Vol. 1, pp. 146-202). London: E and S Livingstone.

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, *9*, 718-27.

Keulen, R. F., Adam, J. J., Fischer, M. H., Kuipers, H., & Jolles, J. (2002). Selective reaching: evidence for multiple frames of reference. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 515-526.

Kinoshita, H., Kawai, S., & Ikuta, K. (1995). Contributions and co-ordination of individual fingers in multiple finger prehension. *Ergonomics*, *38*, 1212-1230.

Klapp, S. T., & Greim, D. M. (1979). Programmed control of aimed movements revisited: the role of target visibility and symmetry. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 509-521.

Kuhn, T. S. (1962). Revolutions as changes of world view. In: *The Structure of Scientific Revolutions.* (Eds. 3th pp. 111-136). Chicago: University of Chicago Press.

Land, M., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities in daily living. *Perception*, *28*, 1311-1328.

Lemon, R. N. (1999). Neural control of dexterity: what has been achieved? *Experimental Brain Research*, *128*, 6-12.

Liberman, A. M. (1970). The grammars of speech and language. *Cognitive Psychology*, *1*, 301-323.

Lukos, J., Ansuini, C., & Santello, M. (2007). Choice of contact points during multi-digit grasping: Effect of predictability of object center of mass location. *Journal of Neuroscience*, *27*, 3894-3903.

Marteniuk, R. G., Leavitt, J. L., MacKenzie, C. L., & Athenes, S. (1990). Functional relationship between grasp and transport components in a prehension task. *Human Movement Science*, *9*, 149-176.

Marteniuk, R. G., MacKenzie, C. L., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm movement trajectories. *Canadian Journal of Psychology*, *41*, 365-378.

Marzke, M. W. (1994). Evolution. In: K. M. B. Bennett, & U. Castiello (Eds.), *Insights into the Reach to Grasp Movement* (pp. 19-35). Amsterdam: Elsevier Science.

Mason, C. R., Gomez, J. E., & Ebner, T. J. (2001). Hand synergies during reach-to-grasp. Journal of Neurophysiology, 86, 2896-2910.

Meegan, D. V., & Tipper, S. P. (1998). Reaching into cluttered visual environments: spatial and temporal influences of distracting objects. *Quarterly Journal of Experimental Psychology A*, *51*, 225-249.

Meulenbroek, R. G., Rosenbaum, D. A., Jansen, C., Vaughan, J., & Vogt, S. (2001) Multijoint grasping movements. Simulated and observed effects of object location, object size, and initial aperture. *Experimental Brain Research*, *138*, 219-234.

Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control. *Neural Networks*, *9*, 1265-1279.

Napier, J. R. (1956). The prehensile movements of the human hand. *Journal of Bone and Joint Surgery*, *British Volume*, *38B*, 902- 913.

Napier, J. R. (1960). Studies of the hands of living primates. *Proceedings of the Zoological Society of London*, *134*, 647-657.

Paulignan, Y., Frak, V. G., Toni, I., & Jeannerod, M. (1997). Influence of object position and size on human prehension movements. *Experimental Brain Research*, *114*, 226-234.

Paulignan, Y., & Jeannerod, M. (1996). Prehension movements. The visuomotor channels hypoyhesis revisited. In A. M. Wing, P. Haggard, & R. Flanagan (Eds.), *Hand and Brain : The Neurophysiology and Psychology of Hand movements.* (pp. 265-282). San Diego: Academic Press.

Paulignan, Y., Jeannerod, M., MacKenzie, C., & Marteniuk, R. (1991a). Selective perturbation of visual input during prehension movements. 2. The effects of changing object size. *Experimental Brain Research*, *87*, 407-420.

Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1991b). Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. *Experimental Brain Research*, *83*, 502-512.

Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1990). The coupling of arm and finger movements during prehension. *Experimental Brain Research*, *79*, 431-435.

Pratt, J., & Abrams, R. A. (1994). Action-oriented inhibition: effects of distractors on movement planning and execution. *Human Movement Science*, *13*, 245-254.

Quaney, M. B., Nudo, R. J., & Cole, K. J. (2005). Can internal models of objects be utilized for different prehension tasks? *Journal of Neurophysiology*, *93*, 2021-2027.

Rosenbaum, D. A., & Jorgensen, M. J. (1992). Planning macroscopic aspects of manual control. *Human Movement Science*, 11, 61-69.

Rosenbaum, D. A., Vaughan, J., Barnes, H. J., & Jorgensen, M. J. (1992). Time course of movement planning: selection of handgrips for object manipulation. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *18*, 1058-1073.

Rumelhart, D. E., & Norman, D. A. (1982). Simulating a skilled typist: a study of skilled cognitive – motor performance. *Cognitive Science*, 6, 1-36.

Salimi, I., Hollender, I., Frazier, W., & Gordon, A. M. (2000). Specificity of internal representations underlying grasping. *Journal of Neurophysiology*, *84*, 2390-2397.

Santello, M., Flanders, M., & Soechting, J. F. (1998). Postural hand synergies for tool use. *Journal of Neuroscience*, *18*, 10105-10115.

Santello, M., Flanders, M., & Soechting, J. F. (2002). Patterns of hand motion during grasping and the influence of sensory guidance. *Journal of Neuroscience*, *22*, 1426-35.

Santello, M., & Soechting, J. F. (1998). Gradual molding of the hand to object contours. *Journal of Neurophysiology*, *79*, 1307-1320.

Savelsbergh, G. J., Whiting, H. T., & Bootsma, R. J. (1991). Grasping tau. *Journal of Experimental Psychology: Human Perception and Performance*, *17*, 315-22.

Savelsbergh, G. J. P., Steenbergen, B., & van der Kamp, J. (1996). The role of fragility information in the guidance of the precision grip. *Human Movement Science*, *15*, 115-112.

Schieber, M. H. (1990). How might the motor cortex individuate movements? *Trends in Neurosciences*, *13*, 440-445.

Smeets, J. B., Hayhoe, M. M., & Ballard, D. H. (1996). Goal-directed arm movements change eye-head coordination. *Experimental Brain Research*, *109*, 434–-440.

Smeets, J. B., & Brenner, E. (1999). A new view on grasping. *Motor control*, *3*, 237-71.

Soechting, J. F. (1984). Effect of target size on spatial and temporal characteristics of a pointing movement in man. *Experimental Brain Research*, *54*, 121-132.

Steenbergen, B., Marteniuk, R. G., & Kalbfleisch, L. E. (1995). Achieving coordination in prehension: Joint freezing and postural contributions. *Journal of Motor Behavior*, *27*, 333-348

Stelmach, G. E., Castiello, U., & Jeannerod, M. (1994). Orienting the finger opposition space during prehension movements. *Journal of Motor Behavior*, *26*, 178-186

Tipper, S. P., Howard, L. A., & Jackson, S. R. (1997). Selective reaching to grasp: evidence for distractor interference effects. *Visual Cognition*, *4*, 1-38.

Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: evidence for action-centered attention. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 891-905.

Tresilian, J. R. (1998). Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension. *Experimental Brain Research*, *120*, 352-368.

Tubiana, R. (1981). Architecture and function of the hand. In: R. T. Tubiana (Ed.), *The Hand*. Saunders (pp. 19-93). Philadelphia.

Ulloa, A., & Bullock, D. (2003). A neural network simulating human reach – to – grasp coordination by continuous updating of vector positioning commands. *Neural Networks*, 16, 1141-1160.

Van Galen, G. P. (1984). Structural complexity of motor patterns: a study of reaction times movement times of hand written letters. *Psychological Research*, *46*, 49-57.

Weir, P., MacKenzie, C. L., Marteniuk, R. G., Cargoe, S. L., & Frazer, M. B. (1991a). The effects of object weight on the kinematics of prehension. *Journal of Motor Behavior*, *23*, 192-204.

Weir, P., MacKenzie, C. L., Marteniuk, R. G., & Cargoe, S. L. (1991b). Is object texture a constraint on human prehension?: kinematic evidence. *Journal of Motor Behavior*, *23*, 205-210.

Wing, A. M., & Fraser, C. (1983). The contribution of the thumb to reaching movements. *Quarterly Journal of Experimental Psychology A*, *35*, 297-309.

Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior*, *18*, 245-260.

Winges, S. A., Weber, D. J., & Santello, M. (2003). The role of vision on hand preshaping during reach to grasp. *Experimental Brain Research*, *152*, 489-498.

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*, 1212-1217.

Wolpert D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks*, *11*, 1317-1329.

Wolpert, D. M., Goodbody, S. J., & Husain, M. (1998). Maintaining internal representations: the role of the human superior parietal lobe. *Nature Neuroscience*, *1*, 529-533.

Zaal, F. T., & Bootsma, R. J. (1993). Accuracy demands in natural prehension. *Human Movement Science*, *12*, 339-345.

Zatsiorsky, V. M., Gao, F., & Latash, M. L. (2003). Prehension synergies: effects of object geometry and prescribed torques. *Experimental Brain Research*, *148*, 77-87.

Acknowledgments

I would like to thank Professor Umberto Castiello for his supervision and for providing the funding and the environment as to perform the research reported in this thesis. Livia Giosa, Veronica Tognin, Federico Tubaldi, Luca Turella are also thanked for helping with data collection. Finally, I would like to thank Gianmarco Altoè and Stefano Massaccesi for statistical advice and technical support, respectively.

APPENDIX A

MANOVA results for both metacarpal-phalangeal (MCP) and proximal interphalangeal (PIP) joints for all digits.

Digit	Joint	Experimental Condition	Time	Experimental Condition x Time
Thumb	MCP	$F_{(1,24)} = 14.122$, $P<.002$	$F_{(9,216)} = 14.540$, $P<.0001$	$F_{(9,216)} = 2.117$, $P<.03$
	PIP	$F_{(1,24)} = 8.922$, $P<.007$	$F_{(9,216)} = 29.322$, $P<.0001$	$F_{(9,216)} = 3.378$, $P<.002$
Index	MCP	$F_{(1,24)} = 2.933$, NS	$F_{(9,216)} = 24.803$, $P<.0001$	$F_{(9,216)} = 1.848$, NS
	PIP	$F_{(1,24)} = 5.613$, $P<.027$	$F_{(9,216)} = 19.340$, $P<.0001$	$F_{(9,216)} = 6.782$, $P<.0001$
Middle	MCP	$F_{(1,24)} = 5.993$, $p<.023$	$F_{(9,216)} = 23.601$, $P<.0001$	$F_{(9,216)} = 1.931$, $P<.05$
	PIP	$F_{(1,24)} = 0.035$, NS	$F_{(9,216)} = 16.656$, $P<.0001$	$F_{(9,216)} = 4.463$, $P<.0001$
Ring	MCP	$F_{(1,24)} = 7.285$, $P<.014$	$F_{(9,216)} = 19.064$, $P<.0001$	$F_{(9,216)} = 0.873$, NS
	PIP	$F_{(1,24)} = 0.298$, NS	$F_{(9,216)} = 21.233$, $P<.0001$	$F_{(9,216)} = 4.574$, $P<.0001$
Little	MCP	$F_{(1,24)} = 9.124$, $P<.007$	$F_{(9,216)} = 36.393$, $P<.0001$	$F_{(9,216)} = 2.059$, $P<.035$
	PIP	$F_{(1,24)} = 1.423$, NS	$F_{(9,216)} = 29.837$, $P<.0001$	$F_{(9,216)} = 2.805$, $P<.005$

Notes. NS = not significant

APPENDIX B

MANOVA results for both metacarpal-phalangeal (MCP) and proximal interphalangeal (PIP) joints for all digits.

Digit	Joint	Experimental Condition	Time	Experimental Condition x Time
Thumb	MCP	$F_{(1,24)} = 17.224$, $P<.0001$	$F_{(9,216)} = 53.512$, $P<.0001$	$F_{(9,216)} = 6.979$, $P<.0001$
	PIP	$F_{(1,24)} = 2.907$, NS	$F_{(9,216)} = 37.725$, $P<.0001$	$F_{(9,216)} = 7.232$, $P<.0001$
Index	MCP	$F_{(1,24)} = 24.048$, $P<.0001$	$F_{(9,216)} = 168.11$, $P<.0001$	$F_{(9,216)} = 39.076$, $P<.0001$
	PIP	$F_{(1,24)} = 3.785$, NS	$F_{(9,216)} = 47.089$, $P<.0001$	$F_{(9,216)} = 10.712$, $P<.0001$
Middle	MCP	$F_{(1,24)} = 19.202$, $P<.0001$	$F_{(9,216)} = 179.944$, $P<.0001$	$F_{(9,216)} = 45.146$, $P<.0001$
	PIP	$F_{(1,24)} = 0.157$, NS	$F_{(9,216)} = 37.183$, $P<.0001$	$F_{(9,216)} = 7.711$, $P<.0001$
Ring	MCP	$F_{(1,24)} = 10.307$, $P<.005$	$F_{(9,216)} = 65.872$, $P<.0001$	$F_{(9,216)} = 17.568$, $P<.0001$
	PIP	$F_{(1,24)} = 2.220$, NS	$F_{(9,216)} = 58.897$, $P<.0001$	$F_{(9,216)} = 7.277$, $P<.0001$
Little	MCP	$F_{(1,24)} = 9.275$, $P<.007$	$F_{(9,216)} = 18.621$, $P<.0001$	$F_{(9,216)} = 16.354$, $P<.0001$
	PIP	$F_{(1,24)} = 4.384$, $P<.048$	$F_{(9,216)} = 73.632$, $P<.0001$	$F_{(9,216)} = 6.508$, $P<.0001$

Notes. NS = not significant

APPENDIX C

Main effects for the MANOVA performed on angular excursion of both metacarpal-phalangeal (MCP) and proximal interphalangeal (PIP) joints for all digits.

Digit	Joint	Object	Distractor Type	Time
Thumb	MCP	$F_{(1,19)}$ = 1.271, NS	$F_{(2,38)}$ = .111, NS	$F_{(9,171)}$ = 46.841, P<.0001
	PIP	$F_{(1,19)}$ = 3.014, NS	$F_{(2,38)}$ = 8.066, P<.002	$F_{(9,171)}$ = 42.704, P<.0001
Index	MCP	$F_{(1,19)}$ = 1.147, NS	$F_{(2,38)}$ = 1.966, NS	$F_{(9,171)}$ = 75.349, P<.0001
	PIP	$F_{(1,19)}$ = 8.524, P<.01	$F_{(2,38)}$ = .423, NS	$F_{(9,171)}$ = 121.544, P<.0001
Middle	MCP	$F_{(1,19)}$ = .181, NS	$F_{(2,38)}$ = .821, NS	$F_{(9,171)}$ = 112.430, P<.0001
	PIP	$F_{(1,19)}$ = 15.478, P<.002	$F_{(2,38)}$ = .958, NS	$F_{(9,171)}$ = 78.363, P<.0001
Ring	MCP	$F_{(1,19)}$ = 42.182, P<.0001	$F_{(2,38)}$ = .082, NS	$F_{(9,171)}$ = 29.710, P<.0001
	PIP	$F_{(1,19)}$ = 3.550, NS	$F_{(2,38)}$ = .087, NS	$F_{(9,171)}$ = 107.454, P<.0001
Little	MCP	$F_{(1,19)}$ = 2.852, NS	$F_{(2,38)}$ = .056, NS	$F_{(9,171)}$ = 11.048, P<.0001
	PIP	$F_{(1,19)}$ = 2.386, NS	$F_{(2,38)}$ = 2.712, NS	$F_{(9,171)}$ = 41.627, P<.0001

Notes. NS = not significant

APPENDIX D

Two- and three way interactions for the MANOVA performed on angular excursion recorded of both metacarpal-phalangeal (MCP) and proximal interphalangeal (PIP) joints for all digits.

Digit	Joint	Object x Distractor Type	Object x Time	Distractor Type x Time	Object x Distractor Type x Time
Thumb	MCP	$F_{(2,38)}$ = .692, NS	$F_{(9,171)}$ = 1.888, NS	$F_{(18,342)}$ = .678, NS	$F_{(18,342)}$ = .973, NS
	PIP	$F_{(2,38)}$ = .234, NS	$F_{(9,171)}$ = 4.856, P<.0001	$F_{(18,342)}$ = 1.004, NS	$F_{(18,342)}$ = 2.496, P<.002
Index	MCP	$F_{(2,38)}$ = .598, NS	$F_{(9,171)}$ = 1.557, NS	$F_{(18,342)}$ = .837, NS	$F_{(18,342)}$ = .532, NS
	PIP	$F_{(2,38)}$ = .361, NS	$F_{(9,171)}$ = 5.934, P<.001	$F_{(18,342)}$ = .499, NS	$F_{(18,342)}$ = 2.049, NS
Middle	MCP	$F_{(2,38)}$ = .017, NS	$F_{(9,171)}$ = 1.262, NS	$F_{(18,342)}$ = 1.692, P<.04	$F_{(18,342)}$ = 2.081, P<.007
	PIP	$F_{(2,38)}$ = .321, NS	$F_{(9,171)}$ =14.212, P<.0001	$F_{(18,342)}$ = 1.005, NS	$F_{(18,342)}$ = .262, NS
Ring	MCP	$F_{(2,38)}$ = .610, NS	$F_{(9,171)}$ =20.526, P<.0001	$F_{(18,342)}$ = .606, NS	$F_{(18,342)}$ = .509, NS
	PIP	$F_{(2,38)}$ = .011, NS	$F_{(9,171)}$ =3.555, P<.0001	$F_{(18,342)}$ = 1.192, NS	$F_{(18,342)}$ = 1.546, NS
Little	MCP	$F_{(2,38)}$ =1.165, NS	$F_{(9,171)}$ = 1.698, NS	$F_{(18,342)}$ = 1.730, P<.035	$F_{(18,342)}$ = .551, NS
	PIP	$F_{(2,38)}$ = .698, NS	$F_{(9,171)}$ = 5.100, P<.0001	$F_{(18,342)}$ = .829, NS	$F_{(18,342)}$ = .727, NS

Notes. NS = not significant

APPENDIX E

Main effects for the MANOVA performed on the angular distances between fingers.

Fingers' abduction angle	Object	Distractor Type	Time
Thumb-Index	$F_{(1,19)} = .056$, NS	$F_{(2,38)} = 4.665$, $P<.016$	$F_{(9,171)} = 154.551$, $P<.0001$
Index-Middle	$F_{(1,19)} = .039$, NS	$F_{(2,38)} = .160$, NS	$F_{(9,171)} = 14.832$, $P<.0001$
Middle-Ring	$F_{(1,19)} = 8.905$, $P<.009$	$F_{(2,38)} = .163$, NS	$F_{(9,171)} = 10.882$, $P<.0001$
Ring-Little	$F_{(1,19)} = 17.310$, $P<.002$	$F_{(2,38)} = 1.677$, NS	$F_{(9,171)} = 3.527$, $P<.0001$

Notes. NS = not significant

APPENDIX F

Two- and three way interactions for the MANOVA performed on the angular distances between fingers.

Fingers' abduction angle	Object x Dystractor Type	Object x Time	Dystractor Type x Time	Object x Dystractor Type x Time
Thumb-Index	$F_{(2,342)}$ = .128, NS	$F_{(9,171)}$ = .416, NS	$F_{(18,324)}$ = 1.564, NS	$F_{(18,324)}$ = 1.544, NS
Index-Middle	$F_{(2,342)}$ = .205, NS	$F_{(9,171)}$ = .099, NS	$F_{(18,324)}$ = 1.225, NS	$F_{(18,324)}$ = .476, NS
Middle-Ring	$F_{(2,342)}$ = .050, NS	$F_{(9,171)}$ = 7.624, $P<.0001$	$F_{(18,324)}$ = 1.645, $P<.049$	$F_{(18,324)}$ = .255, NS
Ring-Little	$F_{(2,342)}$ = .497, NS	$F_{(9,171)}$ = 10.451, $P<.0001$	$F_{(18,324)}$ = 1.616, $P=.054$	$F_{(18,324)}$ = .731, NS

Notes. NS = not significant

APPENDIX G

MANOVA results for both metacarpal-phalangeal (MCP) and proximal interphalangeal (PIP) joints for all fingers.

Digit	Joint	Experimental Condition	Time	Experimental Condition x Time
Index	MCP	$F_{(2,16)} = .314$, NS	$F_{(9,72)} = 7.555$, $P < .0001$	$F_{(18,144)} = .801$, NS
	PIP	$F_{(2,16)} = 1.216$, $P < .027$	$F_{(9,72)} = 4.814$, $P < .0001$	$F_{(18,144)} = .702$, NS
Middle	MCP	$F_{(2,16)} = 1.621$, NS	$F_{(9,72)} = 5.595$, $P < .0001$	$F_{(18,144)} = 1.373$, NS
	PIP	$F_{(2,16)} = .115$, NS	$F_{(9,72)} = 11.949$, $P < .0001$	$F_{(18,144)} = 1.466$, NS
Ring	MCP	$F_{(2,16)} = .069$, NS	$F_{(9,72)} = 5.405$, $P < .0001$	$F_{(18,144)} = 1.761$, $P < .05$
	PIP	$F_{(2,16)} = .440$, NS	$F_{(9,72)} = 4.980$, $P < .0001$	$F_{(18,144)} = 2.132$, $P < .01$
Little	MCP	$F_{(2,16)} = .558$, NS	$F_{(9,72)} = 3.142$, $P < .01$	$F_{(18,144)} = 1.682$, $P < .05$
	PIP	$F_{(2,16)} = .359$, NS	$F_{(9,72)} = 6.230$, $P < .0001$	$F_{(18,144)} = 3.645$, $P < .0001$

Notes. NS = not significant

APPENDIX H

MANOVA results for both metacarpal-phalangeal (MCP) and proximal interphalangeal (PIP) joints for all fingers.

Digit	Joint	Experimental Condition	Time	Experimental Condition x Time
Thumb	MCP	$F_{(4,76)}$ = 1.404, NS	$F_{(9,171)}$ = 54.840, P<.0001	$F_{(36,684)}$ = 5.128, P<.0001
	PIP	$F_{(4,76)}$ = 7.006, P<.0001	$F_{(9,171)}$ = 49.289, P<.0001	$F_{(36,684)}$ = 18.715, P<.0001
Index	MCP	$F_{(4,76)}$ = 3.964, P<.007	$F_{(9,171)}$ = 62.845, P<.0001	$F_{(36,684)}$ = 11.785, P<.0001
	PIP	$F_{(4,76)}$ = 4.325, P<.004	$F_{(9,171)}$ = 84.876, P<.0001	$F_{(36,684)}$ = 18.829 , P<.0001
Middle	MCP	$F_{(4,76)}$ = 6.164, P<.0001	$F_{(9,171)}$ = 64.179, P<.0001	$F_{(36,684)}$ = 6.598, P<.0001
	PIP	$F_{(4,76)}$ = 3.425, P<.02	$F_{(9,171)}$ = 51.464, P<.0001	$F_{(36,684)}$ = 6.702 , P<.0001
Ring	MCP	$F_{(4,76)}$ = 4.841, P<.003	$F_{(9,171)}$ = 63.073, P<.0001	$F_{(36,684)}$ = 4.216, P<.0001
	PIP	$F_{(4,76)}$ = 11.109, P<.0001	$F_{(9,171)}$ = 64.948, P<.0001	$F_{(36,684)}$ = 6.751, P<.0001
Little	MCP	$F_{(4,76)}$ = 7.129, P<.0001	$F_{(9,171)}$ = 34.918, P<.0001	$F_{(36,684)}$ = 5.603, P<.0001
	PIP	$F_{(4,76)}$ = 11.093, P<.0001	$F_{(9,171)}$ = 47.915, P<.0001	$F_{(36,684)}$ = 3.973, P<.0001

Notes. NS = not significant

APPENDIX I

MANOVA results for the angular distances between fingers

Fingers' abduction angle	Experimental Condition	Time	Experimental Condition x Time
Thumb-Index	$F_{(4,76)}$ = 7.148, P<.0001	$F_{(9,171)}$ = 45.575, P<.0001	$F_{(36,684)}$ = 3.255, P<.0001
Index-Middle	$F_{(4,76)}$ = 2.202, NS	$F_{(9,171)}$ = 2.100, P<.04	$F_{(36,684)}$ = 2.499, P<.0001
Middle-Ring	$F_{(4,76)}$ = 4.448, P<.004	$F_{(9,171)}$ = 21.747, P<.0001	$F_{(36,684)}$ = 5.574, P<.0001
Ring-Little	$F_{(4,76)}$ = 1.438, NS	$F_{(9,171)}$ = 15.835, P<.0001	$F_{(36,684)}$ = 2.878, P<.0001

Notes. NS = not significant