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RESEARCH ARTICLE

Control of hand shaping in response to object shape perturbation

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Abstract This study assessed how hand shaping responds to a perturbation of object shape. In *blocked* trials (80% of total), subjects were instructed to reach, to grasp and lift a concave or a convex object. In *perturbed* trials (20% of total), a rotating device allowed for the rapid change from the concave to the convex object or vice versa. In this situation subjects grasped the last presented object. Flexion/extension at the metacarpal-phalangeal and proximal interphalangeal joints of all digits was measured by resistive sensors embedded in a glove. 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 (i.e., over-flexion with respect to the blocked trials) 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 assigns to opposing digits different roles.

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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 central nervous system (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 et al. 1985; Bingham et al. 1986; Iberall and Fagg 1996; Santello and Soechting 1998; Santello et al. 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 maximum grip aperture (e.g., Castiello et al. 1992, 1993, 1998; Paulignan et al. 1990, 1991; Savelsbergh et al. 1991). 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 and Soechting 1998), 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 peak grip aperture as previously reported.

Here, we tackle this issue by providing a description of how hand-shaping (i.e., angular excursion at both metacarpal-phalangeal (*mcp*) and proximal interphalangeal (*pip*) joints for all digits) reacts to an object shape perturbation. In the present experiment, subjects 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 (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 were 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?

Methods

Subjects

Twenty-five subjects (13 females and 12 males, aged 21–29) took part in the experiment. All participants showed right-handed dominance and reported normal or corrected-to-normal vision. All subjects were naïve as to the experimental purpose 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.

Stimuli and apparatus

The stimuli were one concave and one convex wooden-object (Fig. 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 weighed ~100 g. Both the concave and convex objects were accommodated back to back within a device (Fig. 1a, b). A rectangular black paperboard was placed between objects so that only one object at the time was visible (Fig. 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 (Fig. 1b). The onset of object rotation was triggered by a pressure switch, released at the onset of the reach (see below). 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.

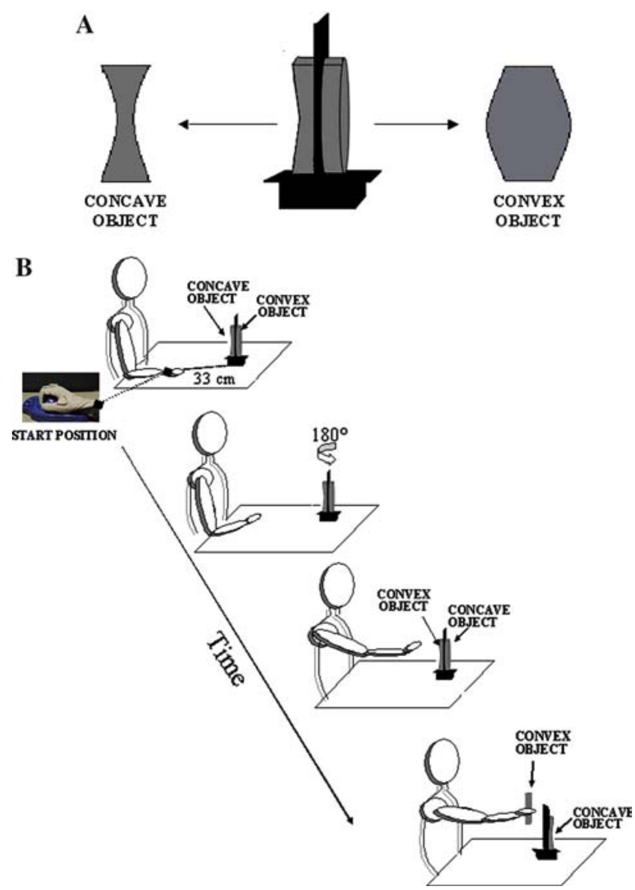

Fig. 1 The objects used as targets in the present experiment and the device by which the perturbation was produced **(a)**. Schematic representation of the subject's posture, the initial hand-posture for the right hand, and an example of the time course for a perturbed trial **(b)**. Figure is not on scale

Procedures

The subject 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 in the start position (Fig. 1b). In this start position, the hand was in a pronated position with the palm towards the table on a pressure switch. To make sure that the initial posture of hand was similar for all subjects across trials, the surface within which the pressure switch was embedded was designed with slight convexities dictating a natural flexed posture of the fingers (see Fig. 1b). Subject was required to reach to, grasp and lift the object after hearing an auditory signal (Hz = 880; duration = 200 ms). The subject was instructed to reach at a natural speed and grasp with all fingers opposing the thumb on the concave/convex sides of the target object. The object was aligned with the subjects' body midline and located at 33-cm-distance from the starting position to the left of the subject's right shoulder. Such positioning allowed for a comfortable reach to grasp movement by avoiding the necessity to adopt an extreme extension of the wrist during the movement itself. When subjects did not grasp the object using all fingers, the trial was discarded and repeated. Subjects 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. 1b). The latter object was then the actual target for the reach and grasp movement (Fig. 1b). We define trials performed in this condition as 'perturbed' trials.

Four types of trial within two 50 trial blocks were administered: (a) *blocked concave* ($n = 40$) in which the subjects reached towards and grasped the concave object; (b) *blocked convex* ($n = 40$) in which the subject reached towards and grasped the convex object; (c) *perturbed convex* → *concave* ($n = 10$) in which the subject 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 subject 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.

Recording techniques

Hand posture was measured by resistive sensors embedded in a glove (CyberGlove, Virtual Technologies, Palo Alto, CA, USA), worn on the right hand. The sensors' linearity was 0.62% of maximum nonlinearity over the full range of hand motion. The sensors' resolution was 0.5°, which remains constant over the entire range of joint motion. The output of the transducers was sampled at 12-ms interval. Angular excursion was measured at *mcp* and *pip* joints of the thumb, index, middle, ring, and little fingers. Before starting the experiment, we recorded the reference hand posture for each subject by asking them to position their right hand flat on the table 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. At the beginning of each trial, the subject's hand contacted a pressure-switch, whose release indicated onset of the reaching movement and 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.

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-subjects factors, was performed. On the basis of previous perturbation studies, we expected 'blocked' and 'perturbed' trials to differ with respect to reach duration (e.g., Castiello et al. 1993; Paulignan et al. 1991). As object shape perturbation did affect reach duration, we time-normalized the duration of the reach. We believe that another advantage of normalizing reach duration is that kinematic differences may be better understood when the occurrence of kinematic events is expressed in terms relative to the overall reach duration. Then, 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 subjects.

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). Main effects were used to explore the means of interest. Bonferroni corrections (alpha level: $P < 0.05$) were applied.

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 is presented separately for reach duration (ANOVA), the pattern of linear correlation, and the pattern of fingers' angular excursion (MANOVAs).

Concave versus 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 (1,366 vs. 1,326 ms; $P < 0.05$). Although for both considered objects the strength of the linear correlation increased during reaching time (see Fig. 2), correlation analysis revealed some differences. For instance, for the concave object, a significant level of correlation was reached from the beginning (i.e., 10–20%) and maintained until the end of the movement for both the *mcp* and the *pip* joints of all digits (Fig. 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. 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 (see Fig. 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).

Convex → concave perturbation

Reach duration

The main factor 'Experimental Condition' was significant [$F_{(1,24)} = 36.475$, $P < 0.0001$]. Reach duration was longer for 'perturbed' (1,498 ms) than for 'blocked' trials (1,366 ms).

Linear regression analysis

Results from linear regression analysis revealed that *r*-values obtained for 'perturbed' trials were generally lower than those obtained for 'blocked' trials (see Fig. 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. 4). For the *pip* joint of the thumb, a significant level of correlation was reached at 30% of reaching duration. For 'blocked' trials, the earlier mentioned joints reached a significant level of correlation from the very beginning to the end of the movement (Fig. 4).

Pattern of angular excursion

Table 1 shows the results obtained from the MANOVAs when comparing 'blocked' and 'perturbed' trials

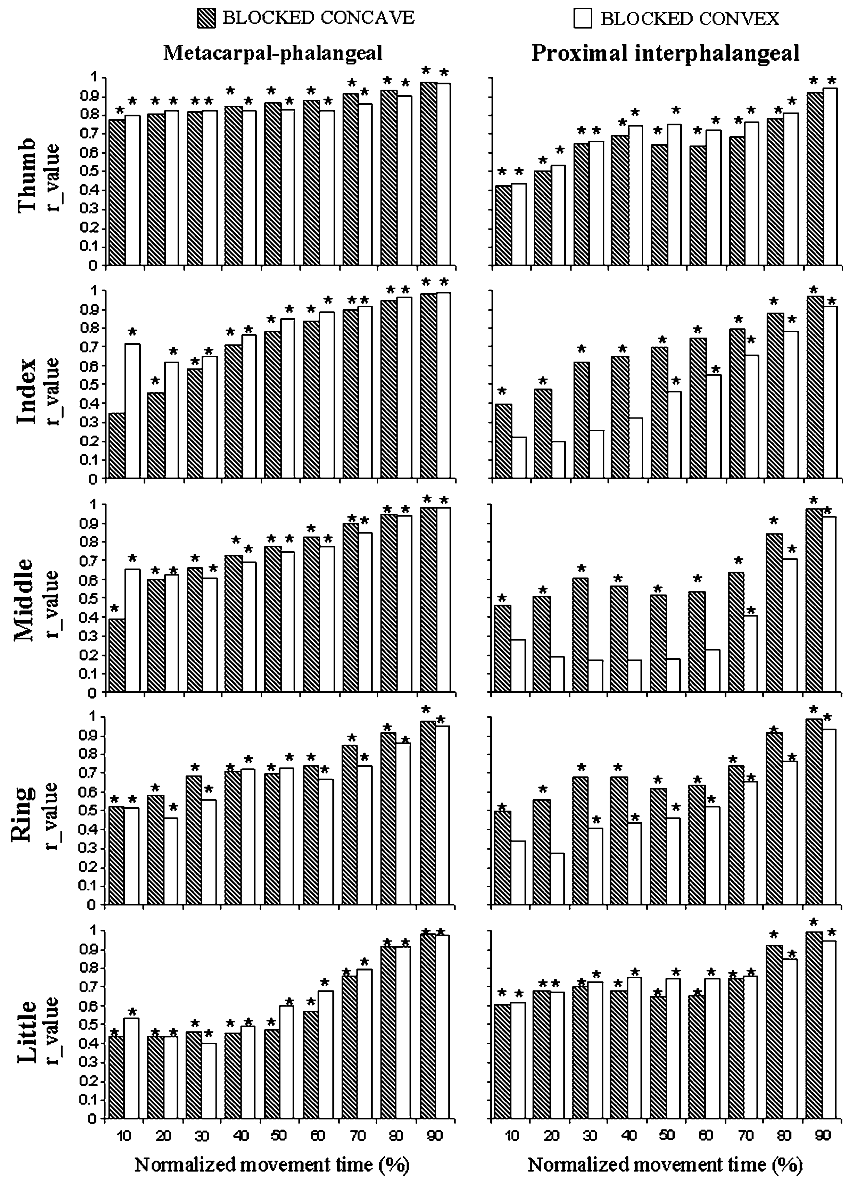

Fig. 2 Correlation coefficients between joint angles during the reach versus joint angles at the end of the movement for 'blocked' trials. *Each panel* shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at the reaching end for the concave (*patterned bars*) and the convex (*white bars*) objects. Data on the *left* and *right columns* correspond to the metacarpal-phalangeal (*mcp*) and the proximal interphalangeal (*pip*) joints' correlation coefficients, respectively, for each digit. An *r* value > 0.397 is significant at $P < 0.05$. *Asterisks* indicate the significant correlation values

ending with the concave object. These analyses 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. For example, the *mcp* of the ring finger showed a greater extension for 'perturbed' (22.6°) than for 'blocked' trials (24.3°) (main factor 'Experimental Condition'; see Table 1). For the remaining joints, the two-ways interaction 'Experimental Condition × Time' was significant (see Table 1). These results indicated that both *mcp* and *pip* joints of the thumb, the middle finger and the little finger, the *pip* joint of 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. 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 of the middle, and the *pip* joint of both the index and the ring finger, and the *mcp* joint of the little finger were generally more extended for 'perturbed' than for 'blocked' trials from 30–40 to 70–80% of the reaching movement (Fig. 5).

Concave → Convex perturbation

Reach duration

The main factor 'Experimental Condition' was significant [$F_{(1,24)} = 36.475$, $P < 0.0001$]. Reach duration was longer for 'perturbed' (1,450 ms) than for 'blocked' trials (1,326 ms).

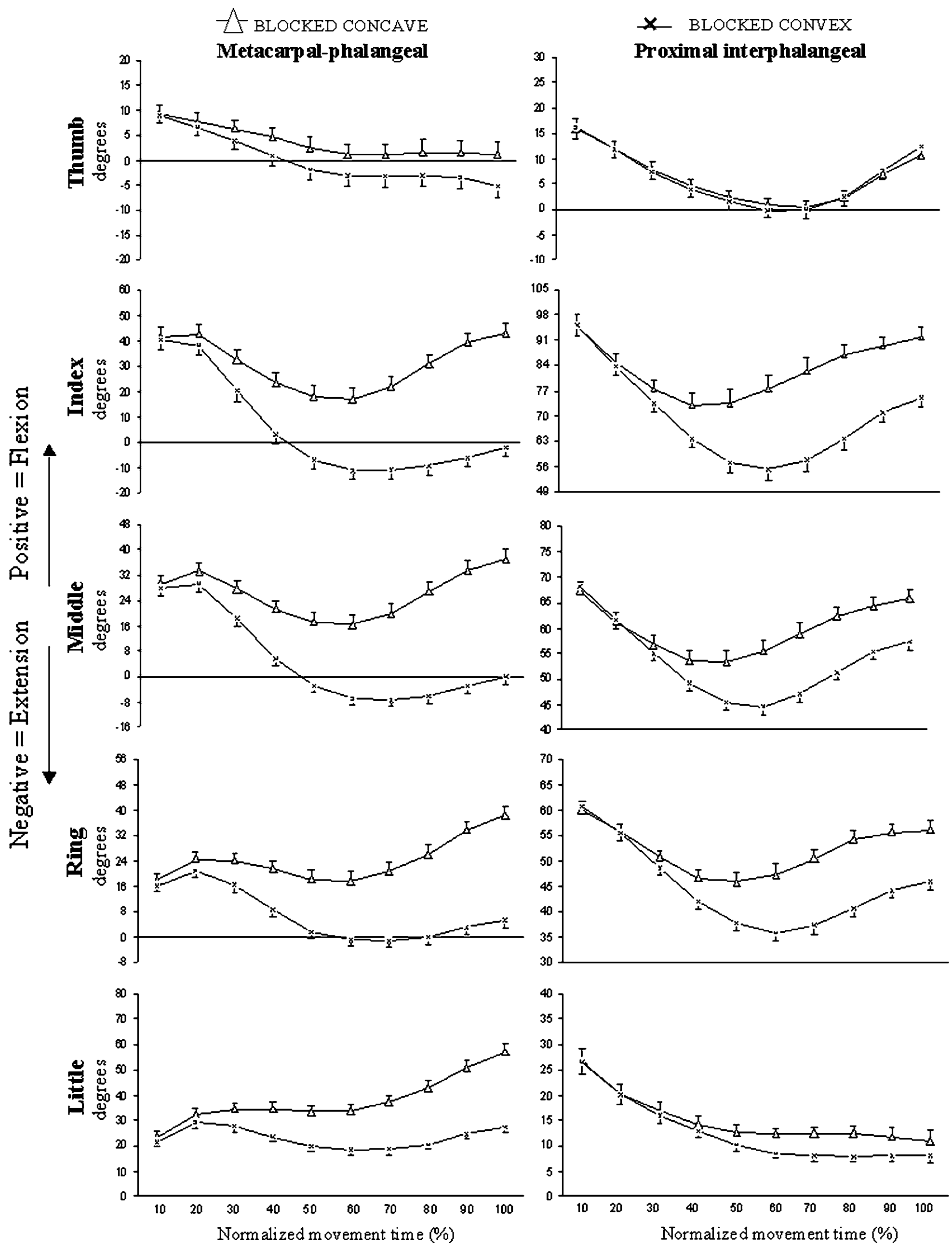

Fig. 3 Time course of finger motion during reaching for 'blocked' trials. *Each trace* denotes average angular excursion across trials and subjects of *mcp* (*left panels*) and *pip* (*right panels*) joints of the thumb, index, middle, ring, and little finger performed in 'blocked' trials for the concave (*empty triangles*) and the convex (*crosses*) object. Positive values correspond to fingers' flexion whereas negative values correspond to fingers' extension. *Bars* represent the standard error

Linear regression analysis

Results from the linear regression analysis revealed that *r*-values were lower for 'perturbed' than for 'blocked' trials (see Fig. 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. 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. 6).

Pattern of angular excursion

Table 2 shows the results obtained from the five MANOVAs performed to compare 'blocked' and 'perturbed' trials ending with the convex object.

As revealed by the significance of the two-way interaction (i.e., 'Experimental Condition' × 'Time') for all analyzed joints the effect of the perturbation on hand shaping varied along reaching time. As depicted in Fig. 7 both the *mcp* and the *pip* joints of all digits were more flexed for

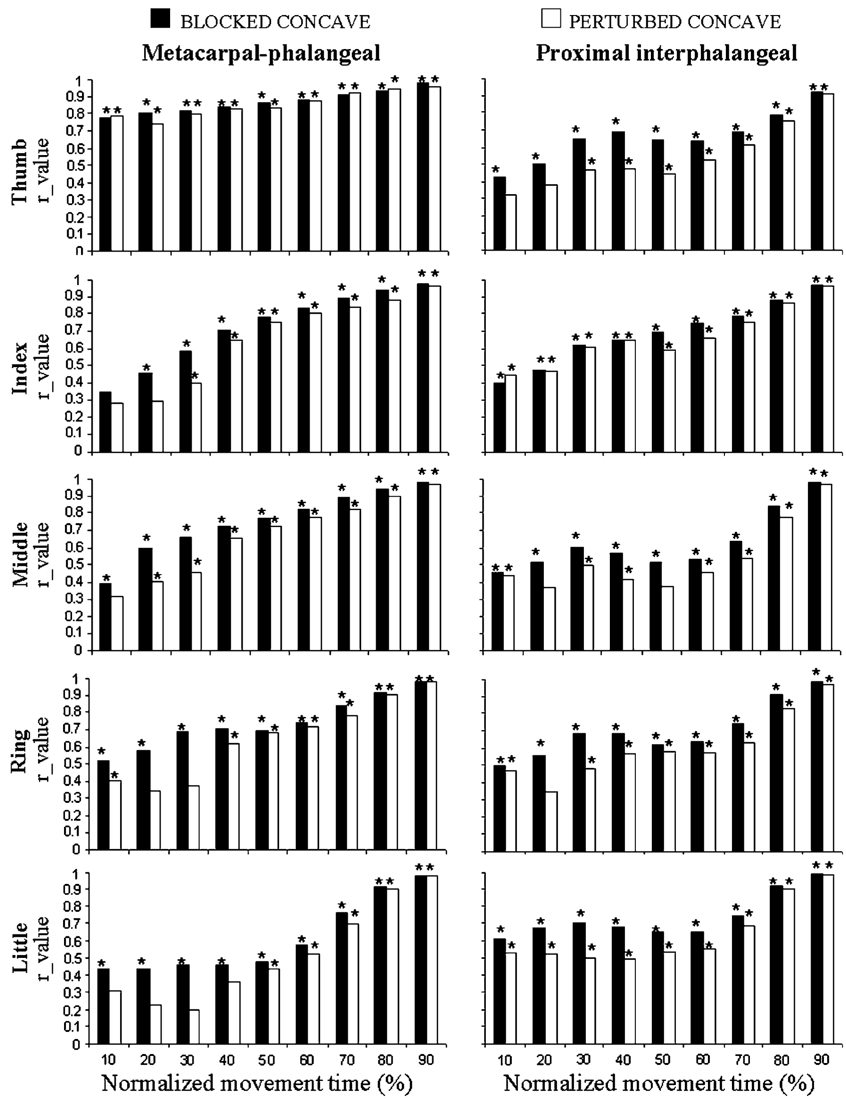

Fig. 4 Correlation coefficients between joint angles during the reach versus joint angles at the end of the movement for 'blocked' concave and 'perturbed' concave trials. *Each panel* shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at the 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 *mcp* and the *pip* joints' correlation coefficients, respectively, for each digit. An *r* value > 0.397 is significant at *P* < 0.05. *Asterisks* indicate the significant correlation values

Table 1 MANOVA results for the main factors 'Experimental Condition', 'Time', and the interaction 'Experimental Condition by Time' for the 'convex-concave' perturbation for both metacarpal-phalangeal (*mcp*) and proximal interphalangeal (*pip*) joints of all digits

Digit	Joint	Experimental Condition	Time	Experimental Condition × Time
Thumb	*mcp*	$F_{(1,24)} = 14.122$, $P < 0.002$	$F_{(9,216)} = 14.540$, $P < 0.0001$	$F_{(9,216)} = 2.117$, $P < 0.03$
	pip	$F_{(1,24)} = 8.922$, $P < 0.007$	$F_{(9,216)} = 29.322$, $P < 0.0001$	$F_{(9,216)} = 3.378$, $P < 0.002$
Index	*mcp*	$F_{(1,24)} = 2.933$, NS	$F_{(9,216)} = 24.803$, $P < 0.0001$	$F_{(9,216)} = 1.848$, NS
	pip	$F_{(1,24)} = 5.613$, $P < 0.027$	$F_{(9,216)} = 19.340$, $P < 0.0001$	$F_{(9,216)} = 6.782$, $P < 0.0001$
Middle	*mcp*	$F_{(1,24)} = 5.993$, $P < 0.023$	$F_{(9,216)} = 23.601$, $P < 0.0001$	$F_{(9,216)} = 1.931$, $P < 0.05$
	pip	$F_{(1,24)} = 0.035$, NS	$F_{(9,216)} = 16.656$, $P < 0.0001$	$F_{(9,216)} = 4.463$, $P < 0.0001$
Ring	*mcp*	$F_{(1,24)} = 7.285$, $P < 0.014$	$F_{(9,216)} = 19.064$, $P < 0.0001$	$F_{(9,216)} = 0.873$, NS
	pip	$F_{(1,24)} = 0.298$, NS	$F_{(9,216)} = 21.233$, $P < 0.0001$	$F_{(9,216)} = 4.574$, $P < 0.0001$
Little	*mcp*	$F_{(1,24)} = 9.124$, $P < 0.007$	$F_{(9,216)} = 36.393$, $P < 0.0001$	$F_{(9,216)} = 2.059$, $P < 0.035$
	pip	$F_{(1,24)} = 1.423$, NS	$F_{(9,216)} = 29.837$, $P < 0.0001$	$F_{(9,216)} = 2.805$, $P < 0.005$

NS not significant

'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. 7).

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.

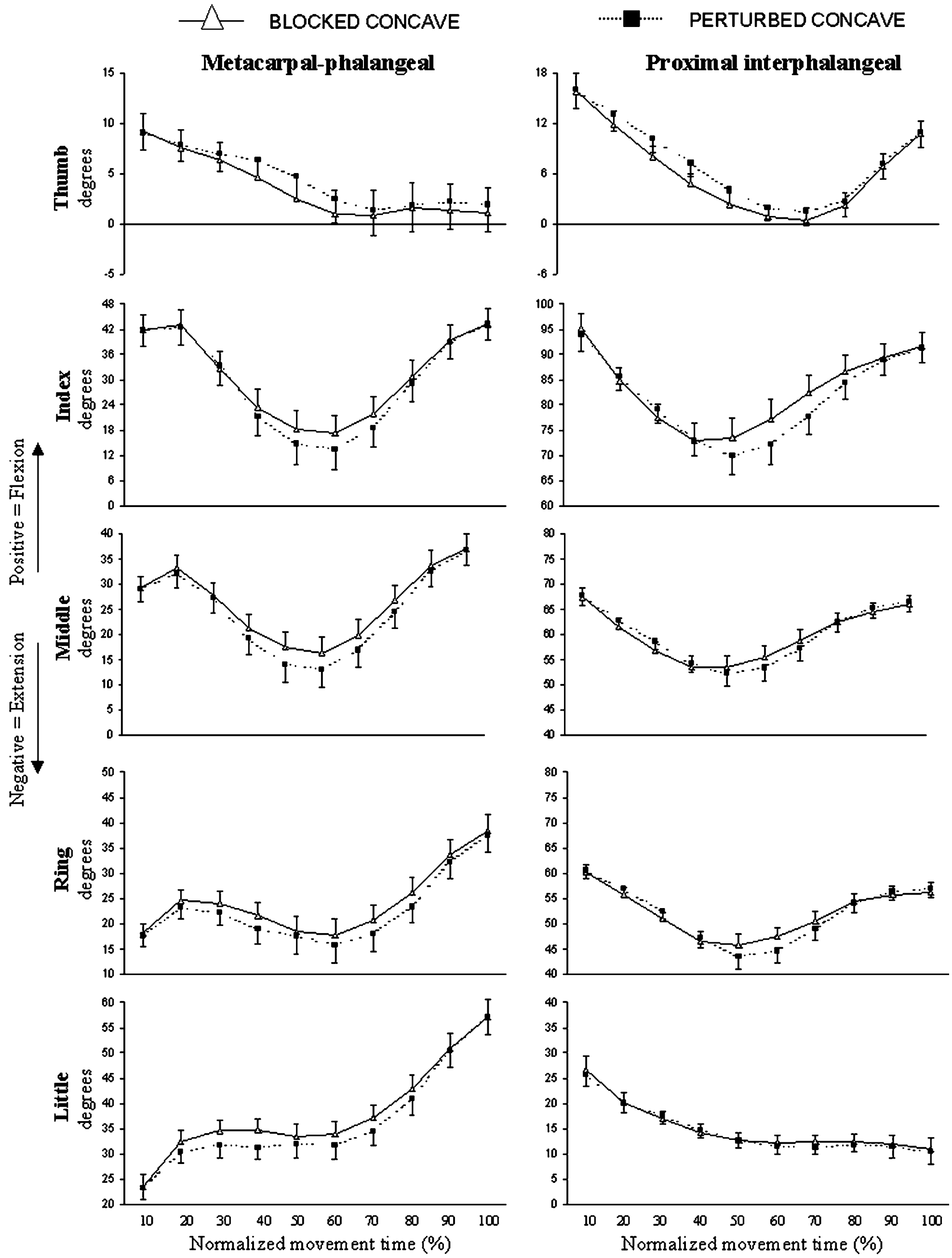

Fig. 5 Time course of finger motion during reaching for 'blocked' concave versus 'perturbed' concave trials. *Each panel* shows the angular excursion averaged across trials and subjects of *mcp* (*left panels*) and *pip* (*right panels*) joints of the thumb, index, middle, ring, and little finger performed in 'blocked' concave (*empty triangles*) and 'perturbed' concave (*filled squares*) trials. Positive values correspond to fingers' flexion whereas negative values correspond to fingers' extension. *Bars* represent the standard error

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

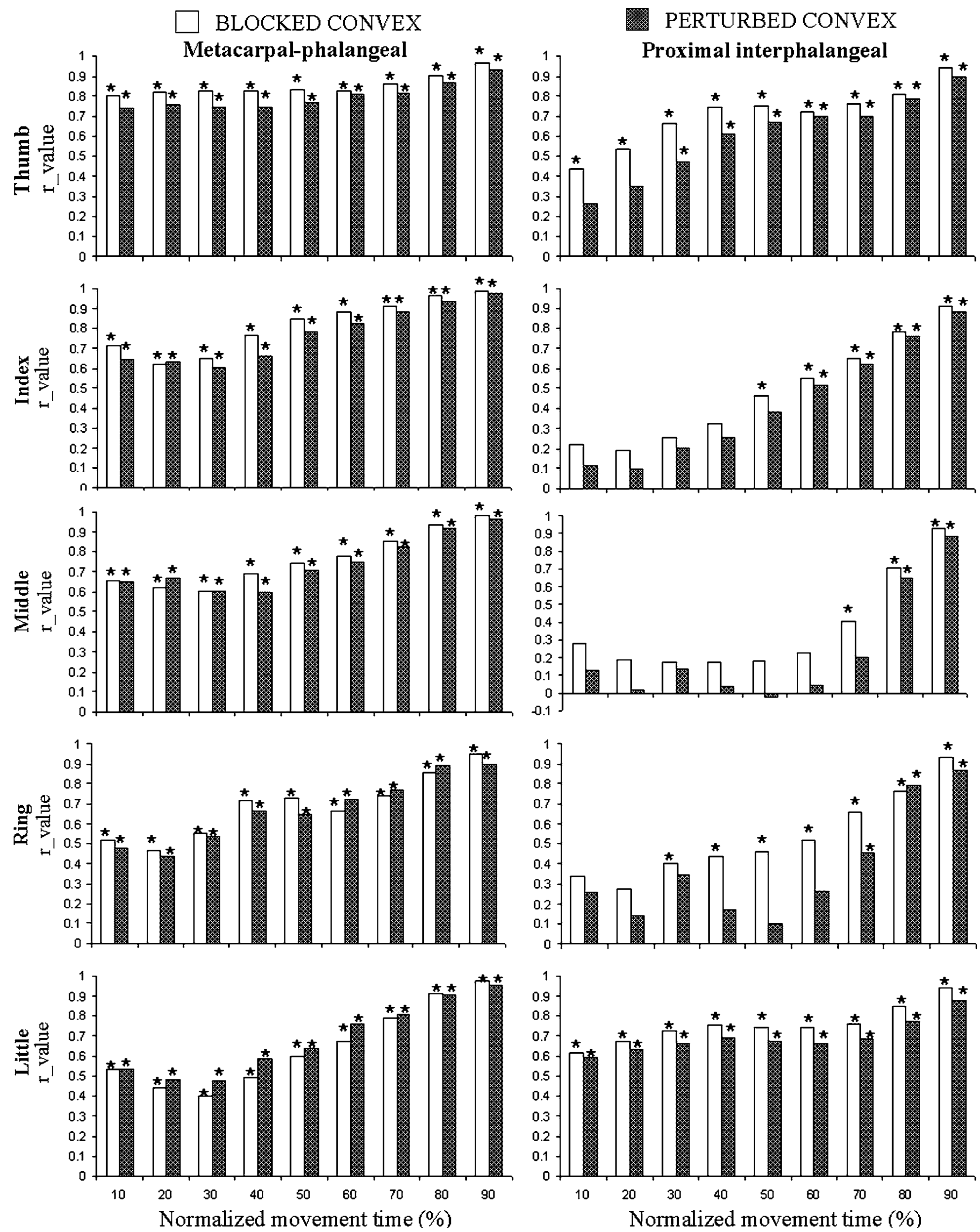

Fig. 6 Correlation coefficients between joint angles during the reach versus joint angles at the end of the movement for 'blocked' convex and 'perturbed' convex trials. *Each panel* shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at the reaching end for the 'blocked' convex (*white bars*) and the 'perturbed' convex (*grey bars*) trials. Data on the *left* and *right columns* correspond to the *mcp* and the *pip* joints' correlation coefficients, respectively, for each digit. An *r* value > 0.397 is significant at $P < 0.05$. *Asterisks* indicate the significant correlation values

Table 2 MANOVA results for the main factors 'Experimental Condition', 'Time', and the interaction 'Experimental Condition by Time' for the 'concave-convex' perturbation for both *mcp* and *pip* joints of all digits

Digit	Joint	Experimental Condition	Time	Experimental Condition × Time
Thumb	*mcp*	$F_{(1,24)} = 17.224$, $P < 0.0001$	$F_{(9,216)} = 53.512$, $P < 0.0001$	$F_{(9,216)} = 6.979$, $P < 0.0001$
	pip	$F_{(1,24)} = 2.907$, NS	$F_{(9,216)} = 37.725$, $P < 0.0001$	$F_{(9,216)} = 7.232$, $P < 0.0001$
Index	*mcp*	$F_{(1,24)} = 24.048$, $P < 0.0001$	$F_{(9,216)} = 168.11$, $P < 0.0001$	$F_{(9,216)} = 39.076$, $P < 0.0001$
	pip	$F_{(1,24)} = 3.785$, NS	$F_{(9,216)} = 47.089$, $P < 0.0001$	$F_{(9,216)} = 10.712$, $P < 0.0001$
Middle	*mcp*	$F_{(1,24)} = 19.202$, $P < 0.0001$	$F_{(9,216)} = 179.944$, $P < 0.0001$	$F_{(9,216)} = 45.146$, $P < 0.0001$
	pip	$F_{(1,24)} = 0.157$, NS	$F_{(9,216)} = 37.183$, $P < 0.0001$	$F_{(9,216)} = 7.711$, $P < 0.0001$
Ring	*mcp*	$F_{(1,24)} = 10.307$, $P < 0.005$	$F_{(9,216)} = 65.872$, $P < 0.0001$	$F_{(9,216)} = 17.568$, $P < 0.0001$
	pip	$F_{(1,24)} = 2.220$, NS	$F_{(9,216)} = 58.897$, $P < 0.0001$	$F_{(9,216)} = 7.277$, $P < 0.0001$
Little	*mcp*	$F_{(1,24)} = 9.275$, $P < 0.007$	$F_{(9,216)} = 18.621$, $P < 0.0001$	$F_{(9,216)} = 16.354$, $P < 0.0001$
	pip	$F_{(1,24)} = 4.384$, $P < 0.048$	$F_{(9,216)} = 73.632$, $P < 0.0001$	$F_{(9,216)} = 6.508$, $P < 0.0001$

NS not significant

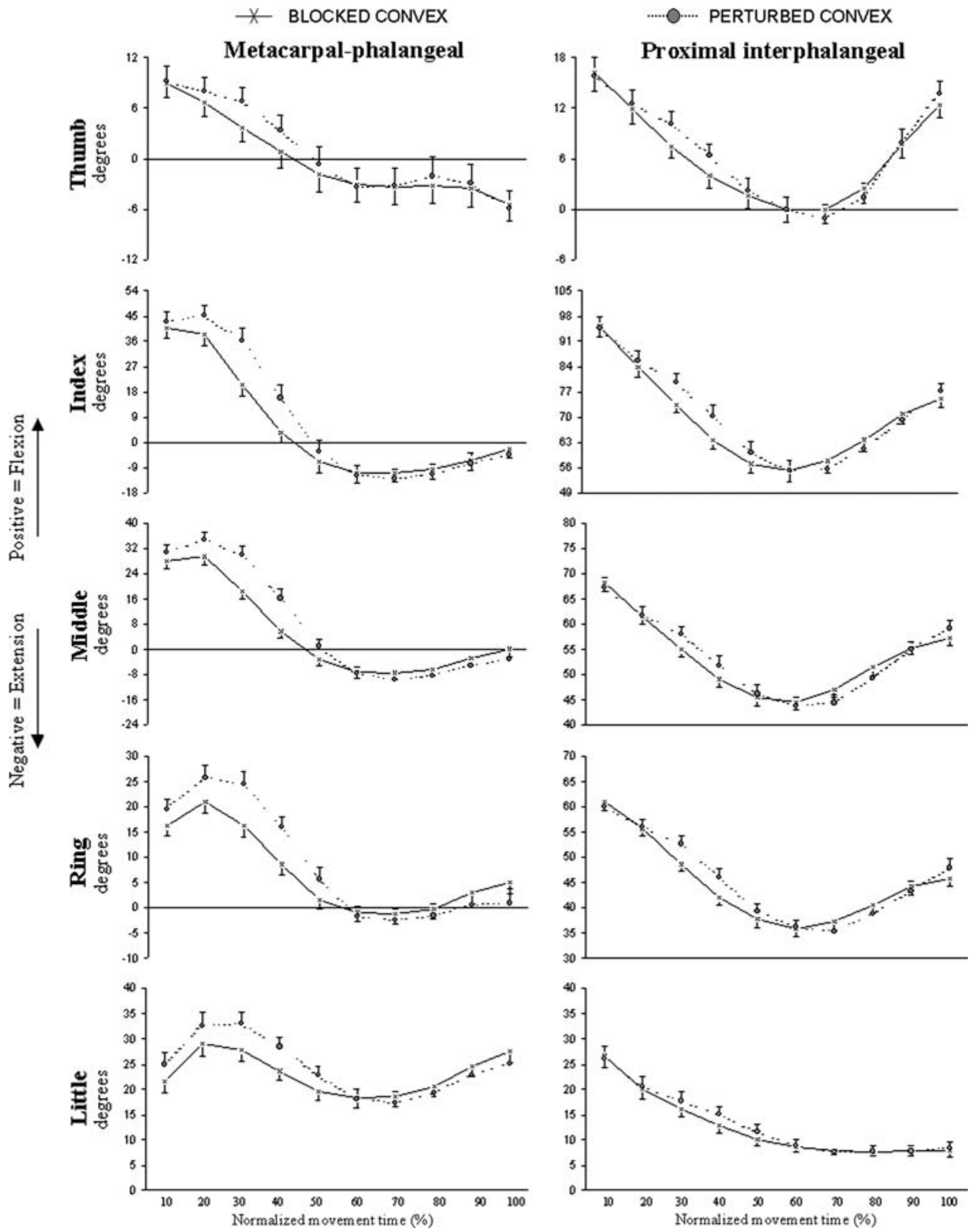

Fig. 7 Time course of finger motion during reaching for ‘blocked’ convex versus ‘perturbed’ convex trials. *Each panel* shows the angular excursion averaged across trials and subjects of *mcp* (*left panels*) and *pip* (*right panels*) joints of the thumb, index, middle, ring, and little finger performed 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

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.

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. 1991), 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. 1991).

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 of 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. 5). In contrast, for the 'concave → convex' perturbation, fingers were more flexed than for the 'blocked' convex trials (see Fig. 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.

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 of 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 (see Figs. 5, 7), it can be noticed that a greater discrepancy was found for trials ending with the convex rather than with the concave object.

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 favored. 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 and 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 modeling (Ulloa and Bullock 2003; see also Hoff and 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. 1991). Importantly, they were able to simulate the differences in the extent of the correction for small versus large and large versus 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.

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* 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 et al. 2001; Galea et al. 2001; Paulignan et al. 1997; Smeets and Brenner 1999; Wing and 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.

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