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Effects of End-Goal on Hand Shaping

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[1]*Dipartimento di Psicologia Generale, Università di Padova, Padova, Italy;* [2]*Department of Kinesiology, Arizona State University, Tempe, Arizona; and* [3]*Royal Holloway, University of London, Egham, Surrey, United Kingdom*

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Ansuini, Caterina, Marco Santello, Stefano Massaccesi, and Umberto Castiello. Effects of end-goal on hand shaping. *J Neurophysiol* 95: 2456–2465, 2006. First published December 28, 2005; doi:10.1152/jn.01107.2005. The aim of the present study was to determine whether hand shaping was affected by planning of an action subsequent to object contact. Ten subjects (5 females and 5 males, ages 19–33) were requested to reach toward and grasp a convex object between the thumb and the four 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. Flexion/extension at the metacarpal-phalangeal and proximal interphalangeal joints of all digits were measured using resistive sensors embedded in a glove. 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 movement 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.

INTRODUCTION

A major theme in motor control is whether contextual factors have an effect on motor behavior. Evidence for such context effects come 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 and Norman 1982), handwriting (Van Galen 1984), manual aiming (Klapp and Greim 1979), finger spelling (Jerde et al. 2003a,b), and prehension (e.g., Cole and Abbs 1986; Gentilucci et al. 1997; Marteniuk et al. 1987; Quaney et al., 2005; Rosenbaum and Jorgensen 1992; Soechting 1984; Stelmach et al. 1994). In general, these context effects indicate that individual movements are often planned not 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 et al. (1987) asked subjects to reach for an object and to either fit it into a similarly sized opening or to 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 and Jorgensen 1992; Rosenbaum et al. 1992).

The above evidence suggests not only that planning plays a role in grasping objects, but also that the execution of prehension, like a variety of other motor behaviors, 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 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 to achieve desired perceptual consequences (e.g., Kawato 1999; Miall and Wolpert 1996). Despite the growing body of evidence for internal models underlying grasping (Quaney et al. 2005; Salimi et al. 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 subjects 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.

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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, i.e., object placement through a tight versus a large niche. Conversely, if context has some influence on the phenomenon of hand shaping, planning different object manipulations should affect the gradual molding of the hand.

Our main results are that the subsequent placement task had an effect on the motion of individual fingers during the reach toward the same object and on the reach duration. In particular, subjects 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 either the large niche were faster than reaches for the other conditions.

METHODS

Subjects

Ten subjects (5 females and 5 males, ages 19–33) took part in the experiment. All participants were right-handed, reported normal or corrected-to-normal vision, and were naive as to the purpose of the experiment. All subjects 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.

Tasks

There were three types of grasping task. For the one object lift task, we used a convex wooden object (see Fig. 1*A*). 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 33 cm from the start location of the hand (Fig. 1*B*) and positioned such that subjects 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 following text), and we used either a convex or a rectangular niche (Fig. 1*A*). 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. 1*A*). 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. 1*A*) The two niches were positioned 6 cm from the object and at a small angle (~3°) relative to it (Fig. 1*B*).

Procedures

Subjects began each trial with the elbow and wrist resting on a flat surface, the forearm horizontal, the arm oriented in the parasagittal plane passing through the shoulder, and the right hand in a pronated

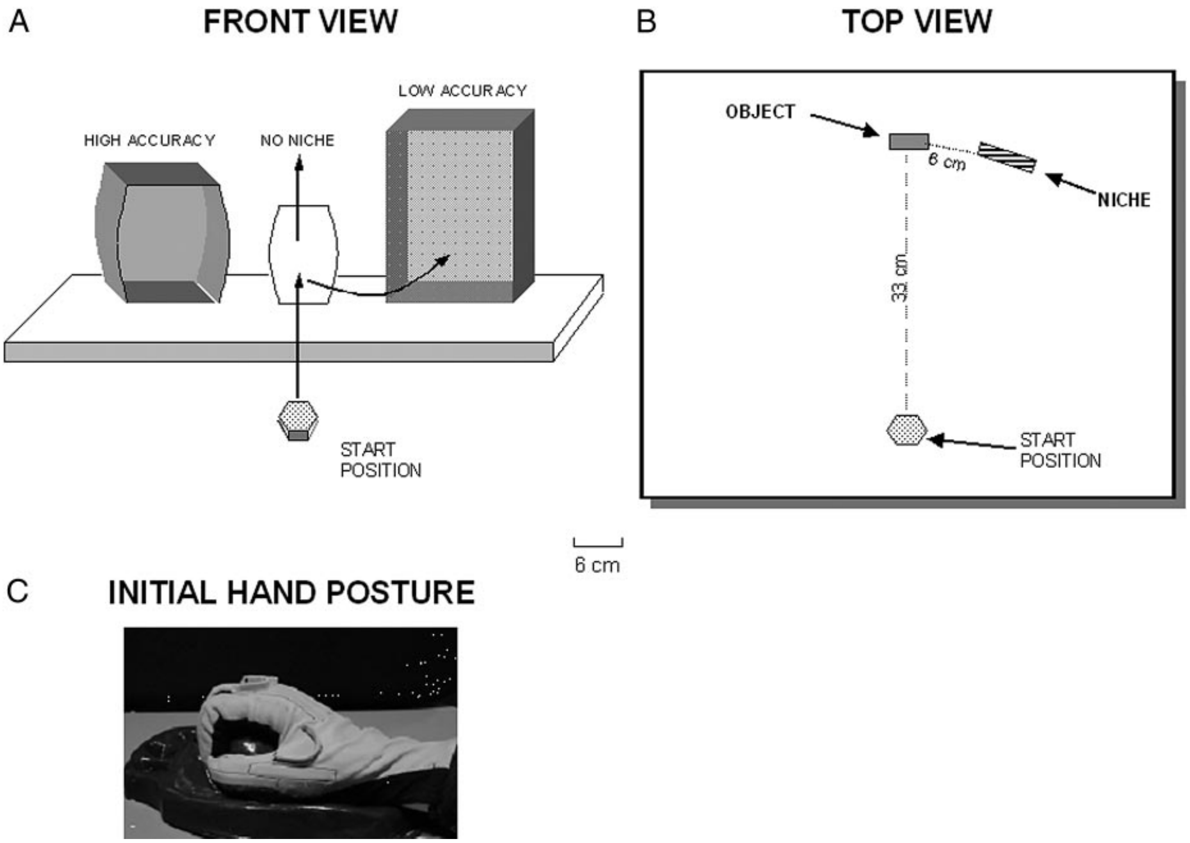

FIG. 1. Experimental set up. *A* and *B*: workspace (front and top view, respectively) and the three experimental conditions [no-niche is equivalent only to the object lift action (arrow direction)]. Although *A* shows both types of niches on both sides of the object, note that only one niche was presented for each block of trials. *C*: initial hand posture.

position with the palm toward the working surface on a pressure switch. To make sure that the initial hand posture was similar for all subjects across trials and conditions, we designed the surface within which the pressure switch was embedded with slight convexities that dictated a natural flexed posture of the fingers (Fig. 1*C*). Subjects were instructed to start the reaching movement after hearing an auditory signal. Subjects were not given specific instructions as to how to clear the surface embedded with the pressure switch. The only instruction given to the subjects was to reach at a natural speed and grasp the object between the thumb and the four fingers of the right hand on the convex sides of the object. The experimenter visually monitored the performance of each trial to ensure subject's compliance to this requirement. When subjects did not grasp the object with the whole hand, the trial was discarded and repeated. We performed three experimental conditions that varied depending on whether subjects were asked to either lift the object (*no. 1*) or place it into a niche (nos. 2 and 3), as well as on the high or low accuracy requirements of the placement task (nos. 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. 1*A*).

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. 1*A*). 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. 1*A*). The niche could be located to the right or to the left of the object.

Each subject 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 subjects.

Recording techniques

Hand posture was measured by resistive sensors embedded in a glove (CyberGlove, Virtual Technologies, Palo Alto, CA) worn on the right hand. The sensor's linearity was 0.62% of maximum nonlinearity over the full range of hand motion. The sensor's resolution was 0.5°, which remains constant over the entire range of joint motion. Angular excursion (resolution of approximately 0.1°) was measured at the metacarpal-phalangeal (*mcp*) and proximal interphalangeal (*pip*) joints of the thumb, index, middle, ring, and little fingers (T, I, M, R, and L, respectively). Before starting the experiment, we recorded baseline hand posture by asking subjects to position their right hand flat on the table and to maintain it in that position while *mcp* and *pip* joint angles of all digits were recorded. The *mcp* and *pip* joint angles were defined as 0° when the finger was straight and in the plane of the palm ("baseline" hand posture), and flexion was assigned positive values. The subject's wrist contacted a pressure switch whose release indicated onset of the reaching movement. The object was placed on a second switch that was released when the object was lifted from the table. Reach duration was computed as the time interval between the release of the two switches. The output of the transducers was sampled at 12-ms intervals.

Data analysis

Data from each trial were time normalized to allow comparisons of hand postures across trials and subjects at different epochs during the reach. Data from one subject were excluded due to technical problems. Preliminary analysis comparing 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 (*mcp* and *pip*) for each digit separately to assess the modulation of their angular excursion in time as a function of experimental condition. Main effects were used to explore the means of interest. Bonferroni corrections (alpha level: $P < 0.05$) were applied. 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.

RESULTS

This section is organized 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.

Qualitative description of hand shaping during reaching

Figure 2, *A–C* shows representative kinematic data from one trial for each of the three experimental conditions. The traces depict the time course of motion at *mcp* joints of each finger.

Figure 2 shows that for the no-niche and the high accuracy conditions (Figs. 2*A* and 2*B*, 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. 2*C*). 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. However, as shown in Figs. 3, 4, and 5, we found that the requirements of the subsequent task elicited distinct patterns of angular covariation (data shown are from one trial of one subject). 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.

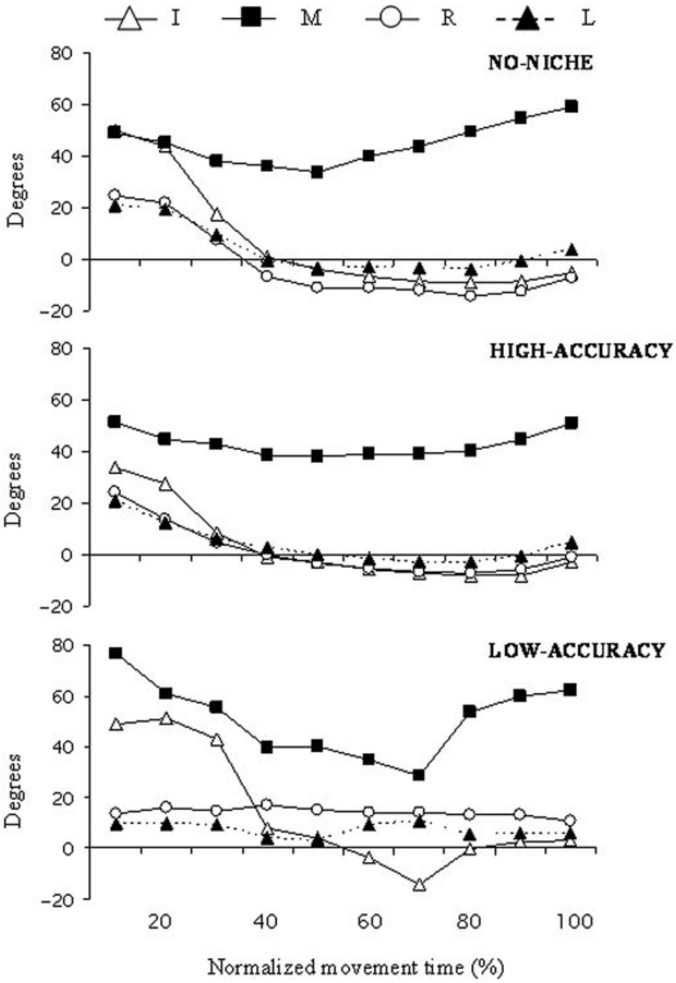

FIG. 2. Time course of finger motion during reaching. Each trace denotes angular excursion of *mcp* joints of the index (*I*), middle (*M*), ring (*R*) and little (*L*) finger (*subject 7*) during one trial (*no. 1*) performed in the no-niche, high accuracy, and low accuracy conditions (*A*, *B*, and *C*, respectively).

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. 6; first, second, and fourth panel from the *top right* column, respectively).

A similar pattern was also found for the *mcp* of the middle finger (Fig. 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. 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. 6; fourth and fifth panels from the *top left* column) and the *pip* joint for the middle and little finger (Fig. 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.

Multivariate ANOVA

As expected, there was a gradual molding of the digits during the approach phase to the object. This behavior was confirmed by MANOVA revealing a significant main effect of the factor “time” for all digits at both *mcp* and *pip* joints (Table 1). Although all digits 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. 7; left and right column, respectively) were characterized by a kinematic pattern that was different from that observed for the other two conditions. To date, the interaction between time and experi-

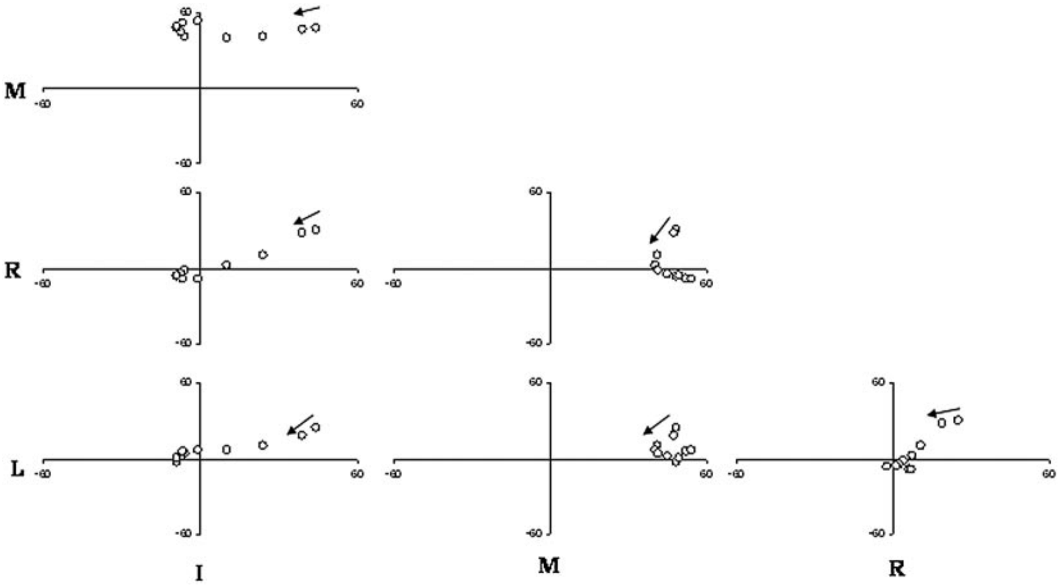

FIG. 3. Covariation in angular excursion of *mcp* joints (no-niche condition). Covariations in angular excursion at the *mcp* joints among digit pairs are shown (I, M, R, and L denote index, middle, ring, and little fingers, respectively). The arrow in each graph indicates the direction of the covariation patterns from the beginning of the movement. The origin of the axes is 0°. Data are from a single trial (*no. 3*) from one subject (*no. 1*).

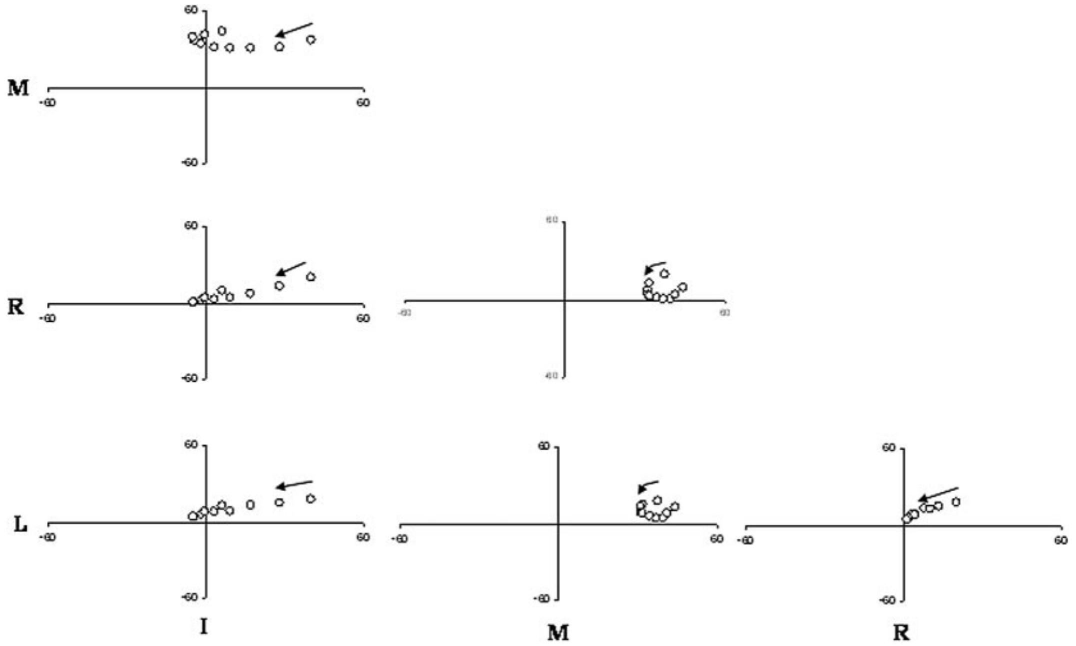

FIG. 4. Covariation in angular excursion of *mcp* joints (high accuracy condition). Same notations as Fig. 3. Data are from a single trial (*no. 3*) from one subject (*no. 1*).

mental condition was significant only for these two fingers ([$F(36,288) = 1.862$, $P < 0.01$], ring finger; [$F(36,288) = 2.384$, $P < 0.0001$], little finger). 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. 7; left column, *top* panel). However, the *mcp* joint of the little finger was the joint mostly affected by our experimental conditions (Fig. 7; right column, *top* panel).

Both *mcp* and *pip* joints of thumb, 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 (100 on the *x*-axis; Fig. 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.

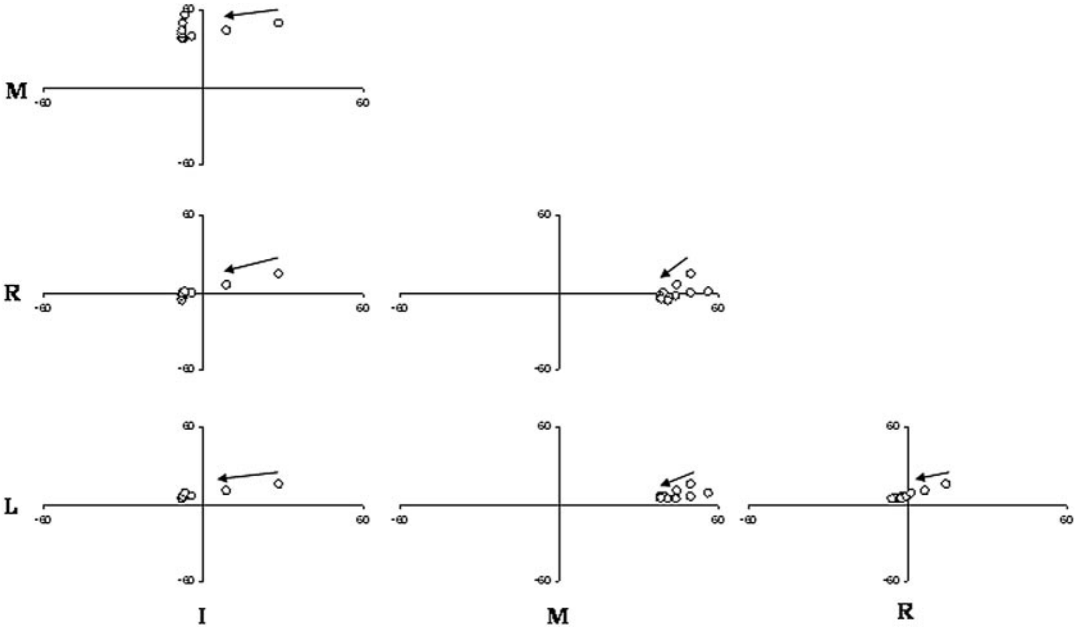

FIG. 5. Covariation in angular excursion of *mcp* joints (low accuracy condition). Same notations as Fig. 3. Data are from a single trial (*no. 3*) from one subject (*no. 1*).

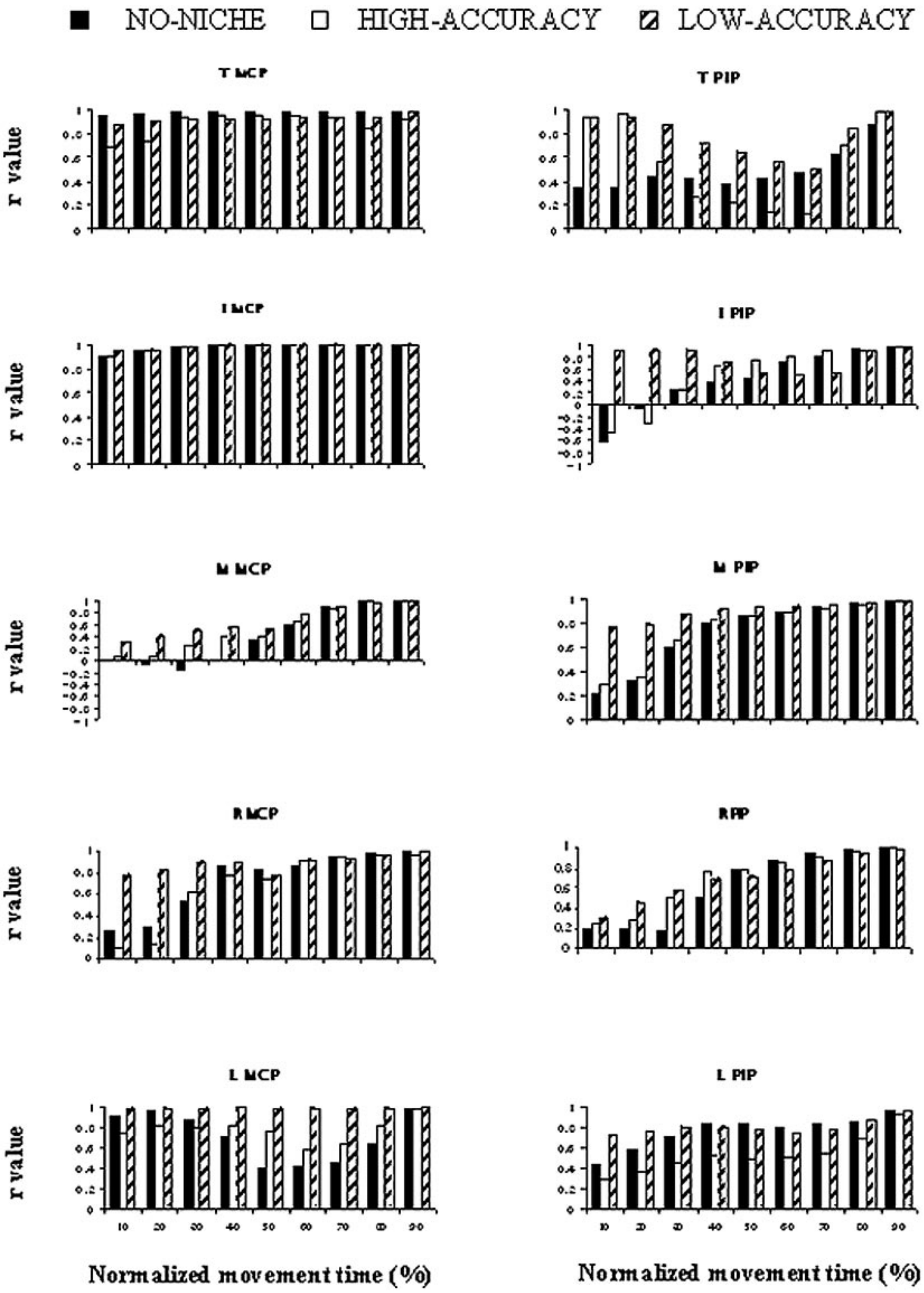

FIG. 6. Correlation coefficients between joint angles during the reach vs. joint angles at contact. Each panel shows the correlation coefficients of the relationships between joint angles during the reach and joint angles at contact. Data on the *left* and *right* columns are *mcp* and *pip* joint correlation coefficients, respectively. T, I, M, R, and L denote thumb, index, middle, ring, and little fingers, respectively. An r value >0.797 is significant at $P < 0.01$.

Reach duration

The duration of reaches was significantly affected by experimental condition [$F(2,178) = 12.98$, $P < 0.0001$]. Multiple comparisons (Bonferroni's correction) revealed that movement duration was longer for the high accuracy than for the low accuracy niche condition (1,129 versus 918 ms; $P < 0.0001$; see Fig. 8). Furthermore, reach duration for the no-niche condition was longer than for the low accuracy niche condition (1,064 vs. 918 ms; $P < 0.0001$; see Fig. 8).

To summarize, the type of task that followed object grasping affected preshaping of the hand during the reach,

TABLE 1. *Mean values of mcp and pip joint angles and MANOVA results*

Normalized movement time, (%)													
Index Finger		70	80	90	100	Middle Finger		90	100	Ring Finger		90	100
		I_MCP						M_MCP				R_MCP	
MEANS (SME)		35.3	36.9	40.1	44.8	MEANS (SME)		53	54.6	MEANS (SME)		−0.1	1.77
10	80.1 (6.1)					10	52.2 (4.9)			10	7.1 (3.1)		
20	65.5 (5.8)					20	47.0 (3.4)			20	5.31 (2.8)		
30	46.9 (4.6)					30	42.7 (2.2)			30	0.75 (2.9)		
40	37.8 (9.4)					40	40.2 (1.8)		*	40	−2.56 (3.4)		
50	35 (9.1)				*	50	40.1 (2.2)		*	50	−2.55 (4.4)		
60	34.7 (8.9)				*	60	42.3 (2.1)	*	*	60	−4.38 (4)		
70	35.3 (8.7)			*	*	70	45.6 (2.2)	**	**	70	−4.33 (3.8)		*
80	36.9 (8.5)			*	*	80	49.2 (2.3)	**	**	80	−2.75 (3.8)		*
90	40.1 (8.1)				*	90	53 (2.3)		*	90	−0.1 (3.7)		
100	44.8 (8)					100	54.6 (2.1)			100	1.77 (3.6)		
		I_PIP						M_PIP				R_PIP	
		46.7	55.9	65.6	69.2			−3.4	1.1			49.8	51.7
10	70.8 (14.8)					10	13.5 (5.9)			10	55 (5.6)		
20	56.2 (10.3)					20	8.3 (5.9)			20	48.8 (4.3)		
30	43.1 (3.5)					30	−0.8 (5.3)			30	42.7 (2.8)		
40	38.3 (2.3)		*	*		40	−7.6 (4.7)			40	39.1 (2.1)		
50	38.0 (3)		*	*		50	−10.2 (4.6)		*	50	38.2 (2.6)		*
60	41.1 (3.3)	*	*	*		60	−10.6 (4.6)		*	60	39.7 (3.2)	*	*
70	46.7 (3.5)			*		70	−9.7 (4.7)	*	**	70	42.4 (3.5)	*	*
80	55.9 (4.3)			*		80	−7.4 (4.5)	*	**	80	46.1 (3.7)	*	*
90	65.6 (5.5)					90	−3.4 (4.5)		**	90	49.8 (3.6)		*
100	69.2 (5.4)					100	1.1 (4.4)			100	51.7 (3.4)		

Asterisks indicate those values which are significantly different. $*P < 0.05$; $** P < 0.01$.

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 subjects responded to the low accuracy condition with faster reaches than those to either grasp and lift or grasp and place the object in the tight niche.

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

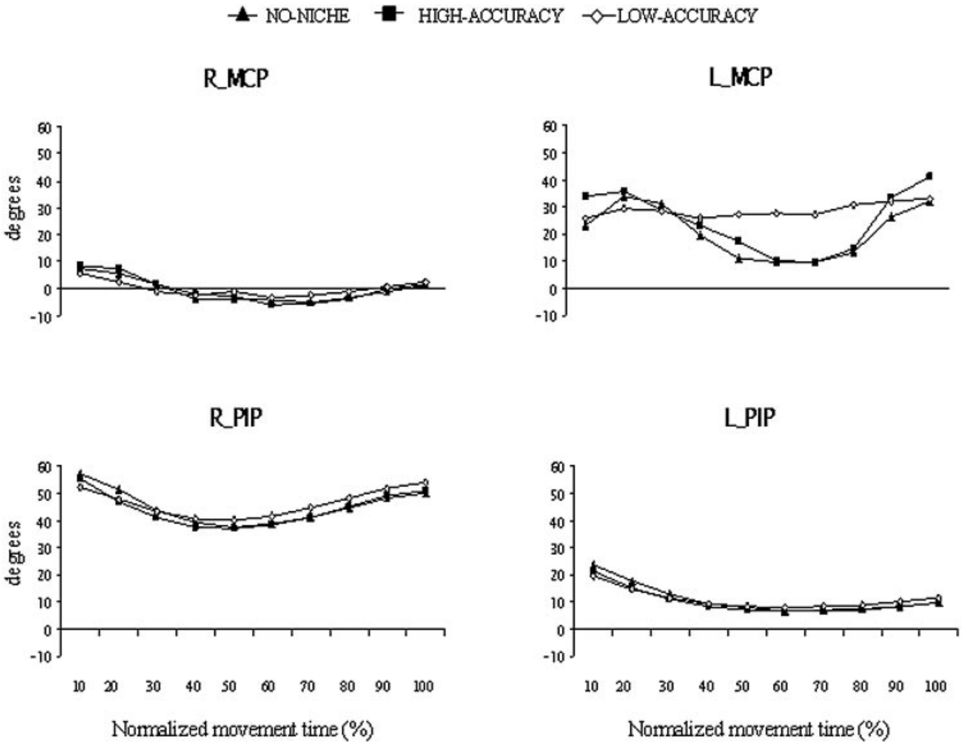

FIG. 7. Time course of digit motion during reaching. Each panel shows the angular excursion averaged across trials and subjects. Data on the *left* and *right* columns are *mcp* (*top*) and *pip* (*bottom*) joint angles for the ring and little fingers, respectively.

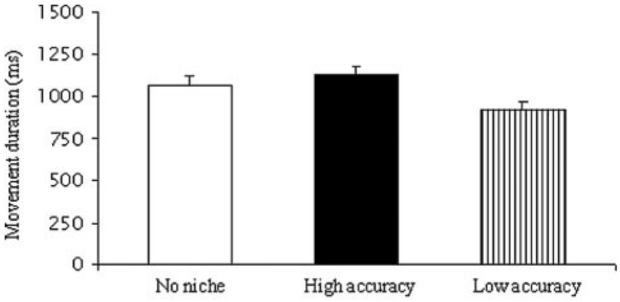

FIG. 8. Reach duration in milliseconds for the 3 experimental conditions. Bars represent ±SE.

leading to distinct patterns of hand shaping. The speed at which subjects 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 subjects plan to manipulate the object following grasping.

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 preshaping during the reach. When this type of niche was presented, participants configured the hand with respect to hand shape on object contact from the very beginning of the movement. In contrast, subjects 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, subjects 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.

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., Mason et al. 2001; Santello and Soechting 1998; Santello et al. 2002; 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 versus 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, subjects 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 subjects). 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.

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 subjects 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 et al. (1997), who found shorter movement durations when subjects 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 subjects approached the object with slower reaches compared with those in the low accuracy condition. We would like to point out that these slower reaches were also accompanied by a more gradual molding 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.

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 subjects 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 and 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 subjects to represent the entire movement sequence in advance of 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 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 et al., 1998). In effector terms, Salimi et al. (2000), based on their examination anticipatory control of fingertips forces during grasping based on the center of mass 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 et al. (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.

Conclusion

The present findings suggest that the gradual modulation of hand shape during reach-to-grasp is affected by the nature of an upcoming task. As the reach component was also affected by accuracy constraints of object manipulation, we conclude that proximal and distal component of the movement are controlled and modulated as a unit. Such modulation appears to be related not only to object contact, but also to planned object manipulation.

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