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RESEARCH ARTICLE

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Reprogramming of grip aperture in a double-step virtual grasping paradigm

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Abstract The present study investigated the control of manual prehension movements in humans. Subjects grasped luminous virtual discs with the thumb and index finger, and we recorded the instantaneous grip aperture, defined as the 3-D distance between the thumb and index finger. Target size could remain constant (single-step trials) or unexpectedly change shortly after target appearance (double-step trials). In single-step responses, grip aperture varied throughout the movement in a consistent fashion. Double-step responses exhibited distinct corrective modifications, which followed the target change with a latency similar to the normal reaction time. This suggests that visual size information has a fast and continuous access to the processes involved in grip formation. The grip-aperture profiles of single-step responses had a different shape when the target called for an increase than when it called for a decrease in the initial finger distance. The same asymmetry was observed for aperture corrections in double-step trials. These findings indicate that increases and decreases of grip aperture are controlled through separate processes, engaged equally by the appearance and by the size change of a target. Corrections of grip aperture in double-step trials had a higher peak velocity and reached their maximum as well as their final value earlier than the aperture profiles of single-step trials. Nevertheless, the total duration of double-step trials was prolonged. These response characteristics did not fit with either of the three corrective strategies previously proposed for double-step pointing movements, which could indicate that grasping and pointing movements are controlled by different mechanisms. However, more data are needed to substantiate this view.

Key words Sensorimotor integration · Motor control · Prehension · Grasping

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Introduction

A number of studies have investigated the control of aimed arm movements using the double-step pointing paradigm. In this approach, subjects point at visual targets that can unexpectedly change their position and, thus, require a correction of the originally planned motor program. It has been shown that the latency of such corrections is less or equal to the normal reaction time (Gottsdanker 1973; Georgopoulos et al. 1981; Prablanc and Martin 1992; de Jong 1995). In fact, if the time between target onset and displacement (inter-step interval, ISI) is very short, responses can already be modified at their onset, and the magnitude of this initial correction is inversely related to the value of ISI (van Sonderen et al. 1988). Taken together, these findings provide strong evidence that visual signals have fast and continuous access to the mechanisms for arm movement control.

In some double-step pointing studies, target displacement called for a substantial change, or even a reversal, of movement direction. It was found that the peak velocity of corrections was higher than that of comparable single-step responses and that total movement duration was prolonged by an amount equivalent to the ISI (Massey et al. 1986; Flash and Henis 1991; de Jong 1995). These results were interpreted as evidence that corrections are accomplished by canceling the original motor program and *substituting* it by a program that moves the hand from its current position to the new target, or alternatively, by maintaining the original program and *superposing* a second one for a movement from the first to the second target.

Other studies used relatively small target displacements and found that peak velocity and total movement duration were similar to those of single-step controls of equal amplitude (Gottsdanker 1973; Pelisson et al. 1986; Flash and Henis 1991; Prablanc and Martin 1992; Komilis et al. 1993). These findings led to the conclusion that corrections are brought about by *amending* the original motor program rather than by formulating a new one. Visual feedback about hand movement seems not to play a major role for these modifications, since the characteristics of double-step responses were similar with and without hand vision (Prablanc and Martin 1992; Komilis et al. 1993).

In summary, the above double-step pointing studies led to the proposition of three possible corrective strategies, namely, the cancellation, superposition, or amendment of the original motor program. The purpose of the present study was to determine whether the same strategies are also employed for corrections of other movement types, in particular, for corrections of the *grasping component* of prehension movements. It is widely accepted that manual prehension of objects is achieved by two distinct components, executed in parallel: a transport component, bringing the hand into the vicinity of the object, and a grasping component, which adjusts the grip aperture (i.e., the distance between participating fingers) such that it matches the object's shape and size (Jeannerod 1981). Grip aperture increases and decreases throughout the course of a movement in a rather stereotyped way, in the presence as well as absence of hand vision (Jeannerod 1984; Bock 1996); these changes of aperture are functionally coupled with the transport component (e.g., Marteniuk et al. 1990; Paulignan et al. 1991), but can also be partially independent if task constraints require it so (e.g., Carnahan and McFadyen 1996; Timmann et al. 1996). Thus, grasping kinematics are consistent enough to suggest the existence of a distinct motor program, yet flexible enough to accommodate different manipulative tasks.

In analogy to the above double-step pointing studies, corrective strategies for the grasping component can be investigated in double-step grasping experiments, where the size rather than the location of targets is unexpectedly changed and the resultant modifications to the time-course of grip aperture are analyzed. This approach has been taken by two previous studies in which target size could change at the time of movement onset, i.e., ISI was set equal to the reaction time. Both studies observed that an *increase* of target size is followed by distinct aperture corrections with a latency of more than 500 ms (Jeannerod 1981) or about 300 ms (Paulignan et al. 1991; Castiello et al. 1992). The total duration of double-step responses towards increasing or decreasing targets exceeded that of single-step controls by 40–180 ms (Paulignan et al. 1991; Castiello et al. 1992). Unfortunately, however, neither study provided information on reaction time, peak velocity of aperture corrections, and latency of corrections towards *decreasing* targets, as would be needed to interpret the findings in terms of the three proposed corrective strategies (see above). It also remained unclear whether corrections towards an increasing and a decreasing target exhibit similar characteristics. These topics are therefore addressed in the present study.

Materials and methods

Human subjects executed grasping movements with their right (preferred) hand, using the experimental setup outlined in Fig. 1. Visual targets were produced on a computer monitor located above the subjects' head and were viewed through a tilted, semi-transparent mirror, such that the virtual target image appeared in a frontal plane at eye level, 40 cm ahead. Mirror transparency was sufficient for subjects to be able to see their hands.

Each trial began with the presentation of a starting disc of 4 cm diameter, presented for a randomly varying interval of 0.8–1.2 s at the center of the right display edge. It was then replaced by a target disc of 1, 4, or 7 cm diameter, located 15 cm to the left of the

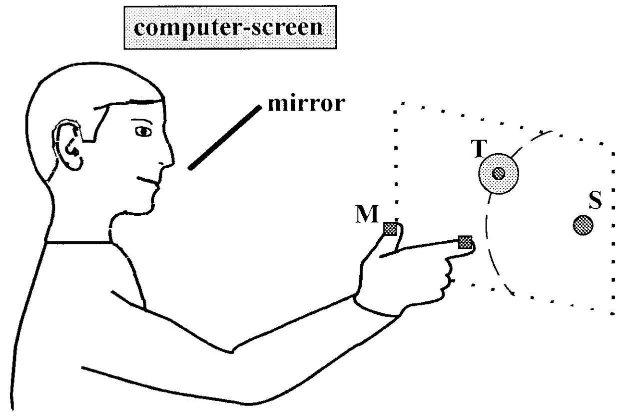

Fig. 1 Schematic view of mirror, computer screen, markers (*M*), and virtual display area (*dotted*). *S* indicates the starting, *T* the target discs. Two possible sizes of T are shown. Actually, only one disc was visible at a time

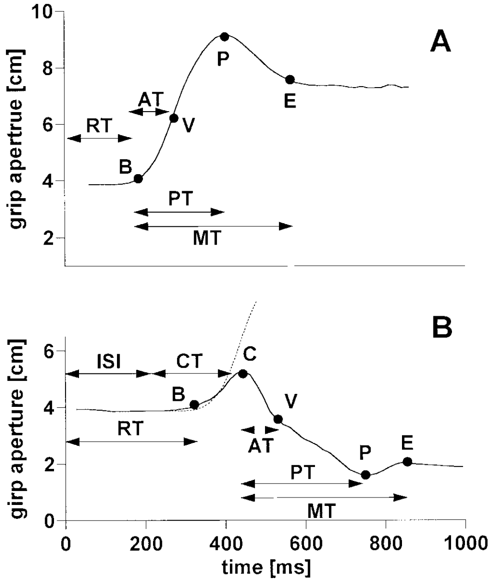

Fig. 2 Schematic grip-aperture profiles for single-step (**A**) and double-step (**B**) trials, with definition of response parameters (for further details see text). *ISI* denotes the interval between target appearance and size change. The *dotted curve* in **B** represents the initial portion of the mean single-step response. *RT* Reaction time, *AT* acceleration time, *PT* peak aperture time, *MT* movement time, *CT* correction time, *B* movement beginning, *C* correction onset, *V* velocity peak, *P* aperture peak, *E* movement end

starting disc, in a randomly varying direction. In single-step trials, the target size remained constant, while in double-step trials, target size changed after an inter-step interval (ISI) of 65 or 214 ms following target appearance. For either trial type, the target was presented for a total duration of 1 s and was then replaced by the starting disc, which initiated the next trial.

Each experimental session consisted of 64 trials. Of these, 48 were single-step trials, in which the target size was continuously large (16 "L" trials), medium (16 "M" trials), or small (16 "S" trials). The remaining 16 were double-step trials, in which the target size was initially large, but soon changed to small (eight "L→S" trials) or vice versa (eight "S→L" trials). The different trial types and ISI values were administered in a mixed, balanced order. To prevent fatigue, a rest break of about 3 min was provided after the first 32 trials of each session.

The subjects' task was to grasp each displayed virtual disc between the thumb and index fingertip as quickly and accurately as possible. Thus, each trial started with the hand near the center right edge of the virtual display, with the thumb and index fingertips about 4 cm apart. Later during the trial, the fingers moved leftwards towards the target and their distance increased, stayed relatively constant, or decreased, depending on target size. It is important to note that, since the starting and target discs were virtual objects, subjects' fingers never made physical contact with them and, therefore, tactile feedback about task performance was absent. This fact distinguished the present work from most previous studies, where subjects grasped real physical objects (see, however, Bock 1996).

Finger position was measured with the Polhemus FASTRAK system, which is based on electromagnetic induction. Two markers (cubes of about 2 cm side length and 17 g weight) were attached to the fingernails of the thumb and index finger, and their 3-D position was recorded contact-free with a spatial resolution of about 0.8 mm and a temporal resolution of 60 marker pairs/s. From these recordings, we calculated the instantaneous grip aperture as the 3-D distance between markers minus the thickness of thumb and index finger (a subject-specific constant determined prior to each session) and also determined grip velocity as the rate of change of grip aperture.

For further analysis, an interactive computer program calculated a number of response parameters for each trial (see Fig. 2). It yielded satisfactory results in 85% of cases; in the remaining 15%, a human operator had to adjust the parameter values by eye. The parameters for the single-step trials were:

- Movement beginning (B): time when grip velocity first exceeded 50 mm/s.
- Maximum velocity (V): time when absolute grip velocity was largest. When grasping a large target, subjects had to *increase* their initial grip aperture; when grasping a small target, they had to *decrease* it. Therefore, peak velocity occurred during grip *opening* for large and during grip *closure* for small targets.
- Aperture peak (P): time of most extreme grip aperture (maximum aperture in the case of large targets, minimum aperture in the case of small targets).
- Movement end (E): time when grip velocity last dropped below 50 mm/s.
- Reaction time (RT): interval between target appearance and B.
- Acceleration time (AT): interval between B and V.
- Peak aperture time (PT): interval between B and P.
- Movement time (MT): interval between B and E.
- Peak velocity (PV): grip velocity at V.
- Peak aperture (PA): absolute difference between apertures at P and B.
- End aperture (EA): absolute difference between apertures at E and B.

For double-step trials, the following parameters were calculated:

- Movement beginning (B): same as in single-step trials.
- Correction onset (C): time when the corrective change of grip aperture first exceeded 5 mm (for details, see Results).
- Velocity peak (V): as in the single-step trials, but in the direction of the second step.
- Aperture peak (P): as in the single-step trials, but in the direction of the second step.
- Movement end (E): as in the single-step trials, but in the direction of the second step.
- Reaction time (RT): same as in the single-step trials.
- Correction time (CT): interval between change in target size and C.
- Acceleration time (AT): interval between C and V.
- Peak aperture time (PT): interval between C and P.
- Movement time (MT): interval between C and E.
- Peak velocity (PV): same as in the single-step trials.
- Peak aperture (PA): same as in the single-step trials.
- End aperture (EA): same as in the single-step trials.

Note that all parameters except B and RT describe the corrective component of double-step responses rather than the whole response. In consequence, the cancellation and superposition strategies, but not the amendment strategy (see Introduction), predict that these parameters have similar values as in the single-step trials.

Ten right-handed subjects participated in the experiment after giving informed consent. Three subjects were female and seven male; they were laboratory students or scientists, 20–42 years of age, and exhibited no sensorimotor deficits except for corrected vision.

Results

Figure 3 shows original grip aperture profiles of single-step trials from one subject, illustrating that responses to large and small targets were not symmetrical: In L trials, grip aperture started to change earlier and faster, exhibited more pronounced dynamic overshoots, and was more accurate. These observations are confirmed by a quantitative analysis of single-step response parameters, as shown in the first and fourth data row of Table 1. Mean reaction time across all repetitions and subjects (RT) was about 50 ms shorter for L than for S trials, peak velocity (PV) was higher and its timing (AT) faster, peak aperture (PA) was larger, and occurred in time (PT) 100 ms earlier. However, the initial swiftness of L responses was offset by a prolonged decay time following the peak, such that movement time (MT) of L and S trials was comparable. The change of grip aperture from movement onset to end (EA) was more pronounced and reflected the target size more accurately in L than in S trials.

For further analysis, each subject's L responses were aligned with respect to AT and then averaged, yielding a mean large-aperture profile. One example is plotted in Fig. 4 along with the same subject's L→S double-step responses. Note that all responses in Fig. 4 share the same initial target size. Accordingly, grip aperture initially increased for all depicted traces. Later in their course, however, L→S responses deviated more and more towards the small target, with the onset of deviations occurring earlier with short than with long ISIs.

To quantify the onset of corrections, C (see Introduction and Fig. 2), an interactive computer routine aligned each individual L→S response with the respective subject's mean large profile and determined the last point before the L→S response deviated from the mean to-

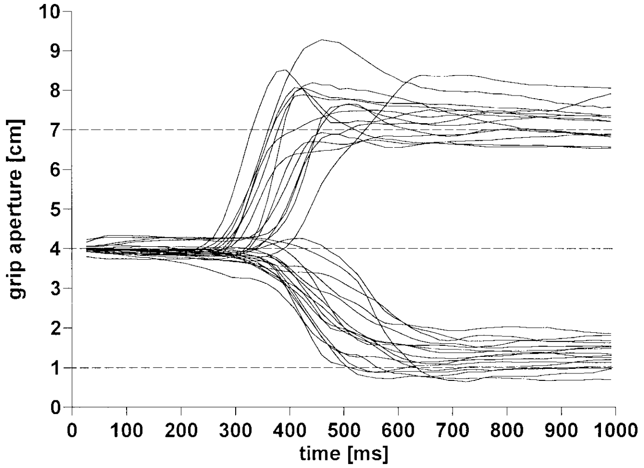

Fig. 3 Original single-step responses from one subject. Each trace represents the aperture profile of one response towards a large or small target. *Horizontal lines* denote the size of the start and target discs

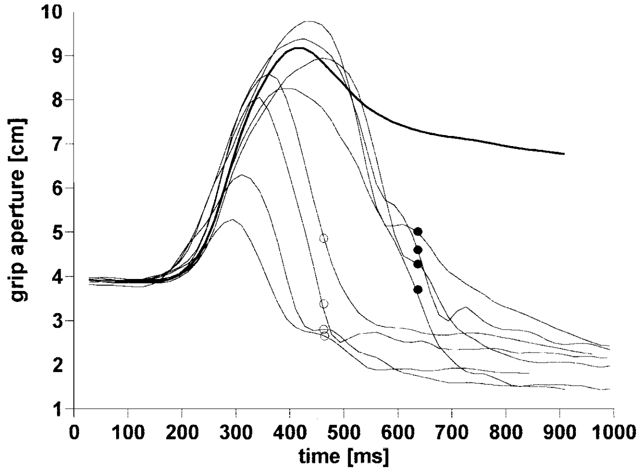

Fig. 4 Original double-step responses with single-step mean. Double-step responses in large-to-small target-change trails (L→S) with inter-step interval (ISI) =65ms (*open circles*) and ISI=214 ms (*filled circles*) are plotted together with the same subject's mean response (*bold trace*). Curves are adjusted relative to the maximal velocity to illustrate similarities of initial profiles

wards the small target by more than 5 mm. In a similar way, the correction onset of S→L responses was quantified by comparing them to the mean small profile. Our computer routine yielded mostly satisfactory results, requiring operator intervention in only about 15% of trials.

The mean reaction and correction times of double-step responses are listed in the second and third row of Table 1 and reveal an intriguing pattern. Considering first the S→L responses, their RT was similar to that of S trials, while their CT was similar to the RT of L trials. This is not surprising, given that S→L responses were initiated by a small, but corrected by a large target. Further from Table 1, L→S responses exhibited the inverse relationship with single-step RTs, which can again be explained by the dependence on target size. It therefore appears that all RT and CT values are similar, once their dependence on target size is taken into account. To substantiate this view, we performed an analysis of variance (ANOVA) with the factors type (levels: single-step RT, double-step RT, double-step CT) and size (levels: small target, large target)[1]. The outcome, summarized in the bottom part of Table 1, confirmed that the effects of type and type*size were not significant. In conclusion, our data provide no evidence for differences between RT and CT, or between CT for increasing and decreasing targets, beyond the dependence on target size already present in single-step trials.

ANOVAs were also performed for each of the other response parameters in Table 1, using the factors type (levels: single-step, double-step) and size (levels: small target, large target).[2] The outcome is again summarized in the bottom part of Table 1. The effects of size confirm the observed differences between L and S trials and extend them to include double-step trials as well: responses towards large targets had an earlier and higher peak velocity, an earlier and higher peak aperture, and a higher final aperture than those towards small targets, while their movement time was not different. Of particular in-

Table 1 Summary of mean values and ANOVA results. *RT* Reaction time, *CT* correction time, *AT* acceleration time, *PV* peak velocity, *PT* peak aperture time, *PA* peak aperture, *MT* movement time, *EA* end aperture. *Top part* presents the mean values across repetitions and subjects of all response parameters for the four different trial types. Dimensions are ms for RT, CT, AT, PT, and MT, cm/s for PV, and cm for PA and EA. *Bottom part* presents the ANOVA *F*-values

	RT	CT	AT	PV	PT	PA	MT	EA
Large	264		113	0.33	227	3.54	336	2.70
S→L	305	260	113	0.38	218	3.28	313	2.61
L→S	268	307	132	0.36	273	2.00	296	1.87
Small	311		152	0.20	307	1.90	320	1.82
Type	0.2$^{\text{n.s.}}$		1.7$^{\text{n.s.}}$	90.1***	6.4**	1.4$^{\text{n.s.}}$	6.8**	0.1$^{\text{n.s.}}$
Size	63.2***		13.5***	42.6***	59.9***	452.9***	3.3$^{\text{n.s.}}$	203.5***
T*S	0.3$^{\text{n.s.}}$		1.6$^{\text{n.s.}}$	22.4***	2.1$^{\text{n.s.}}$	7.2**	0.0$^{\text{n.s.}}$	1.5$^{\text{n.s.}}$

n.s. *P*>0.05; ** *P*<0.01; ****P*<0.001

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[1] Thus, size = small for the RT of S→L trials, size = large for the corrsponding CT, and the reverse holding is true for L→S trials

[2] Since later portions of double-step responses were likely to be predominated by the second target size, we selected size = small for L→S trials, and size = large for S→L trials.

terest in Table 1 are the significant effects of type. They indicate that, for small and large targets alike, there were consistent differences between single- and double-step trials: double-step responses had a higher peak velocity, an earlier peak aperture, and a shorter movement time than the pertinent single-step responses.

The effect of type on MT in Table 1 implies that the *corrective component* of double-step trials (C–E in Fig. 2) was 24 ms shorter than that of single-step responses, while the *total duration* of double-step trials (B–E in Fig. 2) was actually 113 ms longer. This increase in duration, however, amounted to less than the ISI: when subtracting ISI from the total duration of double-step trials, the outcome was 26 ms less than the duration of single-step trials, and this difference was significant in a *t*-test (t=2.34, df=478, P<0.05). It therefore appears that the corrective component of double-step responses is sped up to compensate, at least in part, for the delay caused by the second step.

Finally, from Table 1, we found two significant interaction terms. They explain only negligible portions of the total variance (eta square=0.049 and 0.016, respectively), are difficult to interpret, and may constitute chance results.

Discussion

The present study investigated the execution of grasping movements in a double-step paradigm, where the objects to be grasped could unexpectedly change size shortly after their appearance. As objects, our study employed virtual luminous discs, which allowed us to change their size while keeping their location constant and, thus, to perturb selectively the grasping, but not the transport component of responses. This is a methodological advantage over previous studies using real physical objects (Paulignan et al. 1991; Castiello et al. 1992), where a change of object size was coupled to a slight location change.

Two limitations of our approach should be considered. First, since our objects were generated on a flat computer screen, they provided only few depth cues. Thus, subjects could have misjudged object distance and, consequently, object size. Indeed, the recorded mean finger position was 3 cm in front of the virtual display area, which fits with the findings that subjects underestimated object size (relatively small values of EA in Table 1). However, this limitation is of little concern for the present study, which focuses not on the absolute magnitude of responses, but rather on the differences between trial types. Second, our virtual objects provided no tactile cues about object-finger contact at the end of movement, which may have led to a different movement strategy than found with real objects. Such a difference could explain why dynamic overshoots of grip aperture, typically found by others, were sometimes absent in the present study (see Fig. 3). Interestingly, even studies using real objects found that grasping strategies can differ, depending on the task requirements (Gentilucci et al. 1991); caution is therefore needed when interpreting the present – or any other – findings as general characteristics of the grasping act.

In accordance with previous double-step grasping studies (Jeannerod 1981; Paulignan et al. 1991; Castiello et al. 1992), we observed that responses were corrected in mid-flight towards the new target size. The latency between target change and correction onset was neither larger nor smaller than the reaction time, once the effect of target size on RT was taken into account. This finding supports neither the existence of a refractory period after target appearance nor the existence of high-speed corrective pathways, but, instead, suggests that response correction is accomplished in a manner similar to response initiation. A similar equivalence between correction and reaction times has also been observed in earlier experiments on double-step pointing (Gottsdanker 1973; Georgopoulos et al. 1981; Prablanc and Martin 1992; de Jong 1995).

One aim of the present study was to compare the kinematic features of double-step grasping movements towards a large and a small target. Unexpectedly, we found that the kinematics of *single*-step responses already depended on target size. The same size-dependence was maintained for double-step trials, such that the corrective component of S→L trials resembled an L response, while corrections of L→S trials were reminiscent of an S response. These findings suggest that increases and decreases of grip aperture are controlled by separate processes with different dynamic properties and that the processes are engaged in the same way by the appearance and by the size change of a target.

The main purpose of our work was to determine whether double-step grasping movements obey the same corrective strategies previously proposed for double-step pointing (see Introduction). These strategies have been associated with distinct kinematic characteristics: the substitution and superposition strategies predict that double-step responses have a higher PV than single-step controls and that their total duration is prolonged by ISI, while the amendment strategy expects that PV and total duration of double-step responses are normal. Clearly, our data disagree with response amendment, while, at a first glance, they appear to fit with the other two strategies: both PV and total duration of double-step trials were increased in our recordings. However, grasping duration increased by an amount that was significantly *smaller* than ISI, unlike the above prediction. This finding was further supported by the observed decrease of PT and MT. We therefore conclude that none of the proposed strategies can fully account for the observed kinematics of double-step grasping responses.

One possible explanation for our findings is a modified substitution or superposition strategy, according to which the execution of new, corrective motor programs is *sped up* to partly offset the delay caused by ISI. A modified amendment strategy is also conceivable, which contends that changes to the original motor program take extra time and, thus, prolong total duration by nearly the amount of ISI. Further experiments are required to decide between these alternatives or to propose other ones.

Although the present double-step grasping data did not conform with either of the three corrective strategies proposed for double-step pointing, the discrepancies were not substantial enough to warrant the conclusion that pointing and grasping movements are governed by different processes. Such a conclusion needs further scrutiny in additional experiments, in which double-step pointing and grasping trials are administered to the same subjects in the same apparatus during the same experimental session and in which response parameters are determined by the same algorithms. We are currently preparing such a study.

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