RESEARCH NOTE

E.M. Robertson · R.C. Miall

Multi-joint limbs permit a flexible response to unpredictable events

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Abstract The human arm is kinematically redundant, which may allow flexibility in the execution of reaching movements. We have compared reaching movements with and without kinematic redundancy to unpredictable double-step targets. Subjects sat in front of a digitising tablet and were able to view an arc of four targets reflected in the mirror as virtual images in the plane of the tablet. They were instructed to move, from a central starting point, in as straight a line as possible to a target. In onethird of trials, the target light switched to one of its neighbours during the movement. Subjects made 60 movements using shoulder, elbow and wrist and then another 60 movements in which only shoulder and elbow movement were allowed. By restraining the wrist, the limb was made non-redundant. The path length was calculated for each movement. In single-step trials, there was no significant difference between path lengths performed with and without wrist restraint. As expected there was a significant increase in path length during double-step trials. Moreover this increase was significantly greater when the wrist was restrained. The variability across both single- and double-step movements was significantly less while the wrist was restrained. Importantly the performance time of the movements did not alter significantly for single-step, double-step or restrained movements. These results suggest that the nervous system exploits the intrinsic redundancy of the limb when controlling voluntary movements and is therefore more effective at reprogramming movements to double-step targets.

Key words Pointing · On-line control · Inverse kinematics · Double-step stimulation · Human

E.M. Robertson () · R.C. Miall University Laboratory of Physiology, Parks Road, Oxford OX1 3PT, UK Fax: +44-1865-272-469, e-mail: emr@physiol.ox.ac.uk

Introduction

There has been recent interest in the possibility that predictive strategies are being used by the motor system to bring about controlled voluntary movements (Miall 1995). However, some of the events with which the motor system has to deal are intrinsically unpredictable, for example, if the target suddenly changes its position during a movement. Nevertheless such targets can usually be reached accurately with a high level of control (Pelisson et al. 1986; Soechting and Lacquaniti 1983; van Sonderen et al. 1988). If these changes are particularly extreme or occur late during the execution of the movement, then movements with noticeable points of inflection do result (Georgopoulos et al. 1981). That such random changes in target position are compensated for within a reaction time suggests that the motor command being issued to the limb is being constantly modified (Jeannerod 1988). Others have argued that rather than a single motor command being modified a new command is produced de novo as a result of the new circumstances (Hoff and Arbib 1992). However, even if this is the case, the second command is evoked with a latency significantly shorter than the initial reaction time, suggesting that some aspect of the programming can be bypassed; so the motor command is seen as being flexible and responsive to changes in the goal of a voluntary movement (Jeannerod 1994). The mechanism behind this flexibility remains, at present, unknown. This paper attempts to elucidate a mechanism whereby this flexibility could be produced.

It may be that some of this flexibility derives from the anatomical redundancy of the limb. The fact that a point in space cannot be uniquely specified by a set of joint angles is usually viewed as a problem, called "the degrees-of-freedom problem" (Bernstein 1967). However, it may be that this anatomical redundancy permits the synthesis of flexible motor command, by allowing multiple joint configurations for any given hand position. To test this idea, we examined the effect of reducing the anatomical flexibility of the limb on the ability of subjects to adjust to double-step targets. The results are consistent with the proposal that the ability of subjects to adjust to random changes in the goal of a movement depends critically upon the redundancy of the limb. An abstract of these results has previously been reported (Robertson and Miall 1996).

Materials and methods

Eight neurologically normal, right-handed subjects participated in this study, aged from 22 to 40 years old. All but one of the subjects were naïve as to the purpose of the experiment. The subject sat at an angled digitising tablet (Fig. 1). An angled mirror above the tablet prevented the subject from viewing their hand position but allowed them to view four LEDs as virtual images in the plane of the tablet. These target LEDs were positioned above the angled mirror in an arc of radius 38 cm and were separated from one another by 4 cm. The origin of the circle was the starting point for all movements. The subject held a digitising pen using a power grip. The position of the pen was recorded at 133 Hz by a PC-Pentium as (x, y) co-ordinate pairs; the spatial accuracy of the tablet was 0.25 mm.

Throughout all experimental conditions, forward movement of the shoulder was restrained by a harness. This prevented any displacement of the shoulder axis during the task, making the upper limb equivalent to a triple-jointed, redundant limb when moving in a single plane. To make the limb non-redundant, the wrist was immobilised, using an light-weight orthopaedic wrist restraint (6 g), allowing only elbow and shoulder rotation. The subjects were randomly allocated into two groups of four. The first group performed 60 movements without wrist restraint followed by 60 movements with wrist restraint. The second group did this in reverse order.

The subject was instructed to view the four virtual LED targets in the mirror. When a LED became illuminated, this was the signal for the subject to move in a single, rapid, straight and discrete movement to the point on the tablet that represented the position of the LED (*single-step trials*). When the subject had successfully captured this position, to within 1 cm, the LED was extinguished. For one third of the trials, chosen at random, the illuminated LED changed position during the movement (*double-step trials*). This change in target position was triggered by the hand moving 6 cm from the starting point. This shift was always to an adjacent target, although the direction of the shift was randomly chosen. The amplitude of displacement was always 4 cm (the distance between the LEDs).

Three kinematic parameters were calculated from the movements: the time to make the movement to the LED, the time taken



Fig. 1 Subjects were seated with shoulder restrained while looking in the silvered mirror to see the virtual LED targets. In half of the movements the subjects were also wrist-restrained

Trial-to-trial variability of the trajectories was calculated by first scaling and rotating the paths so as to align the start and end points. The scaling was especially important, because this removed the effects of movement amplitude. The trajectories were then spatially re-sampled and mean paths with standard errors calculated. The standard errors for movements with and without restraint were then compared statistically using Student's *t*-test. Both the single- and double-step trials were subject to this form of analysis. The velocity profiles of all trajectories were also calculated using a numerical differentiation procedure. To compare the velocity profiles, the start of the movement was defined as when velocity exceeded 4% of the maximum velocity. The end point was defined as the velocity falling below this level for the last time. Using these normalised velocity profiles, it was possible to calculate the total movement time and the time required to reach maximum velocity.

Results

We compared the movement kinematics for the two groups, to test whether the order in which they were introduced to the wrist restraint could have influenced their performance. However, no significant differences were found between the group immediately wrist-restrained and the group restrained in the second half of the experiment (P>0.05 performance time, time to reach maximum velocity and path length). We therefore collapsed the two groups into a single group of eight subjects for all subsequent analysis (Table 1).

Effects of restraint

Movements made to single-step targets had almost straight trajectory paths to the targets, regardless of the level of restraint. This is clearly demonstrated by the averaged paths of all eight subjects to target 2 in both the



Fig. 2 Mean paths made by all subjects to a target during standard and perturbation trials. Notice how the path length of the perturbed and restrained (*thickest line*) is greater than any of the other conditions. This feature was statistically significant across all subjects (P < 0.05). *Thinnest line* unrestrained single step; *thin line* restrained single step; *thick line* unrestrained double step, *thickest line* restrained double step

Table 1 Each subject performed 60 movements with and withoutwrist restraint. During both of these sessions, the LED target changed position on one-third of the trials at random, as the subjectreached for the initial target. This procedure generated four differentconditions

Level of restraint	Type of target		
	Single step	Double step	
Unrestrained	Normal	Effects of an uncertain target position	
Restrained	Effects of restraint	Effects of both restraint and an uncertain target position	

unrestrained and the restrained conditions (Fig. 2, Table 2). Moreover the averaged paths in both conditions were also very similar. Statistical comparison of movements to all of the targets found no significant difference in path length between restrained and unrestrained movements (P>0.05). Restraint also did not effect the shape of the velocity profile of movements.

Effects of target changes

In double-step trials, there was a significant increase in the path length of the trajectories (P < 0.05). This effect is clear in the averaged perturbed movements (Fig. 2, Table 2), in this example moving initially towards target 3 and only later moving to target 2. This increase in path length was not consistently reflected in the velocity time profiles, which continued to show only one major peak in velocity. In a few subjects on a few occasions, there were several local velocity peaks. This was the only evidence for the production of discontinuous movements being elicited by the change in target position.

Interaction between restraint and changes in target position

Subjects restrained during double-step movements produced path lengths that were greater than in all other conditions (Fig. 2, Table 2). This was a significant difference when compared with perturbed movements produced without restraint (P<0.05). The velocity profiles were very similar to those observed for the unrestrained double-step trials, with no consistent evidence of discontinuous movements. The performance time in all of these conditions was also found to be similar (P>0.05). Consequently we found a statistically significant increase in mean movement velocity during double-step trials (P<0.05), although there was no effect of interaction between restraint and target perturbation (P>0.05).

Trajectory variability

Restraint of the wrist appeared to affect the ability of subjects to respond to a change in target position. So



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Fig. 3A, B The greater variability of unrestrained movements made to both double- and single-step targets. A box indicates the 25th and 75th percentiles. The line in the centre of the box is the 50th percentile, while the capped bars are the 10th and 90th percentiles. The circular symbols represent the 5th and 95th percentiles A The greater spatial variability associated with unrestrained movements. Each movement made to a single-step target (n = 40) by every subject (n = 8) was spatially re-sampled to give a movement path of 100 co-ordinates. These movements (n = 320)were then averaged together, to give a mean path and associated variance. The variability of both unrestrained (grey) and restrained (black) movements were compared statistically using Student's ttest (P < 0.05). **B** The greater spatial variability of associated with unrestrained movements. Each movement made to a double-step target (n = 20) by every subject (n = 8) was spatially re-sampled to give a movement path of 100 co-ordinates. These movements (n = 160) were then averaged together, to give a mean path and associated variance. The variability of both unrestrained (grey) and restrained (black) movements were compared statistically using Student's *t*-test (P<0.05)

we went on to examine the spatial properties of trajectories produced with and without wrist restraint, in both single- and double-step trials. Those trajectories produced with wrist restraint showed a significant lower spatial variability than unrestrained movements to single- (P<0.05) and double-step targets (P<0.05; Fig. 3, Table 2).

Table 2 The mean and SE across all eight subjects, for three kinematic parameters in each of four conditions. Both level of restraint and type of target were shown to have a statistically significant effect upon pathlength, with a significant interaction between these two factors. While the movement times were not significantly effected in any of the conditions. The spatial variability of the movements was significantly effected by the level of restraint and, as would be expected, by the type of target

Level of restraint	Type of target		
	Single step	Double step	
Path length			
Unrestrained (cm)	39.17 ± 1.46	41.96 ± 1.58	
Restrained (cm)	39.49 ± 1.84	42.69 ± 1.63	
Duration			
Unrestrained (ms)	106.50 ±14.21	90.41 ± 10.54	
Restrained (ms)	114.45 ± 8.22	109.4 ± 9.92	
Spatial variance			
Unrestrained (cm)	0.1438 ± 0.016	0.5382 ± 0.093	
Restrained (cm)	0.1187± 0.013	0.4535 ± 0.083	

Discussion

We have demonstrated that the ability to respond to unpredictable changes in the position of a target during pointing movements was improved by the availability of limb redundancy.

The problems of controlling a multi-joint limb have been widely discussed in the literature (Bernstein 1967). What has been less widely discussed are the potential advantages of a kinematically redundant limb. Here we demonstrated that the ability to respond to random changes in the final target position depends critically upon the number of free joints in the limb.

By using a redundant limb, it is possible for movements to be synthesised that respond flexibly to unpredictable changes in the environment. A change in the spatial location of a target requires the modification or selection of a motor command. These processes depend upon the joints of a redundant limb for their implementation. Consequently when a joint is immobilised these modification procedures can no longer be expressed.

These differences were examined by measuring the path lengths of trajectories from the starting point until the hand velocity fell beneath a threshold. It has previously been demonstrated that subjects attempt to achieve straight or near-straight hand paths (Wolpert et al. 1995). Moreover studies have demonstrated that uncertainty in the final target position has a powerful and consistent effect upon the path length of trajectories. These studies have also shown that the time at which the target is perturbed affects path lengths (Georgopoulos et al. 1981). So, if a target changes position very early during, if not before, the limb movement then the effect upon path length is minimal (Prablanc et al. 1986; Pelisson et al. 1986); but with a later perturbation there is a corresponding rise in the path length. Consequently an increase in path length represents a shift from a desired trajectory. Hence it is reasonable to use this kinematic parameter as a measure of subjects' ability to respond to changes in the final target position.

We found that, when a trajectory is produced by an artificially non-redundant limb to a double-step target, the path length is significantly greater than that produced by a redundant limb. In the latter case the redundancy of the limb has been exploited to allow a modification in the movement trajectory. Thus our data suggests that while subjects can modify their trajectories with a non-redundant limb their corrections are far less effective.

This flexibility is reflected in the variability of movements across trials. Movements in which the limb is non-redundant are significantly less variable than those produced by redundant limbs. This is true for movements to single- and double-step targets. Such an observation is consistent with Fitts's proposal that the statistical variability within a movement reflects the information content of that movement (Fitts 1954). As the number of joints that require control increases, inevitably there is an increase in the information content of the movement. However, in single-step circumstances this increase in trajectory variability in redundant limbs represents an "excessive amount" of control, as both redundant as well as non-redundant limbs produce movements of the same path length. Only during double-step trials does this latent ability to control a joint (in this case the wrist) become of importance, as it permits the statistically significant reduction in path length to a target that has changed position. Perhaps the movement variability represents the latent flexibility of the trajectory.

In addition to this situation *across* several movements a similar phenomena has been reported *within* movements (Georgopouolos et al. 1981). Movements can be roughly divided into an acceleration and a deceleration phase, and it is during the acceleration phase that subjects can most effectively respond to changes in target position. It is also during this acceleration phase that a movement is at its most variable. Consequently it may be that the variability within a trajectory or amongst a series of trajectories reflects the innate flexibility of the strategy being used by the motor system.

Clearly this has an important implication in how movements are represented within the central nervous system. If the joints are exploited in order to make movements flexible then the joints have to be represented centrally. This could argue for an intrinsic or limb-based co-ordinate frame for the calculation of motor commands (Kalaska 1991). A similar conclusion was obtained, by others, when perturbing the spatial orientation of a target rather than its position (Desmurget et al. 1995). The authors found that each orientation of a target was uniquely associated with a particular joint configuration. Importantly this unique association was present even when the target orientation had been modified at movement onset, suggesting that complex movements are encoded using an intrinsic frame of reference.

So we have demonstrated that the ability of the nervous system to express flexible motor commands, which can be altered during the movement, depends upon a redundant limb. This flexibility remains latent during the performance of most movements, although it is expressed in the spatial variability of hand trajectories.

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