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Adjustments of fast goal-directed movements in response to an unexpected inertial load

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Summary. Subjects made fast goal-directed elbow flexion movements against an inertial load. Target distance was 8 or 16 cm, randomly chosen. To exert a force in the direction of the movement subjects had to activate flexors of both shoulder and elbow, but shoulder flexors did not change appreciably in length during the movement. In 20% of the trials the inertial load was increased or decreased without knowledge of the subjects. Until 90–110 ms after the onset of the agonist muscle activity (about 65–85 ms after the start of movement) EMG activity was very similar in all conditions tested. The changes that occured in the EMG from that moment on were effectively a later cessation of the agonist activity and a later start of the antagonist activity if the load was increased unexpectedly. If the load was reduced unexpectedly, the agonist activity ceased earlier and the antagonist activity began earlier. The latency at which EMGs started to change was the same for muscles around shoulder and elbow, for agonists and antagonists and for both distances. All adjustments had the same latency (37 ms) relative to the point where the angular velocity of the elbow in the unexpectedly loaded movements differed by 0.6 rad/s from the expected value. We discuss why simple reflex- or servo-mechanisms cannot account for the measured EMG changes. We conclude that appropriate adjustments of motor programmes for fast goal-directed arm movements start within 40 ms of the detection of misjudgment of load.

Key words: Fast arm movements – Load disturbance – Motor programmes – Sensorimotor integration – Stretch reflex – Human

Introduction

To make a fast goal-directed limb movement one needs to know more than the direction and extent of the movement. The load to be moved is also a very important parameter of the movement. An inertial load can have a dramatic effect on the dynamic behaviour of the limb. It has been shown (Lestienne 1979; Wadman et al. 1979) that the timing and the intensity of the muscle activations can be adapted to a new load condition, even in the case of a negative mass.

In daily life, the mass to be moved is generally not known exactly, so in programming the movement it is likely that the load is over- or under-estimated. To move such loads accurately and fast, there must be a correction mechanism that adjusts the movements for such misjudgments of load. Schmidt and McGown (1980) have shown that the nervous system can indeed correct misjudgments of inertial load. Day and Marsden (1982) showed that this finding also holds for viscous loads.

The explanation favoured by Schmidt (1982) is that there is a linear servo-mechanism superpositioned on the motor programme to correct for load misjudgments. According to his view, a position error in the execution of movement will lead to a correction signal (a change in activation) until the arm has reached the desired position. Day and Marsden (1982) attributed their results to the long latency component of the stretch reflex superpositioned on the motor programme, which is a variant of a servo-mechanism.

Another possibility is that during the movement the programme generator uses the proprioceptive information to alter the planned activity (Arbib 1981), for instance the timing of the switch from agonist to antagonist activation, as suggested by Denier van der Gon (1988). Recently, it has been demonstrated (Pelisson et al. 1986; van Sonderen et al. 1989) that changes in target location can cause reprogramming of an ongoing movement. A percieved misjudgment of the load might cause a similar reprogramming of the movement.

In the research presented we investigated the adjustments made in fast goal-directed movements to correct for an unexpected load. The results are discussed in the light of the suggested mechanisms.

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Methods

Apparatus

The apparatus used in the experiment is described by van den Berg et al. (1987). It consists of a horizontal rail along which a handle can be moved in a straight line over 0.5 m. The handle is attached to a metal belt which runs over two cogwheels. One of these is attached to a microprocessor-controlled torque motor and a digital position encoder. The handle can also be blocked to perform isometric experiments. Strain gauges built into the handle were used to measure the force exerted on the handle in three dimensions.

Two horizontal arrays of LEDs (4 LEDs per cm) placed over the rail were used to give feedback to the subjects. One array (consisting of green LEDs) displayed a target position or force level to be exerted, the other one (red LEDs, placed 1 cm above the other array) displayed the actual position of the handle or the actual force exerted on the handle.

To simulate an inertia the angular velocity of the motor (measured by a tachometer) was differentiated and multiplied by a microprocessor-controlled factor (the mass). The component of force in the direction of the rail was subtracted from the resulting signal to minimize frictional and viscous forces. The difference was fed back to the power amplifier of the torque motor. The resulting static friction was approximately 1N, the viscosity 10 Ns/m. The effective mass could be varied between 0.7 and 20 kg.

EMG's were recorded using bipolar Ag/AgCl surface electrodes, 0.6 cm diameter, placed 2 cm apart over the muscle bellies. The EMG-signals were sampled after they had been band-pass filtered (16–320 Hz), rectified and low-pass filtered (100 Hz). EMG's from four muscles, handle-position and three components of force were all sampled at 256 Hz and stored on disk.

Experimental procedure

Experiments were performed on 6 healthy, right-handed subjects, who gave informed consent. They were seated with their right arm 90 degrees abducted with the arm supported under the elbow joint. The wrist was supinated, immobilised and tightly strapped to the handle. Shoulder angle (θ_1) was between 75 and 90 degrees (0 degrees: upper arm in frontal plane).

In the experiments, EMGs were recorded from the following muscles: the shoulder flexor pectoralis major, the shoulder extensors deltoideus posterior and infraspinatus, the elbow flexors biceps brachii and brachioradialis, and the elbow extensor triceps brachii. In one experiment we recorded the EMG from the anterior part of the deltoideus. Although it is anatomically a shoulder flexor, in the movements it clearly acted as an antagonist. Such deviating behaviour by this part of the deltoideus was also reported in Jongen (1989). In further analysis we treated this muscle as a shoulder extensor.

Each experimental session started with the determination of isometric EMG-torque relations. The subject had his elbow at an angle of 90 degrees (0 degrees: full extension), and was asked to exert a force on the blocked handle, directed along the rail. On the LED array 10 target force levels were indicated, ranging from 0 to 100 N; at each of these force levels the exerted forces and the four EMGs were sampled.

Hereafter the subjects could get accustomed to making fast movements with the handle. The target position was marked by two LEDs. The width of the target region was 12.5% of the movement distance, which corresponds to the accuracy of fast movements with a duration of about 400 ms (Fitts 1954). The subjects were instructed to bring the handle to a standstill in the target region as soon as possible. Thus both the reaction time and the movement time had to be as short as possible. Some of the subjects had visual feedback supplied by the LED arrays, others were deprived of all visual information about their arm position. The experiment consisted of about one hundred fast elbow flexion movements over 8 or 16 cm.

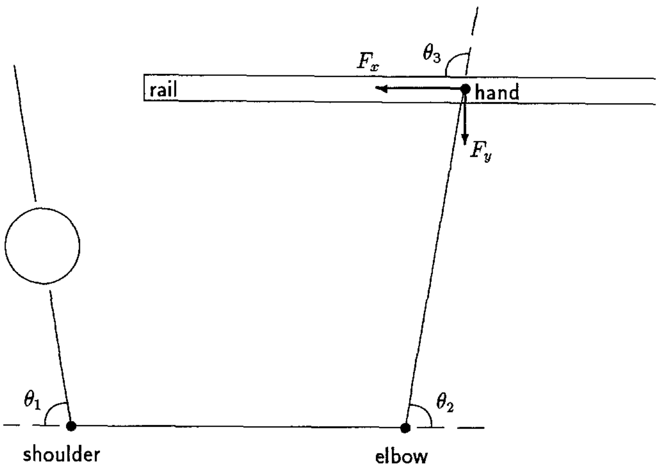

Fig. 1. Top view of the experimental configuration

Each movement started at an elbow angle (θ_2) of approximately 85 degrees, and an angle (θ_3) between lower arm and movement direction of approximately 95 degrees. In this configuration (see Fig. 1), the movement along the rail was initially the result of almost only elbow flexion. During the first 6 cm of movement, which is the most important part for the analysis, the elbow flexed approximately 10 degrees and the shoulder rotated only about 0.2 degrees. In this configuration however, the moments about elbow and shoulder of a force in the direction of motion are the same. Thus, if a subject exerts a force in the direction of motion, both shoulder and elbow muscles have to exert the same torque.

In 80% of the movements, the simulated mass had a standard value, in the other 20% the mass was unexpectedly changed. Not all movements with the standard mass were recorded, we recorded only those standard movements that preceded the unexpectedly loaded movements. The subjects were familiar with all the masses that would occur in the experiment. They knew which one was the standard mass and which were the unexpected ones, and they had made a few training movements with all masses over both distances.

Four experiments were carried out. Five subjects participated in experiment 1, in which the standard mass was about 5 kg, and the unexpected masses were 0.7 and 20 kg. If the adjustment of the movement is a reaction-time process, we would expect the latency of the adjustment to decrease if a subjects does not have to choose his reaction (Houk 1978). So, with two subjects, we repeated the experiment with only one unexpected mass: experiment 2.

In order to investigate the difference between a movement with an expected and unexpected mass, we performed with two subjects an experiment in which the standard mass was 0.7 kg, and the unexpected masses were 5 and 20 kg: experiment 3. We can study the effect of expectation by comparing the standard loaded movements of experiment 3 with the movements of experiment 1 which were unexpectedly loaded with 0.7 kg, and vice versa for the 5 kg load.

In experiment 1–3 the mass was changed at the moment the target position appeared. In this way, the whole movement was made with the same mass. This procedure however gives no reliable information about the moment in time at which the change of load is detected. So, with one subject, we repeated experiment 1 slightly modified: in experiment 4 the mass was changed when the handle had been moved 0.5 cm. Due to the acceleration at this point, the changing of the mass will directly cause a change of acceleration. In this way the start of the disturbance of the movement is better defined, so we can express the latency of an adjustment with respect to the start of the disturbance.

After each unexpectedly loaded movement subjects had a 20 s rest. Subjects could also take a rest after other movements. The total duration of an experimental session was less than one and a half hour.

Data analysis

The force exerted by the hand at 200 ms before the handle had moved 0.5 cm was taken as the background force. The moment, at which the force in the direction of movement had increased 1 N above the background force, was taken as the point for synchronisation. Until this moment, the handle did not move due to friction. In this way, the synchronisation point is independent of the mass. Unless otherwise stated, all times are relative to this synchronisation point, which is referred to as "the start of movement". It is also the zero point on the time axis in the figures. The EMG of the agonists starts (i.e. surpasses 12,5% of burst maximum) approximately 25 ms before the start of movement. The end of movement was defined as the moment at which the velocity was less than 0.05 m/s for at least the next 75 ms.

Velocity and acceleration signals were obtained off-line by digital differentiation of the position after filtering with a fourth-order digital Butterworth filter (Ackroyd 1973). The filter was applied both in forward and reverse direction to prevent phase shift. The effective cut-off frequency was 45 Hz.

Static torques were calculated from force data according to

$$\begin{pmatrix} M_1 \\ M_2 \end{pmatrix} = \begin{pmatrix} l_2 \sin\theta_3 + l_1 \sin(\theta_2+\theta_3) & l_2 \cos\theta_3 + l_1 \cos(\theta_2+\theta_3) \\ l_2 \sin\theta_3 & l_2 \cos\theta_3 \end{pmatrix} \begin{pmatrix} F_x \\ F_y \end{pmatrix}. \quad (1)$$

M_1 and M_2 are the torques about shoulder and elbow, with flexion as the positive direction. F_x is the component of force in the direction of motion and F_y is the component perpendicular to F_x in the plane of the arm, directed to the subject. The angles θ_1, θ_2 and θ_3, defined in Fig. 1, were calculated from the subject's hand position. For this calculation, we measured the position of the shoulder relative to the starting position of the hand, and assumed that shoulder translations were negligible during the experiments. The exerted dynamic torques about the shoulder and the elbow were calculated according to

$$\begin{aligned} M_1 = {} & \ddot{\theta}_1(I_1+I_2+m_2(l_1^2+2d_2l_1\cos\theta_2))+\ddot{\theta}_2(I_2+m_2l_1d_2\cos\theta_2) \\ & -\dot{\theta}_2^2 m_2l_1d_2\sin\theta_2-2\dot{\theta}_1\dot{\theta}_2m_2l_1d_2\sin\theta_2 \end{aligned} \quad (2)$$

$$M_2 = \ddot{\theta}_1(I_2+m_2d_2l_1\cos\theta_2)+\ddot{\theta}_2I_2+\dot{\theta}_1^2m_2l_1d_2\sin\theta_2. \quad (3)$$

As the morphology of the subjects was comparable, we used for all subjects the same estimated values for the parameters in these equations: for the length of the upper and lower arm $l_1 = l_2 = 0.32$ m; for the moment of inertia of the upper and lower arm: $I_1 = 0.054$ kgm^2, $I_2 = 0.060$ kgm^2; for the mass of the lower arm $m_2 = 1.4$ kg and a centre of mass at $d_2 = 0.17$ m from the elbow. This choice of the parameters implies that the calculated torques are a rough estimate, but sufficient for our purposes. The total torque exerted by the muscles is the sum of the calculated static and dynamic components of Eqs. 1–3.

From linear least-squares fits to the data of the isometric experiment EMG-torque relations were derived for the muscles around both joints. With these relations for each muscle the EMG signals can be expressed in the corresponding total torque (Nm) about the joint. Because we defined flexion as the positive torque direction, the EMG of extensors is negative, and more extensor activity thus corresponds to less torque. In this way an indication is given of the effect that changes in the EMG have on the exerted torque.

Force and velocity signals of all recorded movements were examined. Trials in which the subject had clearly not obeyed the instruction (in all load conditions not more than 5% of the trials) were not used for further analysis. For each combination of mass and distance, ensemble-averages and their standard deviations were calculated for the records of position, velocity, acceleration, force, torque and EMG.

To define the point where the ensemble-averaged EMG-records of unexpectedly loaded movements started to deviate from those of standard movements, a *t*-test was performed on the difference of means. Because of the noisiness of the data, a moving average of the difference of means was calculated over an interval of 15.6 ms. Starting at the synchronisation point, the interval was moved until the average of the difference of means was significantly ($p < 0.005$) greater (or less) than zero. The middle of the interval was taken as the point where the signals started to deviate from each other.

This method can slightly over- or under-estimate the start of the EMG-adjustment. If no significant difference was found until 150 ms after the start of movement, no adjustment was assumed to have occurred and the record was not included in the calculation of mean latencies.

t-Tests were also used to compare other ensemble-averaged signals (e.g. velocity or torque) of unexpectedly loaded movements with those of the standard movements. In these cases no moving average was needed. The point where the signals differed significantly $p < 0.005$ from each other was taken as the point where the signals started to deviate.

To test whether a servo-mechanism could account for our results we estimated the feedback delay. Therefore we calculated a normalized cross-correlation function between the EMG-corrections and the kinematic or force error signals for time differences ranging from −110 to 280 ms. The maximum of this correlation function is our estimate of the feedback delay.

In this paper data are always presented as: mean value ± standard deviation (n = number of samples). A sample always refers to a quantity which is the difference of means of two load conditions. The number of samples refers thus to the number of distances, subjects, and muscles involved.

Results

Experiment 1

We first present the results of the experiments with a 5 kg standard mass. This mass could be switched unexpectedly to 0.7 kg or 20 kg at the moment the target was displayed. Five subjects participated in this experiment, three of them were allowed to have visual feedback.

Movement data. Figure 2 shows mean position, velocity, acceleration, force and torque trajectories of movements over 16 cm without visual feedback made by subject TT in this experiment. Irrespective of the load, subjects made one continuous movement. In the movements with both the expected and with the unexpected load, subjects did not direct the exerted forces exactly along the rail, but tended to direct the force somewhat toward their own body. No systematic difference in the direction of exerted force was found between the different load conditions. Vertical forces were negligible.

Without visual feedback, irrespective of the load, subjects made movements that had constant errors up to 15%: undershoot in 16 cm movements and overshoot in 8 cm movements. These errors can be interpreted as an effect of the contraction bias in judging sensory information (Poulton 1979). Movements with an unexpected load were (averaged over all subjects and experiments without visual feedback) 0.9 ± 0.6 cm ($n = 16$) larger than the standard movements. No significant difference in end position was found for the two unexpected load conditions.

When visual feedback was allowed, the target position was always reached. In this condition the movement

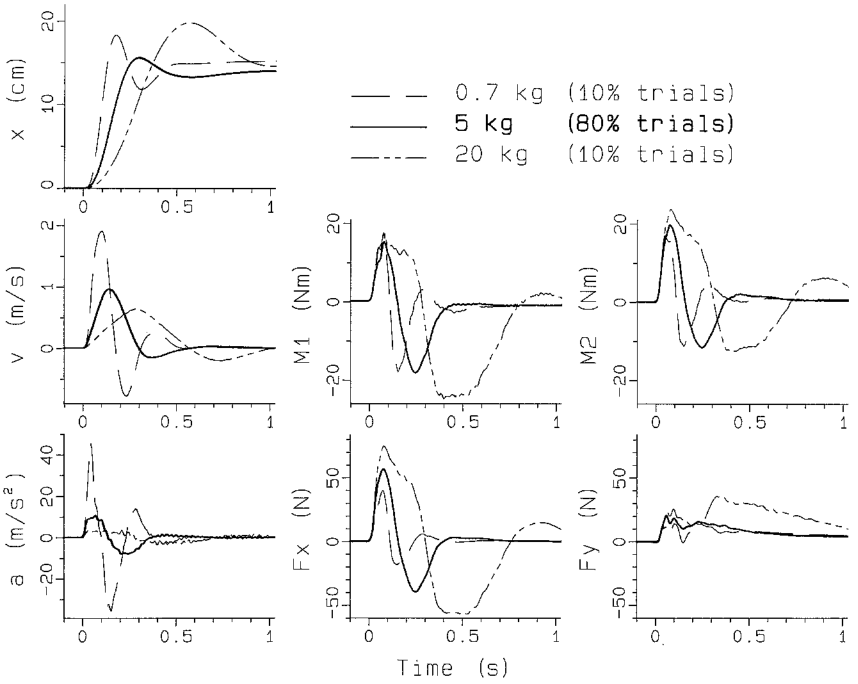

Fig. 2. Ensemble-averages of records of hand-position (x), velocity (v), acceleration (a), torques (shoulder: *M1*, elbow: *M2*) and forces exerted on the handle (F_x, F_y) in experiment 1. The continuous lines (5 kg load, 40 trials executed) are the averages of 10 recorded trials, the dashed lines (unexpected loads, with each load 5 trials executed) are both averages of 5 recorded trials. Results are shown of 16 cm movements made by subject *TT* without visual feedback

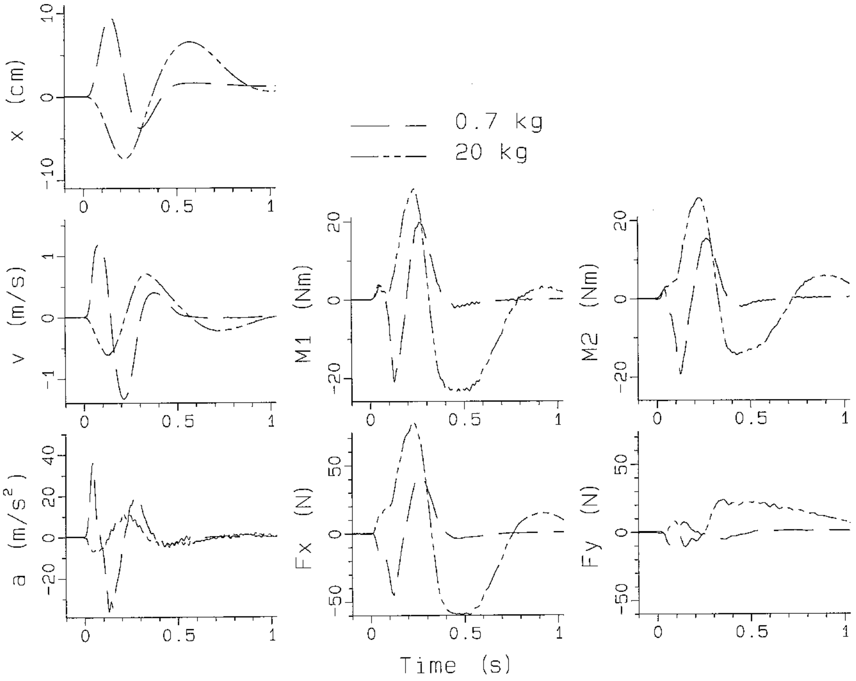

Fig. 3. Difference between the ensemble-averaged movement data of the unexpected loaded and the standard movements in Fig. 2

times of the unexpected 0.7 kg movements were significantly ($p < 0.02$) greater, by approximately 50 ms, than without visual feedback. The same tendency was found for the unexpected 20 kg movements, but for these movements differences in movement times were not significant. The movement time of the standard movements was unaffected by visual feedback.

In Fig. 3 we plotted the difference between the signals of the unexpected loaded movements (Fig. 2, dashed lines) and those of the movements which the subject planned to make (the movements with the standard load: Fig. 2, solid line). Both unexpected masses changed the acceleration (and thus velocity and position) with about the same factor, so absolute changes were larger for the small mass.

The best estimate we can make of the moment when the exerted force of a muscle changed is to use the moment when the torque about that joint changed. For both the elbow and the shoulder, these times are tabulated in Table 1. In both load conditions, a significant change in the torque about the elbow was measured at a shorter latency than in the torque about the shoulder.

These changes in torque could be caused by a change in activation of the muscles around the joint. For the

Table 1. Latencies in experiment 1 at which the exerted torques in unexpectedly loaded movements start to differ significantly from those in movements with the expected load. Times are given relative to the start of movement. The values are averaged over 5 subjects, 2 distances each

Masses (kg)		Start of torque change (ms)	
Standard	Unexpected	Shoulder	Elbow
5	0.7	92 ± 12	67 ± 14 (n = 10)
5	20	112 ± 15	100 ± 15 (n = 10)

shoulder this was the only mechanism that could cause a substantial torque change. The torque data lead us to expect that a change in the activation of the shoulder muscles started about 20 ms earlier in the movements against an unexpected 0.7 kg load than in those against an unexpected 20 kg load.

Not only changes in activation, but also changes of muscle dynamics contributed to torque changes around the elbow. At 70–100 ms after the start of the movement, the different masses caused appreciable differences in the lower arm velocity. Due to the force-velocity relationship for the shortening elbow flexors, torques about the elbow will (under conditions of an unchanged activation) be increased for the 20 kg load and decreased for the 0.7 kg load. The velocity differences were larger in the case of the 0.7 kg unexpected load; this could explain the earlier torque changes in this condition. An examination of the EMG-recordings should reveal whether the force-velocity relationship was the only source of the time difference in the start of the torque changes for elbow and shoulder.

Electromyographic data. The ensemble-averages of the EMG-patterns of the movements in Fig. 2 are shown in Fig. 4. All subjects showed similar EMG-patterns. In both standard and unexpectedly loaded movements a three-burst pattern was distinguishable, although the third bursts were less well pronounced in the movements with the 20 kg mass. The patterns showed roughly the same timing and intensity (expressed in equivalent torque) for the shoulder and elbow muscles. The timing of the activation of the shoulder muscles was also about equal to that of the elbow muscles in the movements with an unexpectedly changed load. In the case of an unexpectedly small mass the first agonist bursts were shortened and the antagonist bursts started earlier. In the case of an unexpectedly large mass, the first agonist bursts were prolonged and the antagonist bursts were delayed. The height of the first agonist and antagonist bursts were not significantly affected by the load change.

So that we can interpret the data in terms of a reflex or servo action superpositioned on an unchanged motor programme, we have plotted the difference in the EMG of the unexpected and standard load conditions for elbow and shoulder flexor and extensor in Fig. 5. Figure 5A shows the adjustments in the case of a smaller mass. Adjustments started at about the same time in the muscles around shoulder and elbow: less agonist and more antagonist, both causing a reduction of the force for the acceleration. Figure 5B shows the reverse in the case of a larger mass: all muscles contribute to an increase in the force for the acceleration. A few EMG-records (of muscles around both elbow and shoulder) did not show an adjustment according to our criteria, but for each subject, at least three out of four records showed an adjustment.

No significant difference was found in the latencies for the muscles around shoulder and elbow, for agonists and antagonists, for both distances and for subjects with

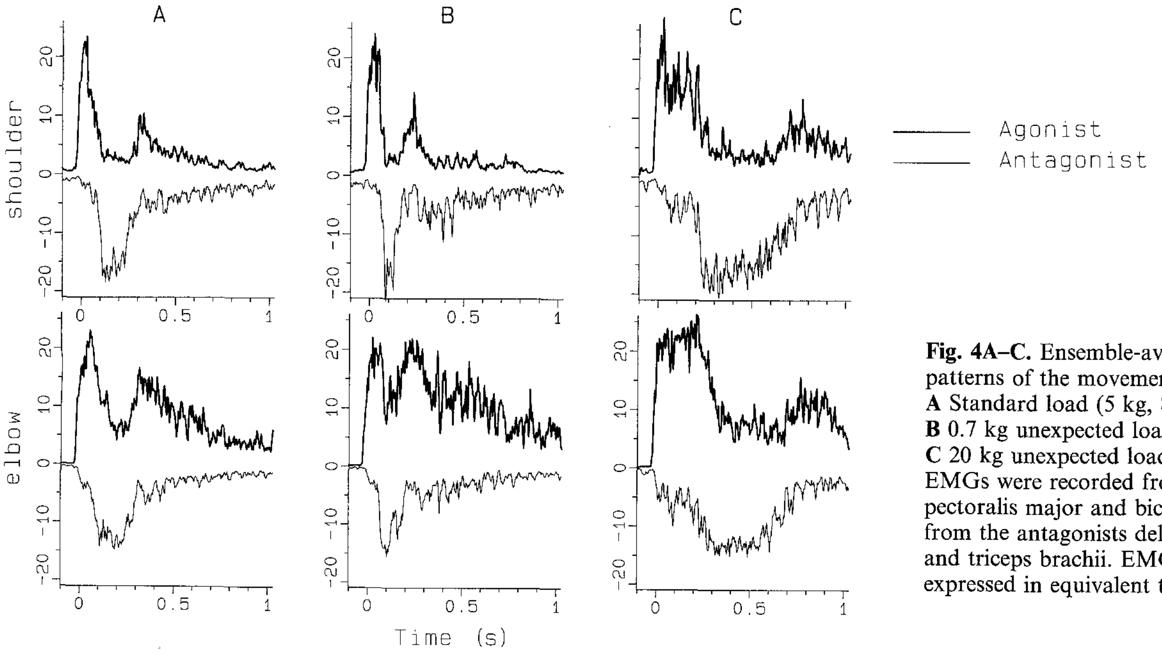

Fig. 4A–C. Ensemble-averages of the EMG patterns of the movements shown in Fig. 2. **A** Standard load (5 kg, 80% of trials), **B** 0.7 kg unexpected load (10% of trials), **C** 20 kg unexpected load (10% of trials). EMGs were recorded from the agonists pectoralis major and biceps brachii, and from the antagonists deltoideus posterior and triceps brachii. EMG-values are expressed in equivalent torque (Nm)

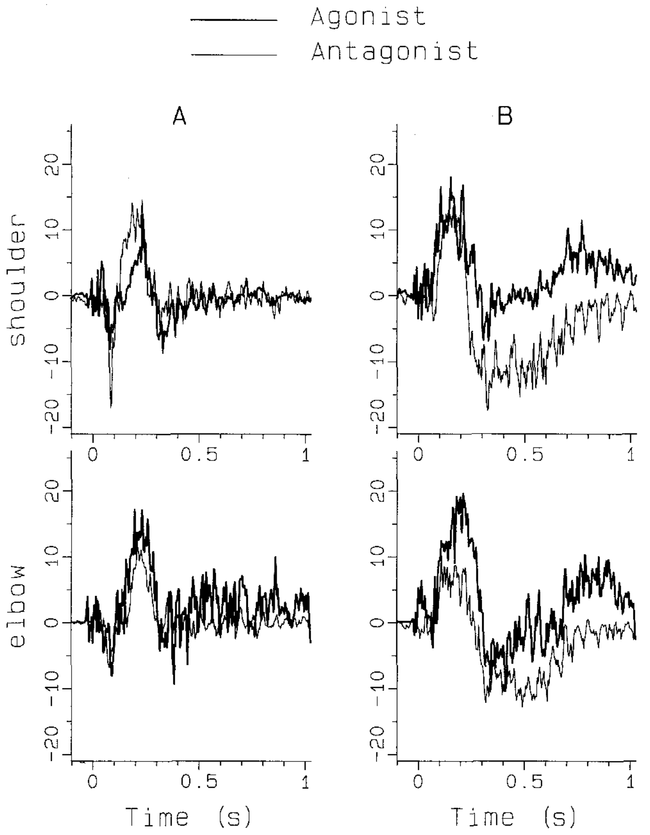

Fig. 5A, B. Difference between the ensemble averaged EMG patterns of the unexpected loaded and the standard movements in Fig. 4. **A** 5 kg standard load and 0.7 kg unexpected load, **B** 5 kg standard load and 20 kg unexpected load. EMG-values are expressed in Nm

and without visual feedback. The EMG-signals of the movements with the 0.7 kg mass began to differ significantly at 68 ± 15 ms ($n = 31$) after the start of movement, for the movements with the 20 kg mass this was at 85 ± 18 ms ($n = 38$). The inter-subject standard deviation of the latencies (for each subject averaged over all muscles and both distances) was 7 ms for both load conditions.

The change in shoulder torque thus started approximately 25 ms after the start of the EMG-adjustment, this time-difference was approximately the same for the two unexpected loads. Although the change in torque started earlier about the elbow than about the shoulder, we found the latencies of the EMG-adjustments to be equal in shoulder and elbow muscles. From this we can conclude that the start of the change in elbow torque was caused by the force-velocity relationship.

Experiment 2

In order to test the effect of eliminating the choice situation, the experiment was repeated under slightly modified conditions. In this experiment only two masses were possible: the standard mass (5 kg) and one unexpected mass. The experiment involved two subjects who had no visual feedback. They knew that only one kind of unexpected mass was possible in this experiment, and had made test movements with this mass and the standard one. If the adjustment in EMG was a reaction time process, we would expect the latencies in this experiment to be shorter than in experiment 1.

The EMG signals in this experiment did not differ significantly from those in experiments with three possible masses. So we do not think that reaction time processes were important in the responses to an unexpected load. The average of the latencies of EMG-adjustments in this experiment and experiment 1 are shown in the upper part of Table 2.

Table 2. Latencies of EMG-adjustments in experiments 1 and 2 (combined) and experiment 3. Times are given relative to the start of movement. Upper part: Average of five subjects (two distances and four muscles) for both load conditions in experiment 1 and two subjects (each for one load condition) in experiment 2. Lower part: Average of two subjects for both load conditions

Experiment	Masses (kg)		Latency of EMG-adjustment (ms)	Adjustment not found
	Standard	Unexpected		
1, 2	5	0.7	67 ± 13 ($n = 39$)	9
	5	20	84 ± 19 ($n = 44$)	4
3	0.7	5	78 ± 18 ($n = 14$)	2
	0.7	20	62 ± 14 ($n = 15$)	1

Experiment 3

So that we could compare planned movements with movements that have been adjusted to an unexpected load, we repeated the experiment with the 0.7 kg mass as the expected load, and the 5 and 20 kg masses as unexpected. Two subjects participated in this experiment; they had visual feedback in both experiment 3 and 1.

In the movements with an unexpected load of 0.7 kg the overshoot for both the 8 and 16 cm movements was more than 2 cm larger than in the movements with the 0.7 kg load when expected. The movement times with both the 0.7 and the 5 kg unexpected loads over both distances were 85 ± 48 ms ($n = 8$) longer than with the same loads when expected. The movement times with the 20 kg load, which was an unexpected load in each experiment, were the same in each experiment.

The latencies of EMG-adjustments in this experiment are shown in the lower part of Table 2. Also in this experiment no difference was found in the latencies for agonists and antagonists, or for shoulder and elbow. The latency of the EMG-adjustment for the unexpected 20 kg load was significantly ($p < 0.01$) shorter than for the unexpected 5 kg load. For the unexpected 20 kg load, the latency of the EMG-adjustment was 22 ms shorter in this experiment (with the 0.7 kg standard load) than in experiment 1 with the 5 kg standard load. This difference is also significantly ($p < 0.01$) if we compare only the values for the two subjects who participated in both experiments. For these two subjects, the latency in experiment 3 with 5 kg as the unexpected load (and 0.7 kg expected) did not differ significantly from the latency in experiment 1 with 0.7 kg as the unexpected load (and 5 kg expected).

Experiment 4

With one subject an experiment was performed in which the mass was switched after the handle had moved 0.5 cm, about 50 ms after the start of movement. At that moment the acceleration was approximately 10 m/s^2, so the change of mass caused a strong disturbance of the ongoing movement.

For these movements it was not appropriate to compute the latencies of the adjustments relative to the movement onset. In this experiment it was better to define the latency of the adjustment as the period of time between the moment at which the ensemble-averages of the velocity start to differ significantly ($p < 0.005$) and the start of EMG-adjustment. By using this method we found for the 0.7 kg unexpected load a latency of 32 ± 17 ms ($n = 6$) and for the 20 kg unexpected load a latency of 34 ± 20 ms ($n = 8$).

For both unexpected loads the latencies are very short. This result made us wonder whether we could also describe the results of the other experiments with one (short) latency.

Detection of an unexpected load

In most experiments, we expressed the latency of adjustments relative to the start of movement. We know that at this point the subject could not have experienced the change of load. This method resulted in different latencies for different unexpected masses. There are two possible explanations for these differences: either they reflect different responses of the central nervous system or the latencies were only seemingly different due to a detection threshold for the load difference.

To test the second possibility we investigated whether we could find identical latencies with respect to one detection point. To do this, we took the start of EMG-adjustment as a new reference point in the records from all subjects and for all experiments. For the ensemble-averages of the position, velocity and force signals, we have plotted in Fig. 6 the absolute difference between the actual and the planned values against the time to the start of EMG-adjustment. In this figure, results are shown of all experiments described in this article. The rationale for this procedure is that, if an absolute threshold is used to detect an unexpected load, this threshold will be surpassed for all 36 traces at approximately the same time before the EMG-adjustment. The level for which the traces have a minimum in the time-variance is thus the most probable detection threshold.

There was no minimum in the time-variance of the absolute force difference, so it was not possible to find a most probable value for a force difference detection threshold. The variance in the time between a fixed velocity difference and the onset of adjustment is smallest for a velocity difference of 0.2 m/s. For all unexpectedly loaded movements we found that the EMG-adjustments started 37 ± 6 ms ($n = 36$) after the moment in time at which the velocity of the unexpectedly loaded movement differed by more than 0.2 m/s from the expected movement. This velocity corresponds to an elbow rotation with 0.6 rad/s angular velocity. In a similar way we found that the most probable detection threshold based on position difference was 0.6 cm (0.02 rad). This point was reached 25 ± 6 ms before the EMG-adjustment.

We have calculated these latencies also for several subsets of our experiments. The latencies did not depend significantly on the sign of the load change or on the standard mass. We can thus describe the results of all experiments very well with one latency.

Servo control?

In a servo-mechanism a controller continuously computes a correction signal from the difference between an

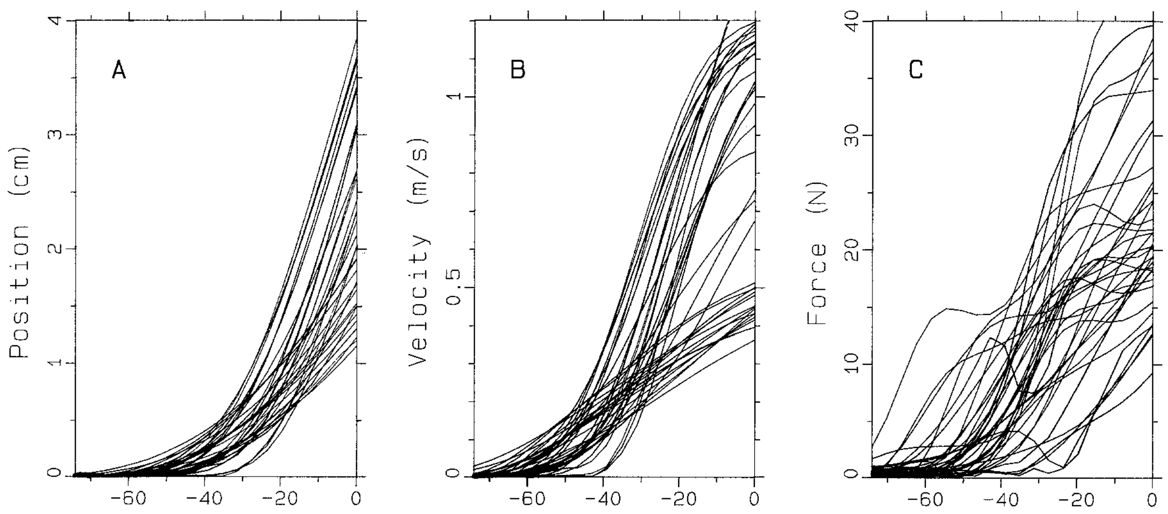

Fig. 6A–C. Absolute value of the difference in ensemble-averages of **A** hand-position (x), **B** velocity (v), and **C** force in the direction of motion (F_x) between standard and unexpected loaded movements. The zero point on the time axis is the start of EMG adjustment (average of three or four muscles). In this figure, results of experiment 1 (20 traces), 2 (4 traces), 3 (8 traces) and 4 (4 traces) are combined output and a reference signal. In the human arm, the correction in the EMG will lag at least 16–18 ms behind the error in kinematical or force variables, due to the conduction times. To account for the experimental results, such a servomechanism must know that a correction of an error in the elbow has to be sent to both the elbow and shoulder. Examples of the possible error signals in our experiments are shown in Fig. 3; the corresponding correction signals are plotted in Fig. 5.

A negative position or velocity servo superpositioned on a motor programme will lead to corrections of errors that are due to misjudgment of the load. Can such a mechanism account for our measured correction signals? One way to test this hypothesis is to estimate the feedback delay from the time of the maximum in the normalized cross-correlation function. If this delay is not in the physiological range of 20–50 ms, then we can reject the hypothesis.

The EMG-adjustments were not well correlated to the position error. The maximum in the cross-correlation functions was 0.45 ± 0.15 ($n = 128$), and was found mainly between -100 and -50 ms. Thus, although the start of the EMG-adjustment was at least 25 ms after the start of the position error, on average the feedback delay was negative, so we can rule out position feedback.

The correlation between the velocity error and the EMG-adjustments was higher: 0.75 ± 0.10 ($n = 128$); it was found at 6 ± 16 ms. This time depended on the value of the standard and unexpected masses. For all experiments with 5 kg standard and 0.7 kg unexpected mass for instance, the maximum was found at -7 ± 7 ms ($n = 52$). So, with some load conditions, the correction signals also preceded the velocity error. Thus neither a position nor a velocity servo-mechanism can describe our experimental results.

Discussion

The results show clear adjustments of the EMG starting at an early stage of the movement. We shall now discuss two questions: how good are these adjustments, and what is the underlying mechanism. To describe this mechanism we need to have answers to two questions. Firstly, we need to know how the nervous system detects that a limb movement is unexpectedly loaded. The second question is: how does the nervous system use this information?

Adequacy of response

The quality of a movement depends on its movement time and its accuracy. The quality of the unexpectedly loaded movements was quite good, but not as good as the movements in which the load was expected. They had either an error in end position or a longer movement time. The error in end position (overshoot in both unexpected load conditions) was also reported by Schmidt and McGown (1981), although in their experiments it was not significant.

In the movements with the standard mass, the direction of the force exerted on the handle was not entirely in the direction of movement. So we could not expect this to be the case in the unexpectedly loaded movements. We conclude that for the unexpectedly loaded movements the EMG-adjustments were qualitatively adequate: shoulder and elbow corrections occurred at the same moment and approximately in the appropriate direction.

Detection of load

We have attempted to answer the question of the detection of load in the results section. The answer was that with an absolute position or velocity threshold we could unify the four latencies in Table 2 and the latencies in the switched mass experiment to one latency. It was not possible to do this with a force threshold. This rules out the possibility that cutaneous inputs from the hand are the basis for the adjustments. The latencies relating to absolute position and velocity thresholds both characterize the experimental data quite well. An important question is: which of these two latencies is realistic from a physiological point of view?

An argument in favour of a velocity threshold is the fact that 0.6 rad/s is very easy to perceive (Sittig et al. 1985), whereas a position difference of 0.02 rad is not (Crowe et al. 1987). Furthermore, results of vibration experiments (Sittig et al. 1987) indicate that afferent velocity information is used for the control of fast movements. Another argument for velocity detection is that position detection leaves only 25 ms time for transportation and computation. The velocity threshold leaves more computational time (37 ms) for the nervous system. So the most probable interpretation of our results is that an adjustment becomes visible in the EMG 37 ms after an angular velocity difference of 0.6 rad/s has been detected between planned and actual velocity.

The latencies we found are about the same as the latency Wadman et al. (1979) reported for an unexpected infinite mass. Exact comparison is not possible due to the different ways in which the start of EMG bursts and EMG differences were defined. We take the opportunity here to react to some misinterpretations of Wadman's experiment. Several authors concluded from the 100 ms 'unchangeable' EMG, combined with movement times of about 150 ms, that proprioceptive information is useless in fast goal-directed movements. They did not take into account that according to their definitions the movement started at least 50 ms after the EMG-onset. In this experiment we have shown explicitly that although the EMG was unchanged for about 100 ms, proprioceptive information did adjust the movements.

Now that we have established that adjustments were probably made on the basis of velocity information, we must try to find out by which mechanism the velocity difference was measured. Since the movements in our experiments were almost pure elbow flexion, the velocity of the hand could only have been measured by means of the spindles in the muscles around the elbow: either in the shortening agonists or in the lengthening antagonists.

In muscle vibration experiments (Capaday and Cooke 1981; Sittig et al. 1987) only antagonist vibration disturbed the movement. Lennerstrand and Thoden (1968), however, showed that in cat static fusimotor stimulation was capable of maintaining muscle spindle firing during muscle shortening. This is also possible at high velocities, although during shortening at high velocities in a normal moving cat spindle endings tended to fall silent (Prochazka et al. 1979; Appenteng et al. 1982). No experimental information exists about spindle firing at high shortening velocities in man.

How can the nervous system conclude from the afferent information that the actual velocity is different from the planned velocity? Detection of the unexpected load by antagonist receptors would require a comparison of the actual spindle signals with the expected signals. In the case of agonist receptors another possibility exists: α-γ-coactivation so that the muscle spindles give a constant output at the desired velocity (Matthews 1972). For this mechanism, the γ-activation has to correspond to the planned velocity, whereas the α-activation corresponds to the force. As the actual velocity depends on the combination of force and load, this mechanism requires that the activation of the α-motoneurons is controled independent from that of the γ-motoneurons. So it does not differ in complexity from a comparison of the actual spindle signals with the expected: in both methods an expected velocity signal is required in addition to the α-activation.

Mechanism underlying the adjustments

We have shown that a linear position or velocity servo superpositioned on the ongoing motor programme cannot describe the measured EMG-adjustments. Can the adjusted EMG-patterns be completely described by a change of the timing of the EMG-bursts?

In the experiments of Wadman et al. (1979) with expected inertial loads, the time coarse of the EMG-pattern varied with the load, while the intensity of the activations remained the same. Our measurements also showed roughly the same features with unexpected inertial loads (Fig. 4B,C). This favours the hypothesis that the timing of the activations is adjusted to the new load conditions.

If the adjustment of the activations consists only of a delayed or an earlier than planned switch from agonist to antagonist activation, we would expect the adjustment in the case of an unexpected larger load to start at the planned moment for the switch. In experiment 3, however, we found that the start of the adjustment depended on the size of the larger load. Thus an adjustment of the timing of the motor programme has to be more flexible than only a delayed or earlier than planned switch from agonist to antagonist activation.

Another possible mechanism underlying the adjustment in the EMG is that these adjustments are a manifestation of a stretch reflex mechanism. To what extent can the adjustments in our experiments be explained by stretch responses?

In the elbow flexion movements investigated in this study, the pectoralis major is activated to prevent shoulder extension. Sensors located in these muscles cannot sense a change in load, so autogenic reflexes will not cause an adjustment in these muscles. A reflex mechanism however may well be involved, because it has been shown that stretch responses can also be present in muscles that are not stretched. Such responses have been found for instance in a thumb flexor after arm displacement (Traub et al. 1980), in the pectoralis major after thumb extension (Marsden et al. 1981), in the biceps after elbow flexion (Lacquaniti and Soechting 1986), in the triceps brachii after elbow extension (Johansson and Westling 1988), and in the same muscle after elbow pronation (Gielen et al. 1988). The latencies of these responses ranged from 35 to 50 ms.

Not all features of the adjustments in our experiments, however, can be attributed to stretch responses. In many experiments in which these responses have been studied, the threshold for the adjustments in fast movements (0.6 rad/s) is not reached within the response latency. This means that either the stretch response is caused by another mechanism or the threshold of the stretch response depends on dynamic conditions.

The stretch reflex is probably a manifestation of a more general response, which can be modulated in accordance with the specific task and expected perturbations. Nashner (1976) showed that subjects were able to modulate the long latency reflex gain following changes in the postural task. Traub et al. (1980) showed that both loading and unloading of the long thumb flexor could cause reflex activity in this muscle, depending on the task the subject was performing. Nichols (1989) has demonstrated that changing the activation of ankle muscles in cat can change heterogenic reflex action from excitatory to inhibitory.

The experiments of Abbs and Gracco (Abbs and Gracco 1984; Gracco and Abbs 1985) on disturbance of speech movement showed coordinated responses of upper and lower lip muscles to a disturbance of lower lip position. They did not record EMG responses with a latency of the perioral reflex, but found coordinated EMG-adjustments with latencies ranging from 22–75 ms. The contributions of autogenic and nonautogenic responses to the corrections depended on the time between disturbance and voluntary muscle activation. They interpreted the flexible responses as a manifestation of an open-loop predictive mechanism for the control of complex motor actions. Probably, tuning of the long latency reflex to the specific task and to possible disturbances is the basis of this mechanism.

Most authors argue that a polysynaptic pathway is involved in the coordinated responses they have found. For a response to be adequate however, a polysynaptic pathway is not necessary. Versatile heterogenic monosynaptic connections can also account for the reported responses. Fritz et al. (1989) have reported strong heterogenic monosynaptic Ia connections in the cat forelimb. Recently, Cavallari and Katz (1989) have reported monosynaptic projections from muscles acting around the wrist to biceps and triceps in man. To decide wether these monosynaptic connections are versatile enough to account for the various experimental results, more physiological data are needed.

Our statement that the activation is adjusted 37 ms after the angular velocity differs by 0.6 rad/s from the planned value, does not imply that after that moment the activations cannot be changed. It is more likely that at that moment only a rough correction of the activations is made. During the rest of the movement, the activations will be continuously adjusted to new information about the movement. Van der Meulen et al. (1989) argued that in undisturbed fast goal-directed arm-movements the activation is also adjusted during the movement to compensate for initial variability. The same was found by Bootsma and van Wieringen (1990) for an attacking forehand drive in top table-tennis players.

We conclude therefore that motor programmes of fast goal-directed movements can be adjusted in a very flexible way to unexpected load conditions. Our experimental results can be explained in terms of a flexible stretch response, but not in terms of simple reflex- or servo-mechanisms.

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