# Perturbations of Fast Goal-Directed Arm Movements: Different Behavior of Early and Late EMG Responses

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**ABSTRACT.** Subjects made fast goal-directed elbow flexion movements against an inertial load. Target distance was 8 or 16 cm, randomly chosen. In 20% of the trials, the inertial load (the mass) was increased or decreased without the subject's knowledge. The change of mass elicited appreciable electromyographic (EMG) responses in elbow muscles as well as in shoulder muscles. The latency of these responses was 25–35 ms, relative to the point at which the velocity of the hand differed by more than 0.2 m/s from the velocity in the control trials.

Whether these responses could be altered during fast movements was tested by giving instructions to the subject or by changing the mass during the movement instead of just after the start.

The first 25 ms of the response were found to depend only on the velocity change induced by the perturbation, not on the instruction to the subject, regardless of the phase of the movement. The part of the response with a longer latency (60 ms) could have a sign opposite to that of the early response, anticipating future effects of the mass change. Instructions to the subject to stop the movement if the mass was unexpectedly large had a slight effect on this late response but no effect on the early response.

The sequence of an early stereotyped response and a flexible late response resembles the sequence of responses to muscle stretch, which makes it likely that the same neural circuits are used. The responses seem more adequate for correcting for changes in inertia than for correcting for position errors. Probably, the stretch reflex is an epiphenomenon of a mechanism that is tuned for dealing with changes in inertia.

Key words: arm, ballistic movements, human, inertial load, instructions, motor program, stretch reflex

n daily life, we generally do not know the precise mass (inertia) of objects that we wish to move. The mechanism underlying our ability to cope with this uncertainty is therefore quite relevant in motor control. In Smeets, Erkelens, and Denier van der Gon (1990), we showed that if the mass to be moved during a fast goal-directed arm movement differed from the one the subject expected at the start of the movement, the EMG patterns adjusted to the actual mass during the movement. We argued that the adjustments observed were caused by a difference between expected and actual velocity or position. The observed EMG responses were such that if the movement was slower than expected, because of a heavy mass, the agonist activities were increased and the antagonist activities were decreased; and vice versa for a light mass. These findings were consistent with earlier experiments (Angel, 1975). Not previously reported were the short (< 35 ms) latency of the changes in EMG and the fact that similar responses were found in muscles that did not change their length in the experiment. Because of the unexpected mass, the agonists shortened at a lower velocity than they had during unperturbed movement execution: They were stretched in comparison with their lengths in movements with the expected mass. This relative muscle stretch led us to argue that the observed responses and the stretch reflex could be manifestations of the same mechanism.

This hypothesis, however, contradicts two rather generally accepted notions about the stretch reflex. The first notion is that a short latency stretch reflex occurs only in muscles that are stretched. Recent experiments, however, revealed that muscles that are not stretched can show a short latency reflex (Smeets & Erkelens, 1991). The sec-

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ond notion is that the stretch reflex is suppressed during fast movements: Research on the stretch reflex in muscles around the ankle (Gottlieb & Agarwal, 1980) and elbow (Soechting, Dufresne, & Lacquaniti, 1981), and in jaw muscles (Erkelens, 1983), has shown that during fast movements, the gain of the stretch reflex was almost zero. In our experiments, however, we found substantial EMG responses. This difference could have been a result of different underlying mechanisms; however, it could also be caused by differences in the instructions to the subjects and in the duration of the perturbations. An interesting aspect of these studies on the stretch reflex during fast movements is that they all reported changes in the response amplitude during the movement. Probably, these time-dependent changes can be found in the responses to an unexpected mass as well. We therefore decided to investigate the response to unexpected masses at different parts of the movement.

The experiments in this article were meant to give a more comprehensive characterization of the response to an unexpected mass during fast goal-directed movements. We investigated three new aspects of the responses during fast goal-directed movements: whether similar EMG responses could be found in all phases of the movement, whether these responses could be changed by instructions to the subject, and whether we could find differences between responses with short and long latencies. By comparing these results with the characteristics of the stretch reflex, we were able to get more evidence for our hypothesis that the stretch reflex and the responses to an unexpected mass during fast goaldirected movements are manifestations of the same mechanism. For this comparison, the instructions for the subjects in our experiment must be comparable with the instructions used in reflex experiments.

In daily life, there are many situations in which the best response to an unexpectedly low velocity of the hand during an arm movement is to increase the effort of the movement. This is, for instance, the case if one wants to move a carton of milk that contains more milk than expected. This is the response we found in our previous experiments. In some situations, however, the best response is to stop the movement. For instance, if one wants to open a door that might be locked, a low velocity of the hand may indicate that it is really locked. In that case, there is not much point in increasing one's effort to open the door. So two more or less natural instructions can be used: Always move to the target (carton-of-milk instruction), and Stop the movement if you encounter an increased resistance (locked-door instruction).

In the locked-door instruction, the perturbation is a trigger for changing the aim of the movement instead of opposing the perturbation. Stretch reflex experiments using perturbations in the direction of a planned movement (Evarts & Granit, 1976; Wadman, Boerhout, & Denier van der Gon, 1980) are more or less analogous to the locked-door paradigm: The subjects are told not to oppose the perturbations. In these experiments, the stretch reflex elicited by the perturbation would be counterproductive. The conclusion from these experiments was that the long latency component (LL; > 50 ms) of the stretch reflex could be suppressed completely by the instruction, but the short latency component (SL; 25–50 ms) remained unaffected.

In this study, we tested to what extent the EMG responses elicited by a change of inertia during a fast goaldirected movement depended on whether or not they were optimally suited for the actual situation. To investigate this, we used a natural load: the inertia. The force resulting from inertia changes depends on the acceleration. To compare perturbations with the same sign, we compared an increase of inertia just after the start of movement with a decrease of inertia after about half the movement had been completed (mimicking the loss of something during a movement). Both changes in inertia resulted in a force directed against the movement. Thus adequate responses had the same sign: more flexor activity and less extensor activity. In this way, any effect of asymmetries between loading and unloading responses was excluded.

If our hypothesis that the responses are based on the same mechanism as the stretch reflex is correct, the first component of the response will be stereotyped, whereas the late components will be more flexible.

# Method

#### Apparatus

The apparatus used in the experiment was described by van den Berg, Mooi, Denier van der Gon, Gielen, and van der Meulen (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 that runs over two cogwheels. One of these is attached to a microprocessor-controlled torque motor, a digital position encoder, and a tachometer. 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.

We used two horizontal arrays of light-emitting diodes (LEDs) (four LEDs per cm), placed above the rail, to give feedback to the subjects. One array (consisting of green LEDs) displayed a target position or force level; 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, we differentiated the angular velocity of the motor; this derivative was multiplied by a microprocessor-controlled factor (the mass). This signal was fed back to the power amplifier of the torque motor. We fed back to the power amplifier the component of force in the direction of the rail to minimize frictional and viscous forces. The remaining static friction was approximately 1 N; the viscosity, 10 N s/m. The effective

mass could be varied between 0.5 and 20 kg. Because the handle was moving on the rail, the simulated mass was only inertial, without differences in weight.

Bipolar silver/silver chloride surface electrodes—0.6 cm diameter, placed 2 cm apart over the muscle bellies—were used to record EMGs. The EMG signals were sampled after they had been band-pass filtered (16–320 Hz), rectified, and low-pass filtered (10 ms). EMGs 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 8 healthy subjects (7 right-handed, 1 left-handed, mean age, 24 years); 2 of them participated in all experiments reported in this article. All subjects gave informed consent. They were seated with their preferred arm 90° abducted; the arm was supported under the elbow joint. The wrist was supinated, immobilized, and tightly strapped to the handle. The rail was positioned parallel to the upper arm; shoulder angle ( $\theta_1$ , see Figure 1) was between 75° and 90° (0°: upper arm in frontal plane). EMGs were recorded from the following muscles: shoulder flexor musculus (m.) pectoralis major; shoulder extensor m. deltoideus posterior; elbow flexor m. biceps brachii; and elbow extensor m. triceps brachii.

Each experimental session started with measurements of isometric EMG-torque relations. The subject had his elbow at an angle of 90° (0°: 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 EMGs were sampled.

Hereafter, the subjects became accustomed to making fast movements with the handle and with the inertia changes that could occur. The target position was marked by two LEDs; the width of the target region was 12.5% of the movement distance. 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. All subjects had visual feedback supplied by the LED arrays, and could see their arm.

Each movement started at an elbow angle  $(\theta_2)$  of approximately 85° and an angle  $(\theta_3)$  between lower arm and movement direction of approximately 95°. In this configuration (see Figure 1), the movement along the rail was initially the result of almost pure elbow flexion. An experiment consisted of about 100 fast elbow flexion movements over 8 or 16 cm, chosen at random.

In 80% of the movements, the simulated mass had a constant value during the whole movement. In the other 20%, the mass was unexpectedly changed after the hand had moved a certain distance. Not all movements with the standard mass were recorded; we recorded only those standard movements that preceded the unexpectedly

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loaded movements. The subjects were familiar with both the masses that would be encountered in the experiment. They knew which one was the standard mass and what would happen if the mass was changed unexpectedly. They had also made a few training movements with both masses over both distances. Subjects could take a rest after each movement. The total duration of an experimental session was less than 1.5 hr.

Four experiments were carried out (see Table 1). Five subjects participated in Experiments 1 and 2 (in one session). In these experiments, the standard mass was 0.5 kg, and the mass could be changed to 7 kg after 0.2 cm. In Experiment 1, the subjects were instructed to always move as fast as possible to the target. In Experiment 2, they were instructed to stop the movement and move back to the starting point as fast as possible if they experienced a larger load.

Experiments 3 and 4 were designed to test the effect of changes in inertia at a later stage of the movement. To get an increase of the force (as in Experiments 1 and 2) by changing the inertia in the middle of the movement, one must decrease the inertia. Five subjects participated in Experiment 3, 2 of whom had participated in Experiment 4. In Experiments 3 and 4, the mass was always 7 kg during the first 4 cm of the movement. In 20% of the trials, the mass was switched to 0.5 kg at that point. For 8-cm movements, the velocity was almost maximal at the switching point, so the changes in mass affected only the deceleration. The change in mass, with unchanged muscle forces, will therefore cause a faster decrease in the velocity. For 16-cm movements, the mass changed in the last part of the acceleration phase. The change in mass, with unchanged muscle forces, will therefore first cause a faster increase in the velocity and then a faster decrease of the velocity.

In Experiment 3, the subjects were instructed to always move as fast as possible to the target and, thus, to counteract the too large deceleration. In Experiment 4, the subjects were instructed that if they experienced a change in mass, they had to move back to the starting point as fast as possible.

Experiment	Position (cm) of mass change	Mass (kg)			Number of
		Standard	Unexpected	Instruction	subjects
1	0.2	0.5	7	continue	5
2	0.2	0.5	7	return	5
3	4.0	7	0.5	continue	5
4	4.0	7	0.5	return	2

## Data Analysis

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

the number of subjects.

The torques associated with a force  $\vec{F}$  exerted by the hand follow from geometry:

$$T_{1} = F_{x}[l_{2} \sin \theta_{3} + l_{1} \sin(\theta_{2} + \theta_{3})] + F_{y}[l_{2} \cos \theta_{3} + l_{1} \cos(\theta_{2} + \theta_{3})].$$
(1)

$$T_2 = F_x l_2 \sin \theta_3 + F_y l_2 \cos \theta_3. \tag{2}$$

 $T_1$  and  $T_2$  are the torques about shoulder and elbow, respectively, with flexion as the positive direction.  $F_x$  is the component of  $\vec{F}$  in the direction of motion, and  $F_y$  is the component perpendicular to  $F_x$  in the plane of the arm. The length of upper and lower arm  $(l_1 \text{ and } l_2)$  were measured; the angles  $\theta_1$ ,  $\theta_2$ , and  $\theta_3$ , defined in Figure 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.

In the absence of external forces, the exerted torques about the shoulder and the elbow can be derived by solving the Lagrangian equations of motion, which leads to

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$$T_{1} = \theta_{1}[I_{1} + I_{2} + m_{2}(l_{1}^{2} + 2d_{2}l_{1}\cos\theta_{2})] + \ddot{\theta}_{2}(I_{2} + m_{2}l_{1}d_{2}\cos\theta_{2}) - \dot{\theta}_{2}^{2}m_{2}l_{1}d_{2}\sin\theta_{2} - 2\dot{\theta}_{1}\dot{\theta}_{2}m2l_{1}d_{2}\sin\theta_{2}.$$
(3)

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$$T_{2} = \ddot{\theta}_{1}(I_{2} + m_{2}d_{2}l_{1}\cos\theta_{2}) + \ddot{\theta}_{2}I_{2} + \dot{\theta}_{1}^{2}m_{2}l_{1}d_{2}\sin\theta_{2}.$$
(4)

We estimated the moment of inertia of the upper and lower arms  $(I_1 \text{ and } I_2)$ , the mass of the lower arm,  $m_2$ , and the position of its center of mass,  $d_2$ , using the subject's body weight and length of upper and lower arm (Winter, 1979). The total torques exerted by the muscles are the sum of the torque components of Formulas 1–4. These calculated torques can show some systematic errors because of small translations of the shoulder during the experiment and errors in estimating the moment of inertia.

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 (N m) about the joint. Because we defined flexion as the positive torque direction, the EMG of extensors is negative; more extensor activity thus corresponds to less torque. In this analysis, we treated m. biceps brachii and m. triceps brachii as muscles acting only around the elbow. Because the torques about elbow and shoulder in our experiments were almost equal, neglecting the biarticular nature of these muscles had negligible effect.

Force and velocity signals of all recorded movements were examined. Trials in which the subject had clearly not obeyed the instruction to move as fast as possible (in not more than 5% of the trials under all load conditions) were not used for further analysis. For each combination of mass and distance, we calculated ensemble averages and their standard deviations for the records of position, velocity, acceleration, force, torque, and EMG. For this averaging, individual trials were synchronized at the position the mass could change (t = 0 in Figures 2, 3, 5, and 6). All muscles and all subjects were analyzed independently, without use of the EMG scaling.

The EMG response signal was obtained by subtracting the ensemble-averaged EMG records of standard movements from those of the movements in which the mass had changed. We performed a t test on the EMG response to define the point at which the response started to deviate from zero. Because of the noisiness of the data, averaging was needed.

A moving average of the response was calculated over an interval of 15.6 ms. The reference point for the laten-

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cies of the EMG responses was the velocity threshold: the point where the difference in velocity between the two load conditions exceeded 0.2 m/s (Smeets et al., 1990). Starting at this point, the interval was moved until the average of the response was significantly (p < .005) larger (or less) than zero. The middle of the interval was taken as the point where the EMG signals started to deviate from each other. If no significant difference was found until 150 ms after the threshold was exceeded, no adjustment was assumed to have occurred and the record was not included in the calculation of mean latencies. Changing the averaging interval or the significance level has a systematic effect on the latencies: Leaving out the averaging over the 15.6-ms interval resulted in about 5ms-longer latencies and fewer responses; changing the significance level (to p < .05) resulted in about 5-msshorter latencies (and some more responses). The .005 probability level was chosen to prevent noise from being regarded as a response.

As this method can introduce systematic errors in the estimated latencies, we have compared the results with the results of an alternative method without any averaging over time. For this we used the scaling of EMG to calculate ensemble averages of the responses (expressed in N m) of all muscles and all subjects in an experiment, whether or not the individual responses were significant according to the standard analysis. Synchronization point for averaging all the responses was the velocity threshold. The latencies according to this method were always within 5 ms from the average latency of our standard analysis. From this observation, we concluded that the systematic errors introduced by our analysis were in the same order of magnitude as the time-resolution of the experiment.

Torque changes can result not only from changes in muscle activation but also from direct mechanical reactions. If the torque changes result mainly from changes in muscle activation, we would expect a good correlation between torque changes and EMG responses, with a delay of about 70 ms (Soechting & Roberts, 1975). As an estimate for the delay between the EMG responses and the resulting torque changes, we used the maximum of the normalized cross-correlation function between the sum of the EMG responses in the muscles about a joint and the torque change about that joint. The values for both the elbow and shoulder were calculated. In this article, data are always presented as mean value ± standard deviation (n = number of differences of means analyzed). The number n thus refers to the product of number of distances, subjects, and muscles involved.

# Results

## Mass Increase Near Start of Movement

In Experiments 1 and 2, the mass changed just after the start of movement in 20% of the trials. The only difference between Experiments 1 and 2 was the instruc-

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tion to the subjects. In Experiment 1, the subjects always had to move the handle to the target as fast as possible. In Experiment 2, the subjects were told that if they experienced an unexpectedly large load, they had to stop the movement as soon as possible and move their hand back to the starting position. This new instruction had a slight effect on the standard movements; these effects differed among subjects. The subject whose data are presented in Figure 2 and 3 made movements with a slightly higher maximum velocity in Experiment 2 than in Experiment 1. For some of the subjects, however, the maximum velocity was higher in Experiment 1.

The left parts of Figures 2 and 3 show the kinematics of the 16-cm movements of 1 subject. In both experiments, the change of mass induced a lower velocity. The velocity difference between the two load conditions (right part of the figures) in Experiment 2 started to differ systematically from the velocity difference in Experiment 1 about 180 ms after the mass change (Figure 4a). From that moment on, the velocity decreased more in Experiment 2 than in Experiment 1. The result was that the velocity in Experiment 2 changed sign about 300 ms after the change of mass, and the hand moved back to the starting position. The maximum velocity during the movement back was only half of the maximum velocity during the movement to the target. The time taken to return to the starting position with the increased mass in Experiment 2 was much longer than that to reach the target in Experiment 1. The subjects reported that they found it impossible to obey the instruction in Experiment 2.

An adequate response to a larger load in Experiment 1 would be to increase the activity of the flexors and to decrease the activity of the extensors for about 100 ms. In Experiment 2, an adequate response to the load change would be to brake the movement as quickly as possible, and thus to decrease the activity of the flexors and increase the activity of the extensors. To reveal the effect of the instruction on the EMG responses, we have compared the EMG records of both experiments.

Examples of EMG records and calculated torques are plotted in the right part of Figures 2 and 3. In both experiments, the response started in the same direction: more flexor activity and less extensor activity. The response in the activity of the muscles resulted in torque changes with about the same time-course. Because the torque about the elbow  $(T_2)$  is influenced by the effect of muscle shortening on the exerted force (force-velocity relation), we also present the torques about the shoulder  $(T_1)$ .

In Experiment 1 and Experiment 2, the EMG activity of all muscles changed, on average, 37 ms and 34 ms, respectively, after the velocity threshold (for the standard deviations, see Table 2). The latency of the response was thus unaffected by the instruction. Because all subjects and all muscles showed almost the same response (no systematic difference between flexors and extensors or



**FIGURE 2.** Example of ensemble averages of records of hand position (x), velocity (v), force in direction of motion  $(F_x)$ , shoulder torque  $T_1$ ), and elbow torque  $(T_2)$ , and the m. biceps and m. triceps EMG records for movements in Experiment 1. In this experiment, the subjects were instructed to always move as fast as possible to the target. The zero on the time axis corresponds to the moment the mass was changed. Results are shown of 16-cm movements made by Subject HM. Continuous traces represent standard movements (0.5-kg load, 40 trials executed); dotted traces show trials in which the mass changed to 7 kg immediately after the start of movement (10 trials). The dashed-dotted traces on the right show the differences between the signals of the standard movements and the unexpectedly loaded movements depicted on the left. The scales of the axes on the left and right parts of the figure are identical; only the positions of the zeroes vary. The wiggles in the torque signals around t = 0 are an artifact resulting from the filtering of the calculated acceleration signal.

between shoulder and elbow), we calculated the ensemble average of all responses. In Figure 4b, the average of all the responses of the different muscles and different subjects over both distances is plotted for Experiments 1 and 2.

To find the moment at which the instruction had an effect on the EMG activity, we compared the EMG responses to the perturbation in both experiments. On average, these responses were not significantly different until 61 ms after the velocity threshold, about 25 ms after the first significant response. Thereafter, the EMG responses in Experiment 2 gradually deviated from the responses in Experiment 1 (see Figure 4b). After 110 ms, the variations in the responses in Experiment 1, suggesting voluntary responses (Houk, 1978). Note that the sign of the response changed within 100 ms, before the perturbation of velocity or force had changed sign (Figures 2–3).

In Experiments 1 and 2, the maximum of the normalized cross-correlation function between the measured EMG response of muscles around a joint and the calculated torque response around that joint was  $0.71 \pm 0.15$ (n = 40). This maximum was found at a delay of  $61 \pm 15$  ms (n = 40) between EMG response and torque response. Soechting and Roberts (1975) reviewed several experiments on the phase difference between activation and resulting torque for the biceps and triceps muscles. For frequencies corresponding to activations with about the same duration as in our experiments, the reported phase lags were in the range 55 and 85 ms. As our result was in this range, it is very likely that the torque changes indeed were mainly caused by changes in muscle activation.

#### **Mass Decrease During Movement**

The mechanical effect of a mass change is not the same during the whole movement. Depending on the sign of the torques at the moment the mass is changed, a decrease will lead to a higher or lower velocity than planned. In Figure 5, examples are plotted of the average traces of normal 8-cm trials and of 8-cm trials in which the mass was changed. In these movements, the mass changed close to the point of maximum velocity. The change of mass thus did not influence the acceleration phase. In the deceleration following the mass change, the velocity decreased so much that it reversed sign: The hand moved backward.

In the 8-cm trials in which the mass was unexpectedly decreased, the EMG started to differ, on average, 23 ms after the velocity threshold, which was reached 20–50 ms after the change of mass. The change consisted of an increase of the flexor EMG and a decrease of the extensor EMG, both with a large amplitude, and resulted in less extension torque. The sign of the response was appropriate to compensate for the change of mass. Thus the EMG also adjusted to unexpected load conditions during the deceleration of a movement.

In the 16-cm movements (Figure 6), the mass changed during the acceleration; that change led to a higher velocity than planned. At that moment (30-50 ms prior to) to the start of the deceleration), the extensors were already active for the deceleration. The generated extension torques decreased the velocity so much that, as in the 8-cm movements, the hand moved back. An adequate response to this disturbance would be to anticipate the large devia-

tions that will occur during the deceleration, by decreasing the activity of the extensors and increasing the activity of the flexors as soon as possible.

Perturbed Fast Arm Movements

The EMG records showed that the first response did not anticipate: The first significant responses (average latency, 32 ms) counteracted the measured velocity difference and the activity of the extensors was increased and that of the flexors decreased. Although the amplitude of this adjustment was low and reached significance in only 13 out of 20 registrations, it was clearly present in the average of all subjects and muscles (Figure 7). About 40 ms later (average latency, 71 ms), the EMG adjusted significantly in the other direction, counteracting the prior excessive antagonistic activity. It is important to notice that at this moment, the velocity difference had not yet changed sign and was clearly positive at a normal reflex latency (25 ms) before this moment. So, the late response was not just proportional to the difference of the actual and expected velocity.

The perturbation in Experiment 3 moved the hand in the direction of the start position. So very little mechanical effort should have been needed to execute the task of Experiment 4. Two subjects participated in this experi-



**FIGURE 3.** An example of a 16-cm movement in Experiment 2 (same subject and same electrode placing as in Figure 2). Ensemble averages of movements made by subjects who were instructed to stop the movement and move back to the starting point as fast as possible if they experienced a larger load. Continuous traces represent standard movements (0.5-kg load, 40 trials executed); dotted traces show trials in which the mass changed to 7 kg immediately after the start of movement (10 trials). The dashed-dotted traces on the right show the differences between the signals of the standard movements and the unexpectedly loaded movements depicted on the left.

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**FIGURE 4.** Effect of instruction on the responses. A. Example of the effect on the velocity difference (the same curves as in Figure 2 and Figure 3, plotted in one graph). The difference instruction had no effect until about 180 ms after the mass change. **B.** Average effect of instruction on the EMG response in Experiments 1 and 2. The average was taken over 5 subjects, four muscles, and two distances. In this figure, error bars indicate the standard error of the mean, and t = 0 indicates the moment the velocity threshold was exceeded. The difference between the instructions in Experiment 1 and 2 affected the responses about 60 ms after t = 0.

ment; the perturbations were the same as in Experiment 3, but now the instruction to the subject was, "If the load changes, move your hand back as soon as possible." Although it was mechanically easy, the subjects reported that the task was very difficult, and they often made errors in task execution.

The EMG responses in Experiment 4 were not significantly different from the responses in Experiment 3 for at least 150 ms after the velocity threshold. The EMG during the 16-cm movements in this experiment responded to the mass change with a negative response at 32 ms and with a positive response at about 77 ms. Because the subject had been instructed to move his hand back, this positive response (increase of torque) did not seem very adequate.

As in Experiments 1 and 2, the EMG responses in Experiments 3 and 4 resulted in a change in the calculated

torques. The average delay between EMG and torque was  $51 \pm 10 \text{ ms} (n = 20)$ ; the maximum of the normalized cross-correlation was  $0.68 \pm 0.14$  (n = 20). Thus, also in this experiment, it seems that the torque changes can be attributed to the EMG response.

# Discussion

The results of our experiments showed that during both the acceleration and the deceleration of fast goaldirected movements, the EMG patterns adjusted to a change of mass. These EMG responses could have about the same amplitude as EMG bursts of an unperturbed movement, and were associated with large changes in the exerted torques. The initial part (25 ms) of the response was stereotyped: This part seemed a direct result of the difference between actual and planned velocity. Later parts varied with the instruction to the subject and with the phase of the movement in which the mass changed.

An interesting aspect of this study was the experience reported by the subjects. Most subjects reported that in Experiments 1 and 3, their hand had reached the target before they had realized what to do about the change of mass. On the other hand, subjects complained that it was impossible to obey the instruction to go back to the start in Experiments 2 and 4; it seemed as if their arm had its own goal. These different experiences reflect the different levels of control that are involved in the task. Changes of environmental variables do not require any conscious intervention; the peripheral motor system corrects before the error is perceived. On the other hand, programming a new target in response to a perceived mass change will be executed after you decide where your hand should go.

#### Latencies

We have expressed the latency of the responses relative to the time at which the velocity difference exceeded a threshold of 0.2 m/s. This threshold is an estimate of the change in mechanical spindle input that will, around the onset of a fast movement via spinal connections, significantly change the motoneuron output (Smeets et al., 1990). This velocity threshold is much higher than the velocity reached in many experiments on the stretch reflex. A physiological basis for this high threshold presumably lies in the response characteristics of the muscle spindles. Spindle responses depend not only on muscle length and velocity but also, for instance, on the history of muscle length and velocity (Baumann & Hulliger, 1991; Gregory et al., 1990) and on the amount of  $\gamma$  activation. The velocity difference at which the spindle output starts to differ detectably can thus depend on the phase of the movement at which the load is changed.

Another complicating factor was that we measured the position and velocity of the handle. The complicated mechanics of the skin, connective tissues, and tendons causes delays between the kinematics of the handle and the kinematics of the muscles. Therefore, the latencies expressed relative to the velocity of the handle can overesti-

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TABLE 2      Summary of the Latencies (Relative to the Velocity Threshold) at Which the EMG Records of the Unexpectedly Loaded Movements Started to Differ Significantly From Those of the Standard Movements							
Experiment	Distances	Sign of response	Start signifiant EMG difference (ms)	n	Adjustment not found		
1	both	+	37 ± 10	37	3		
2	both	+	$34 \pm 11$	34	6		
Difference $2 - 1$	both		61 ± 17	33	7		
3	8 cm	+	$23 \pm 9$	20	0		
4	8 cm	+	$22 \pm 9$	8	0		
3	16 cm	_	$32 \pm 9$	13	7		
4	16 cm		$32 \pm 9$	5	3		
3	16 cm	+	$71 \pm 14$	19	1		
4	16 cm	+	$77 \pm 9$	7	1		

Note. The latency of the response was determined for each recording; these latencies were averaged across subjects and muscles. In the column labeled sign of the response, + indicates that the response showed more activity in the agonists and less activity in the antagonists; - indicates the reverse response. In the 16-cm movements of Experiment 3 and 4, the latencies of two subsequent responses are given. In the column labeled *Experiment*, difference 2 - 1 indicates the difference between the EMG signals of the unexpectedly loaded movements of Experiment 2 and those of Experiment 1.



**FIGURE 5.** An example of the 8-cm movement in Experiment 3, in which the subjects were instructed to always move as fast as possible to the target. Subject JS. Continuous traces represent standard movements (7-kg load, 40 trials executed); dotted traces, trials in which the mass changed to 0.5 kg (10 trials) after 4 cm. The dashed-dotted traces on the right-hand side show the differences between the signals of the standard movements and the unexpectedly loaded movements on the left. For further information see Figure 2.

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**FIGURE 6.** The 16-cm movement of the same subject in the same experiment as in Figure 5. In this experiment, the EMG of the biceps did not show the significant negative response 40-75 ms after the change of mass that was visible in most recordings (see Figure 7).



mate the latencies relative to spindle output. It is possible that the mechanical delay depends on the phase of movement. Therefore, the different latencies of the first response we reported (22–37 ms) do not have to correspond to different latencies respective to the spindle signal. In this respect, it is interesting to note that in experiments on stretch responses caused by perturbations smoother than a torque-step, the reported latencies of the first stretch response were much larger than in the experiments with step-like perturbations.

The latencies of the first EMG responses during fast movements (22–37 ms) can thus correspond to the latency reported for the SL component of the stretch reflex. The latencies of the parts of the responses that were more adequate for the situation (67–77 ms) could correspond to the latency of the LL component of the stretch reflex. Corresponding latencies suggest that both responses are based on the same pathways. This suggestion makes it interesting to look for other similarities between the responses to load perturbations during movements and the stretch reflex.

## Stretch Reflex?

The SL component of the stretch reflex is found to be very robust, depending almost only on the initial state of the muscles and the amplitude of the perturbation and not on the instruction to the subject (for muscles around the elbow, Evarts & Granit, 1976; Gielen, Ramaekers, & van Zuylen 1988; Smeets & Erkelens, 1991; Wadman et al., 1980). These characteristics apply also to the first component of the responses in our experiments: The instruction had no effect on the early responses, and it persisted even when it did not counteract the perturbation.

The LL component of the stretch reflex is more versatile. It can be suppressed if this benefits task execution (Evarts & Granit, 1976; Wadman et al., 1980), and it is better directed against the perturbation than the SL com-

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ponent is (Gielen et al., 1988; Smeets & Erkelens, 1991). The LL component of the stretch reflex is a term usually used for a period starting 25–35 ms after the beginning of the SL response. In Experiment 2, the new instruction had an effect on the reflex amplitude about 25 ms after the first response.

In Experiments 2 and 4, the new instruction to the subject had a modest effect on the late component of the response; as a result, task execution in these experiments was poor. In stretch reflex experiments (Evarts & Granit 1976; Wadman et al., 1980), on the contrary, instructions had very large effects on the late component of the response. An explanation for the difference could be that afferent information is not only used to compensate for large perturbations, as in our experiment, but also contributes to the control of normally executed movements. So, normal movements would be impossible if the gain of the reflexes were set too low. The task of a goal-directed movement thus includes an instruction to oppose perturbations. In stretch reflex experiments, however, variations of the reflex gain do not interfere with the ability to hold the arm against a constant load, so there is no resistance to variation of the reflex gain in such an experiment.

The implicit reflex gain instruction included in the present task is probably the explanation for the low gain of the stretch reflex during fast movements (Erkelens, 1983; Gottlieb & Agarwal, 1980; Soechting et al., 1981). Fast movements of the ankle occur during running; in this situation, the purpose of muscle activation is to deliver a force, not to reach a certain position. Perturbation of position is therefore probably no reason for changing muscle activation. In fast jaw-closing movements, position perturbation indicates an unexpected obstacle in the mouth; extra muscle activation in this situation could damage the teeth. The elbow flexion movements in the experiments of Soechting et al. (1981) were also not goal directed; No target position was indicated; the subjects only had to flex their arm as fast as possible. So, in all these experiments, the task to move fast could have included an implicit "do not oppose perturbations" instruction. Our fast movements were goal directed, requiring a high reflex gain. The gain of the SL reflex was indeed very high: In Figure 5 its amplitude is almost equal to that of the initial antagonist burst.

In the 16-cm movements of Experiment 3, the sign of the late response (60-100 ms) was opposite to the sign of the early response. Stretch reflexes in which the early and late components had opposite signs were also reported by Gielen et al. (1988) and by Soechting and Lacquaniti (1988). The sign of the EMG responses in Experiment 3 switched in the middle of the antagonist burst. In our previous experiments, in which the mass was unexpectedly low from the start of the movement (Smeets et al., 1990), the sign of the response changed just before the middle of the antagonist burst. It could be that the sign (and amplitude) of the long-latency response is programmed with the movement sequence. In experiments

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on reflexes elicited by nerve stimulation during walking, such a phase-dependent reversal of the long latency component has been reported by Yang and Stein (1990). The sign of some stretch responses can also change for a short period when catching a ball (Lacquaniti, Borghese, & Carrozo, 1991).

The change of response amplitude in our experiments seems very adequate. The amplitude of the early responses was low (and the late responses had an opposite sign) when the perturbing force changed sign (inertia changed halfway through the acceleration: the 16-cm movement of Experiments 3 and 4). The amplitude of the early responses was high (and the late responses had the same sign) when the perturbing force lasted a long time (all other conditions). The functionality of the variation of the stretch reflex gain in compensating force pulses during movements (Erkelens, 1983; Gottlieb & Agarwal, 1980; Soechting et al., 1981) has never been revealed. Probably, the stretch reflex is not designed to compensate for force pulses.

Variations in inertia are very common to a limb: For instance, a change of the elbow angle changes the inertia of the arm (see Equations 3 and 4). So, one could argue that a control system for arm movements should be designed to deal with these variations in inertia. The effect of a change in inertia on a movement depends on the phase of the movement: The force is proportional to the acceleration of the arm. A control system that is designed to deal with such changes should therefore have a phasedependent gain. Furthermore, such a control system would be able to predict future effects of the inertia change. The control of goal-directed arm movements indeed uses such a predictive mechanism: The EMG responses to changes of inertia advance errors in position and velocity (Smeets et al., 1990). Reformulating our original hypothesis, we can hypothesize that the stretch reflex is a laboratory artifact of a control mechanism that is meant to cope with variations in inertia, and not with step changes in an external force. Following this hypothesis, we can now understand the reported time-varying properties of the stretch reflex (e.g., Soechting et al., 1981) as an epiphenomenon of the functional gainvariation of the (inertia-error-based) control system.

The mechanical function usually attributed to the SL reflex is to maintain stiffness by compensating for muscle yielding (Nichols & Houk, 1976). Mechanical experiments on which this conclusion was based were done on SL reflexes in muscles that were stretched by the perturbation. In our experiments, the mass change did not lead to muscle stretch and thus did not induce yielding. So, no extra muscle activation was necessary for the maintenance of muscle stiffness. In all our experiments, however, the start of the EMG response was followed by a large torque response. The mechanical effect of early EMG responses is thus clearly more than only stiffness maintenance. Direct measurement of the mechanical effect of EMG responses during movements, and in mus-

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cles that are not stretched by the perturbation, would probably yield quite different results than those of the experiments by Nichols and Houk (1976).

In conclusion, we can describe the response to perturbations of fast goal-directed movements as consisting of three stages. The early EMG response (latency 25-35 ms) in a direct reaction to a change in spindle firing. Later parts (latency 60-70 ms) of the response can be more adequate for the specific situation: The gain can vary drastically, and even change sign. Finally, instructions to change the goal of the movement, depending on its load, can trigger voluntary responses at latencies of about 110 ms. This sequence corresponds to the sequence of responses to muscle stretch and makes it indeed likely that the same neural circuits are used. As control mechanisms for fast goal-directed movements have to be very fast, only responses with short latencies are suited for this task. The stretch reflex is probably just an epiphenomenon of a mechanism meant for the control of fast goaldirected movements.

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