Behavior of the stretch reflex in a multi-jointed limb

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When an external perturbation acts on a segment of a multi-jointed limb, angular motion results in all limb segments which are inertially linked to the one which is perturbed. In such a situation, different hypotheses on the functional role of the stretch reflex lead to different predictions on reflex responses by the stretched muscles. These predictions were examined experimentally and it was found that the EMG responses of elbow muscles evoked by forces applied to either the upper arm or the forearm were not uniquely related to changes in elbow angular position. They were instead correlated with the direction of changes in the net elbow torque resulting from the perturbation.

Beginning with the original description by Liddell and Sherrington[11], the muscle stretch reflex has been studied extensively. Customarily, a functionally isolated muscle is stretched or shortened in acute preparations, or alternatively a single limb segment is displaced by applying force perturbations and motion of other segments is restricted[2,4,6,8,10,13]. In general, however, perturbations applied to one limb segment result in angular motions of all segments of the limb. Thus, angular motion of a limb segment can result from perturbations applied proximally as well as distally to that joint.

In this general case, the reflex response in muscles acting at each of the joints is largely unknown[16,24]. Furthermore, there is no reason to believe that results obtained under experimental situations when motion is restricted to a single muscle or a single limb segment can be extrapolated to the more general case. In particular, many muscles cross more than one joint and there may be convergence of afferent input from muscles acting at different joints[3]. Furthermore, from a functional point of view, different hypotheses concerning the functional utility of the stretch reflex lead to qualitatively different predic-tions concerning the particular muscles reflexively activated when motion of all limb segments is permitted. Thus, one cannot expect even the observation of Liddell and Sherrington[11], namely that a muscle which is stretched is activated and a muscle which shortens is relaxed, to hold true under all conditions.

In this note, we shall begin by detailing the predictions of some of the hypotheses concerning the stretch reflex in the case when motion of more than one limb segment is permitted. We will then present experimental data obtained when perturbations are applied either to the upper arm or to the forearm of human subjects, both segments being free to move.

As regards the function of the stretch reflex, Merton[15] construed the reflex loop comprising muscle spindles and alpha motoneurons as a length servo, the spindles providing negative feedback of muscle length and its derivatives. With some modifications, this point of view has also been taken by a number of other authors[13,14,23]. Another point of view (load compensation hypothesis) holds that the stretch reflex acts to counteract externally applied loads[4,18]. Finally it has also been suggested that the stretch re-

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flex acts to regulate muscle stiffness[17]. Stein[22] has recently reviewed evidence for and against each of these hypotheses.

The upper part of Fig. 1 shows schematically the angular motion at the shoulder and at the elbow which results when an external force is applied to the
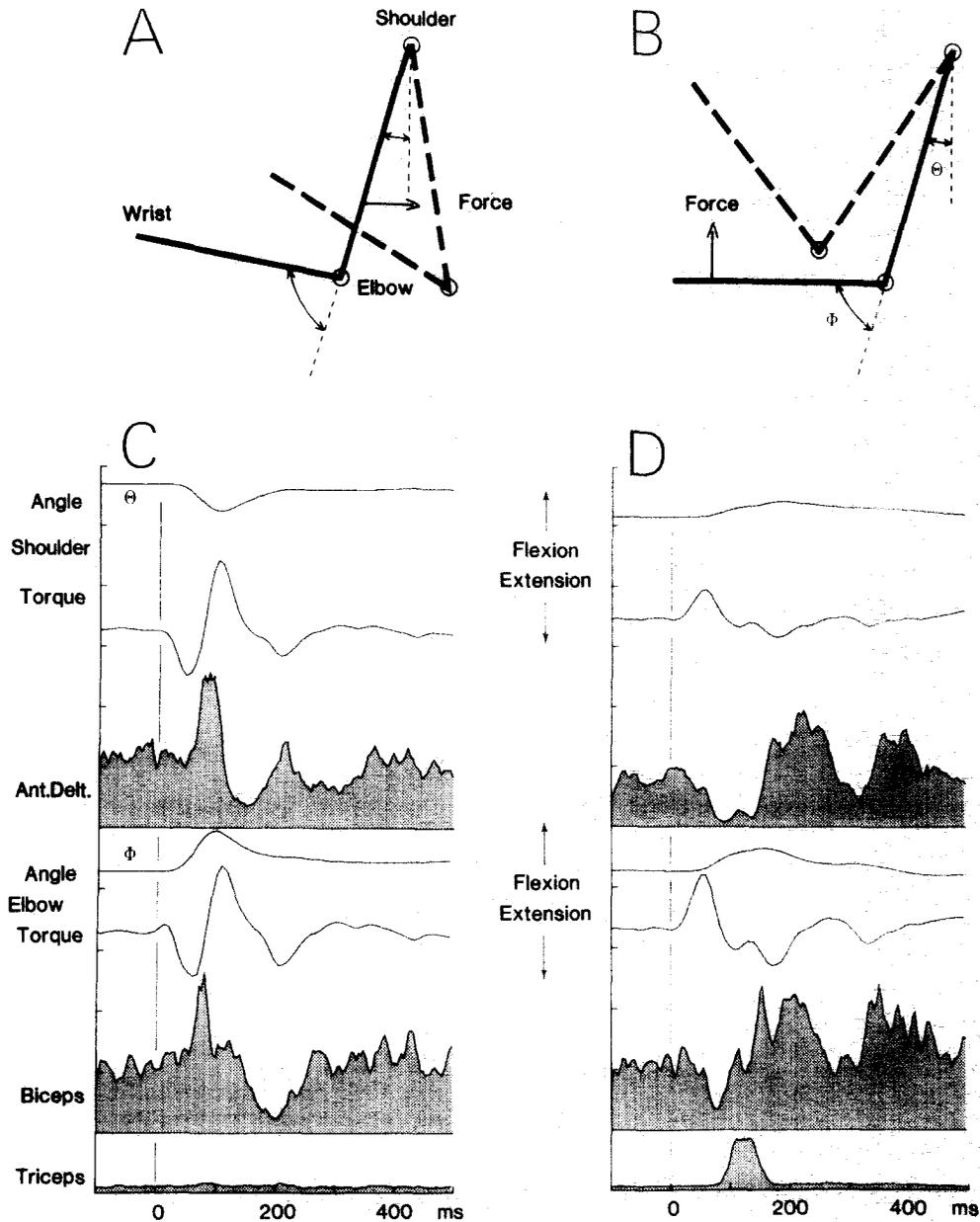

Fig. 1. On the top, schematic diagram of the arm movement which results when a force is applied to the upper arm (A) and to the forearm (B). The initial position of the limb is indicated by the continuous lines. θ is the angle of shoulder flexion, measured relative to the vertical, ϕ the angle of elbow flexion. As a consequence of the applied force, both limb segments are set into motion; heavy dashed lines indicate their position at some time after the application of the force. Note that shoulder extension and elbow flexion is produced in A, flexion of both joints in B. Parts C and D show representative results obtained in the conditions diagrammed in A and B, respectively. Traces, from top to bottom, depict shoulder angle (θ), shoulder torque (T_s), rectified EMG activity of anterior deltoid, elbow angle (ϕ), elbow torque (T_e), biceps and triceps EMG. The force consisted of a 50 ms pulse applied at $t = 0$. One division equals $10°$ (θ, ϕ), 20 N-m (T_s), 5 N-m (T_e), 15 μV (biceps), 25 μV (triceps and anterior deltoid in C), 50 μV (triceps and anterior deltoid in D). Initial shoulder angle is about $20°$, initial elbow angle about $40°$.

upper arm or to the forearm and both segments are free to move. In Fig. 1A a backward force applied to the upper arm results in shoulder extension, as indicated by the heavy dashed lines. At the same time, the elbow also flexes, because of the dynamic coupling which exists between the two limb segments[9,20]. When an upward force is applied to the forearm (Fig. 1B), elbow flexion also occurs, this time however in conjunction with forward flexion at the shoulder. Thus, in both cases illustrated, the applied perturbation produces elbow flexion but the direction of shoulder motion is opposite.

If the stretch reflex functions as a length-servo, one would expect reflex activation of the stretched elbow extensors and relaxation of the elbow flexors which shorten in both of the conditions shown in the figure. At the shoulder, instead, one would expect reflex responses which are oppositely directed, according to where the force is applied. Thus, shoulder flexors would be activated in the case illustrated in Fig. 1A, whereas they would relax when an upward force is applied to the forearm (Fig. 1B). The predictions are summarized in the first row of Table I, a (+) indicating reflex activation of flexors and a (−) their depression.

Load compensation is generally taken to mean a reflex response opposing external loads applied to a given limb segment. In Fig. 1A, the force applied at the upper arm produces an extensor torque at the shoulder. However there is no torque due to external forces at the elbow, since the force is applied proximally to that joint. Thus, this hypothesis would predict reflex activation of shoulder flexors and no response in elbow flexors or extensors (as indicated by a (0) in Table I). In Fig. 1B, instead, the upward force applied to the forearm exerts a flexor torque at both the shoulder and elbow, and one would expect depression of shoulder and elbow flexors.

A different interpretation of the load compensation hypothesis is that the reflex is a response to changes in the total torque acting at the joint, including both torque components due to external forces as well as those due to the passive visco-elastic properties of muscle. Even though there are no external torques applied to the elbow, torque at the elbow will change as a result of muscular contributions when the force is applied proximally to the elbow, as in Fig. 1A. As indicated in the figure, the force applied

TABLE I

Theoretical predictions of stretch reflex behavior

	Fig. 1A		Fig. 1B	
	Shoulder flexors	Elbow flexors	Shoulder flexors	Elbow flexors
Length-servo	+	−	−	−
External load	+	0	−	−
Net torque	+	+	−	−

to the upper arm results in elbow flexion by virtue of the dynamic coupling between the two limb segments. Thus, elbow extensor muscles will be stretched. As a consequence of their visco-elastic properties, restoring forces will develop and there will be a net increase in extensor torque at the elbow joint.

Mathematically, torque at the shoulder (T_s) and elbow (T_e) is given by

$$T_s = (I_s + I_e + 2A\cos\phi)\ddot{\theta} + (I_e + A\cos\phi)\ddot{\phi} - \\ - A\sin\phi(\dot{\phi}^2 + 2\dot{\phi}\dot{\theta}) + B\sin\theta + C\sin(\theta + \phi) \quad (1)$$

$$T_e = I_e\ddot{\phi} + (I_e + A\cos\phi)\ddot{\theta} + A\sin\phi\dot{\theta}^2 + C\sin(\phi + \theta) \quad (2)$$

according to Newtonian mechanics. I_s and I_e are the moments of inertia of the upper arm and of the forearm. These coefficients, as well as A, B and C, are constants and can be computed on the basis of anthropometric data[20]. The terms with leading coefficients B and C represent gravitational torque. Typical values for the coefficients are: $I_s = 0.40$, $I_e = 0.15$ and $A = 0.18$ kg-m², $B = 12$ and $C = 5$ kg-m²/s². We have adopted the convention that a torque tending to produce flexion at the shoulder or elbow is positive.

These equations make explicit the inertial coupling which exists between the forearm and the upper arm. From equation (2) one can see that motion at the elbow can occur even when there is no torque at the elbow ($T_e = 0$). Thus, if the elbow were a frictionless hinge, the force applied to the upper arm (as in Fig. 1A) would produce backwards extension ($\ddot{\theta} < 0$) at the shoulder, and the elbow will flex ($\ddot{\phi} > 0$) so that there is a cancellation of the terms in eqn. (2). Since the elbow is not a frictionless hinge, extensor torque at the elbow will result from the visco-elastic restoring forces of the stretched elbow extensors. As a consequence, the elbow will flex by a smaller

amount than it would if visco-elastic forces were absent*.

Under this interpretation of the load compensation hypothesis, one would predict activation of elbow flexors in Fig. 1A to counteract the extensor torque at the elbow, contrary to the other two hypotheses so far considered. The contribution of the external load to the net torque will instead dominate at the shoulder in Fig. 1A; it will also dominate at both shoulder and elbow in Fig. 1B.

Thus, as summarized in Table I, all 3 of the hypotheses we have discussed give the same prediction when an upward force is applied to the forearm (Fig. 1B), namely a depression of activity in shoulder and elbow flexors. They also predict reflex activation of shoulder flexors when a backward force is applied to the upper arm (Fig. 1A). The predictions regarding elbow flexors in this latter situation are different, however: activation, depression or no change are to be expected according to the hypothesis considered.

Experiments as outlined in Fig. 1A and B were performed on human subjects to see which of the predictions best describes reflex behavior at the elbow. A force was delivered to the distal part of either upper arm or forearm by means of a flexible cable. One end of the cable was attached to a molded brace fitted to the upper arm or the forearm, the other end was wound around the rim of a flywheel attached to the shaft of a DC torque motor. At random times, 50 ms duration pulses were delivered, with the subjects seated and instructed to maintain the position of their limb approximately constant. EMG activity of biceps, triceps and anterior deltoid was recorded by means of surface electrodes. Elbow angle (φ) was measured by means of a goniometer. The instantaneous position of two points on the upper arm in space was measured by means of ultrasound emitters and 3 orthogonal linear microphones[19]. From these data, shoulder angle (θ) was computed trigonometrically. The methods are fully described elsewhere[19,20]. EMG activity was sampled at 500 Hz. For each experimental condition 20 trials were averaged, EMG activity being rectified for this purpose. The net torques at the shoulder and at the elbow were computed

according to equations (1) and (2) after numerical differentiation of the kinematic data.

Parts C and D of Fig. 1 show representative results obtained in each of the two conditions diagrammed in A and B, respectively. Each panel shows the temporal changes in the mean value of the indicated variables. At the shoulder, given the applied perturbations, both angular position and net torque change in the extensor direction in C and towards flexion in D. In agreement with all 3 hypotheses outlined above, the EMG responses of anterior deltoid to the perturbation are also opposite in the two cases. In C, muscle activity increases with a latency of about 50 ± 10 ms (SD) (mean value over 4 subjects and 23 experiments) from the time of application of the torque pulse and peaks at 80 ± 10 ms. In D, anterior deltoid activity is depressed at a similar latency (3 experiments in 3 subjects). The timing of these responses is comparable to that reported in single joint studies for various muscles[2,8,13].

Elbow flexion occurs in both C and D but the initial changes in elbow torque are in opposite directions. In Fig. 1C, elbow torque changes in the extensor direction while in Fig. 1D the change is toward flexion. The responses of biceps and triceps to the perturbation are also drastically different in the two cases. When the force is applied to the upper arm as in C, biceps activity increases at 40 ± 10 ms with a maximum at 70 ± 10 ms. Triceps activity remains low throughout, showing no appreciable modulation. When the force is applied to the forearm as in D, on the contrary, biceps activity is depressed at about the same latency. Triceps increases at 75 ± 5 ms with a maximum at 135 ± 5 ms. These results were found consistently in all subjects and experiments. As a quantitative estimate of the changes in biceps activity, we measured its maximum deviation from the basal activity (mean EMG amplitude computed over the 100 ms period preceding the pulse). The average value over all experiments was 22 ± 8 μV for the experiments corresponding to Fig. 1A, and -17 ± 8 μV for those corresponding to Fig. 1B.

The two experimental conditions symmetrical to those of Fig. 1 were also investigated in the same

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* To simplify the presentation, we have neglected the influence of gravitational forces in the discussion above. Thus, it is strictly valid only when the arm lies in the horizontal plane. When it lies in the vertical plane, a constant amount of torque must be produced at the elbow and the shoulder to counteract the gravitational forces. The changes in the terms involving acceleration and velocity dominate changes in the gravitational terms in the experimental situations considered.

subjects. When a downward force was applied to the forearm, anterior deltoid and biceps activities increased at about the same latencies. When a forward force was applied to the upper arm, inducing upper arm flexion and forearm extension, anterior deltoid was depressed at a latency of about 50 ms. Over the first 100 ms after the onset of the perturbation, biceps showed a modulation in activity whose average change was not statistically significant. There was, however, a late depression of biceps at a latency of 105 ± 10 ms and an activation of triceps at about the same time (15 experiments in 3 subjects). Thus, even though the latencies are longer, the significant changes in biceps and triceps activities just described (biceps depression and triceps increase) are roughly reciprocal to those reported for the experiments of Fig. 1C.

In summary, the responses of both biceps and triceps to the perturbations applied at the upper arm or forearm were poorly related to the changes in elbow angular position. Therefore, the length-servo hypothesis, according to which stretch of a muscle should result in its reflex activation, and vice versa, does not predict the experimental data. Similarly the load compensation hypothesis holding that elbow muscles should respond only when an external load acts directly at that joint, failed to predict the results.

The initial changes in biceps and triceps activities did, however, correlate with the direction of the changes in net torque at the elbow joint caused by the perturbation. For example, in Fig. 1C, where a net extensor elbow torque results from the perturbation, biceps activity increases, whereas there is a decrease in biceps activity and an increase in triceps activity when the initial change in elbow torque is towards flexion (Fig. 1D). Thus, our findings are in qualitative agreement with the hypothesis that the reflex acts to oppose changes in net torque at the elbow joint.

Therefore, it is possible that the adequate stimulus

(or input variable) for the reflex is net joint torque. Even though this parameter is not encoded in the output of a single receptor population, it could conceivably be derived from an appropriate combination of the activity of muscle spindles, Golgi tendon organs and joint and cutaneous receptors. However, our results do not preclude the possibility that the input leading to the reflex contraction is derived from a weighted sum of changes in elbow and shoulder joint angles, as might result from a convergence of muscle spindle afferents from anterior deltoid and biceps onto biceps alpha motoneurons. For example, in the cat hindlimb, there is a convergence of spindle afferents from knee flexors and hip extensors[3]. A further possibility arises from the fact that biceps and triceps span the shoulder joint as well as the elbow joint[5]. Given the anatomical arrangement of the muscles, a 1° change in elbow angle results in a change in biceps muscle length which is about twice as large as that produced by a 1° change in shoulder angle. Thus, the overall length of biceps will decrease when a backward force is applied to the upper arm (Fig. 1A and C). Nevertheless, it is possible that, locally, some fibers in biceps may be stretched and that the overall response reflects such differential sensitivity to stretch[1,12]. Another interpretation of our results is that there exists a synergistic linkage between biceps and anterior deltoid, such that they are automatically coactivated. Such synergies have been found to exist during reaction time arm movements[21]. (Note that all such interpretations would make it difficult to ascribe a unique functional significance to the behavior of the stretch reflex.)

In conclusion, whatever the nature of the input variable to the reflex or its functional significance, it is obvious that the responses can be understood only if the dynamical state of the whole limb is considered.

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