

# The Human Motor Control System's Response to Mechanical Perturbation: Should It, Can It, and Does It Ensure Stability?

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**ABSTRACT.** From among the diverse meanings of stability, the one the author adopts here is that the effects of a perturbation are opposed, and therefore small effects remain small. Except in linear systems, however, instability need not lead to unbounded motion and may actually be desirable when maneuverability is important. Moreover, properties of nerves, muscles, and tendons present serious challenges to stabilization. A review of observations from the motor control literature reveals that responses to perturbations in many common situations assist rather than resist the perturbation and are therefore presumably destabilizing. The observations encompass situations of position maintenance as well as impending or ongoing movement. The author proposes that the motor control system responds to a sudden perturbation by a pattern of muscle activity that mimics an accustomed voluntary movement, oblivious of stability considerations. What prevents runaway motion in the face of short-term instability appears to be voluntary intervention.

*Key words:* perturbation, posture, reflexes, stability, voluntary movement

If *stability* is taken to mean the avoidance of disastrous events such as falling down, crashing into a wall, or otherwise getting hurt in responding to a push, then the answer to the question posed in the title is unexceptionable: The motor control system should try to prevent such events—which it normally can, and most often does. Indeed, it is commonly assumed that the neural responses of the motor control system to mechanical perturbations, which are encountered in everyday life, are designed to ensure stability. But the meaning of stability underlying that assumption is usually far more stringent: The system must resist with sufficient vigor even the smallest of mechanical disturbances because if it fails to do so then their effect—it is believed—will grow uncontrollably. That belief is justified for linear systems,<sup>1</sup> which are the mainstay of a large part of

the highly successful classical control systems theory of engineering practice. Instability in a linear system indeed implies that any disturbance, even if only transient and amounting in magnitude to no more than ambient noise, will cause the output to either grow exponentially in magnitude or oscillate with exponentially increasing amplitude, crashing eventually against the ceiling or floor of its possible range. It is no wonder that instability has acquired a menacing connotation, and stability, in the stringent sense, is viewed as the *sine qua non* of successful control.

Concepts that underlie the design of conventional, linear control systems, however, are not always relevant to biological motor control. In particular, stability in the sense of quick resistance to disturbances often may not be necessary for successful control of movement—or even of posture. In support of that contention, in this article I review observations reported in the literature showing that in many common situations the immediate neural response to perturbation fails to oppose—and, in the short term, may even exacerbate—the effects of perturbation. Those observations lead me to argue not only against the once influential analogy, proposed in 1953, between the role of afferent feedback in motor control and its role in the negative-feedback control systems of contemporary engineering practice (Merton, 1953, 1972) but also against the broader assumption that, insofar as afferent input has any effect on the motor output (e.g., in the context of equilibrium-point control), its effect should be such as to resist any and all perturbations so that runaway motion can be prevented.

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An example may help clarify the issues to be examined. Consider the task of upright, quiet standing. The requirement that the body's center of gravity must lie within the base of support is a necessary but not sufficient condition of equilibrium. Equilibrium is ensured only by certain specific muscle moments about each of the relevant joints. The muscle activity confers some stiffness and damping to the joints, which contribute to resisting any external perturbations and thus promote stability.<sup>2</sup> That contribution is inadequate, however, whereas a high stiffness is required to prevent small disturbances from the upright position from being magnified in runaway fashion by the action of the gravitational moment (Loram & Lakie, 2002; Morasso & Sanguineti, 2002). How, then, can a fall be prevented? One option, albeit a costly one in energetic terms, would be to co-contract mutually antagonistic muscles so that joint stiffness increases; the stiffness could stabilize the upright posture, in the stringent sense. Another would be to tailor the reflex responses of the motor control system so that every perturbation is resisted forcefully enough and fast enough so that it does not grow in size; that resistance, too, could stabilize the upright posture, in the stringent sense. Still another option—for which I will argue, and which is the one the motor system actually adopts—would be to live with the instability but rely on the inertia of the body to slow down the falling movement, thereby affording sufficient time for a voluntary, corrective response that eventually checks the fall. In the last option, the reference, upright position would be considered unstable, but no runaway motion would result. One cannot assume that the ability to accomplish the goal of not falling down can be explained by the fact that stretch reflexes, which do resist the perturbation (although not forcefully and fast enough), may be operating.

I examine not only in the context of maintenance of position but also during voluntary movement whether the early responses of the motor control system are such as to resist perturbations. One will see that the responses do not always resist all the effects of a perturbation and may in fact exacerbate some of them. Moreover, in many circumstances, the ability to resist perturbations is questionable, and even the desirability of doing so cannot, in general, be taken for granted. Before considering those issues, however, it is important to specify what I mean here by the term *stable*, given the bewildering variety of its meanings.

### What Does *Stable* Mean?

The following partial list of various distinct meanings of stable is based on readings from the motor control literature and on an informal survey of colleagues: (a) prevented from moving by external restraint; (b) not moving although free to move; (c) moving, but only within a small range; (d) moving, but only within a defined range (i.e., bounded); (e) secure or safe; (f) reliable; (g) enduring; (h) not having a history of falls; (i) maintaining articular relationships without damage or irritation; (j) moving with little variability on successive attempts; (k) showing little random or chaotic

motion; (l) maintaining contact with the environment without “chattering”; (m) having sufficient damping to not show oscillatory motion; (n) showing sustained oscillatory motion but with little drift in frequency; (o) able to return to reference after perturbation; and (p) tending to return to reference after perturbation.

The mathematical literature, too, admits of several concepts of stability. In a textbook on differential equations, Rouche and Mawhin (1980) noted that, “without doubt, there is no concept in current usage that has furnished more mathematical variations” (p. 3). To illustrate the variations, here is a list of qualifiers found to precede the word *stability* in mathematical texts dealing with differential equations, dynamical systems, analytical mechanics, and control systems theory: (a) Lyapunov, (b) Poincaré, (c) Laplace, (d) asymptotic, (e) uniform, (f) orbital, (g) attractive, (h) total, (i) dynamic, (j) neutral, (k) structural, (l) global, and (m) bounded-input/bounded-output (Gopal, 1984; Jordan & Smith, 1999; Rouche & Mawhin; Strogatz, 1994; Struble, 1962; Török, 2000).

In this article, I adhere to the meaning of stability used quite commonly for nonlinear systems, and universally for linear systems, which, implicitly or explicitly, informs many studies of the motor control system's responses to perturbations. In this definition, small effects of a perturbation on a trajectory are posited to remain forever small, whether they are in states of maintained position or movement. Technically, this is Lyapunov stability, according to which an infinitesimally small variation in the state of the system at time  $t_0$  remains infinitesimally small for all subsequent times  $t > t_0$ , which is to say that it does not grow into a substantial difference.<sup>3</sup> (The variation in state at  $t_0$  could be caused by a perturbation or noise, or it could reflect different initial conditions.) Conversely, in a Lyapunov unstable system, the smallest of variations will grow into a substantial one; and, if the system is linear, then it will grow inexorably toward infinity, that is, unboundedly.

For nonlinear systems, however, Lyapunov instability does not necessarily imply unbounded growth; the system might still exhibit a bounded-input/bounded-output stability (herein called *boundedness*). Stability and boundedness cannot be equated, even though they are essentially equivalent in the special case of linear systems (Gopal, 1984). In general, a postperturbation trajectory that starts out by departing increasingly from the unperturbed trajectory (or reference position) can nevertheless be respectably self-limiting and can thus avoid a crash against the ceiling or floor of its possible range. Boundedness can result, for example, when, with increasing output, the system's amplification factor decreases, or the damping increases, or when the system dynamics includes chaotic attractors.

More pertinent to biological motor control, the initial response to a perturbation may aggravate rather than oppose the effects of the perturbation; but despite that manifestation of instability, responses occurring later—for example, voluntary responses—may allow the achievement of the

task. In the strict sense, the trajectory will be considered unstable in such cases. In upright standing, for example, perturbations from the vertical position could be allowed to grow, rendering the position unstable, without resulting in a fall.

### Should the Motor Control System Ensure Stability?

There is long-standing precedent for regarding instability as desirable for the control of movement in certain conditions. In a zoologist's perspective of the dynamics and control of bird flight, R. H. J. Brown (1963) noted that birds lack a vertical fin. Conspicuously present near the tails of airplanes and gliders, the vertical fin confers stability against disturbances in the direction of flight (yaw). Unlike airplanes, therefore, birds have an inherently unstable physical system. That is an advantage, according to Brown, because if a stabilizing vertical fin were present in the bird, the fin would resist any attempt to quickly turn left or right. In a finless, unstable organism, however, the slightest nudge toward the desired direction is self-amplifying, allowing the bird to turn quickly, and thus giving it greater maneuverability. If the self-amplifying turn continues unboundedly, then a correction by the motor control system is needed eventually.

A tradeoff between stability and maneuverability has long been known to airplane designers, and deliberate instability has been incorporated in the design of certain military aircraft.<sup>4</sup> In the biological context too, there have been recent discussions of that tradeoff, examining, in addition to flight (Dudley, 2002), other forms of movement, such as terrestrial locomotion in multilegged organisms (Full, Kubow, Schmitt, Holmes, & Koditscheka, 2002) and aquatic locomotion in fish (Weihs, 2002). In the human motor control literature, however, the issues of whether and when the motor control system might ensure stability and when, in the interest of maneuverability, it may destabilize (or decline to stabilize an unstable physical system) have hardly been mentioned.

Even when maneuverability is not of primary importance, stability would appear to be an overly stringent requirement because it demands that after a small perturbation, the values of the motion variables at any instant of time should be close to what their unperturbed values would have been at that instant. Would it not suffice, for example, if the hand was briefly disturbed while drawing a shape, that the hand returns to the undisturbed spatial path, without the motor control system's ensuring that every point reached on the path is close to where the hand would have been at the same instant without the disturbance? If that would suffice, then the motor control system need not ensure stability. That the perturbed motion should stay close to the unperturbed path, but the values of the perturbed variables at each instant of time can continue forever to depart substantially from what they would have been without the perturbation, is what the mathematical literature demands in the case of rhythmic, limit-cycle motion in nonlinear systems. That

notion is referred to as *Poincaré* (or orbital) stability, which is a weaker requirement than Lyapunov stability. Unfortunately, we cannot adopt Poincaré stability as the standard for motor control because, by its definition, it pertains only to periodic behavior (Jordan & Smith, 1999; Török, 2000).

Although the focus in this article is on responses to external perturbations, it is noteworthy that anticipatory adjustments to internal perturbations also need not necessarily resist motion (Tyler & Hasan, 1995). Bagesteiro and Sainburg (2002) compared pointing movements performed with the dominant and nondominant arms to targets that required motion about the elbow but not the shoulder. On the dominant side, there was less muscle activity at the shoulder to resist the intersegmental interaction and, consequently, greater shoulder motion, which was unnecessary for the task. It was the nondominant side that showed less unnecessary motion. That finding suggests that greater dexterity goes with sacrifice of resistive responses in favor of reduced muscle activity.

In short, frank instability may be desirable when high maneuverability is necessary, and in some situations responses to perturbation that help restore some but not all aspects of the unperturbed motion can suffice. Thus, the motor control system does not necessarily have to ensure stability.

### Can the Motor Control System Ensure Stability?

A challenge to stability arises from the sluggish response of muscle force to change in muscle activation commanded by the motor control system. If muscle activation changed rhythmically with a frequency of around 5 Hz, the fluctuation in muscle force would lag so much as to be out of phase with the fluctuation in muscle activation (Baratta, Solomonow, & Zhou, 1998). For that frequency, then, the muscle would in effect reverse the sign of any feedback effect, rendering the corresponding frequency component of noise self-amplifying. Unless the effectiveness of the feedback was very small, the system would be unstable. Another threat to stability is presented by nerve-conduction delays in the negative-feedback loop, again because of the phase lag. A simulation study has shown that the unstable oscillatory behavior that arises in a reflex pathway containing phase lags, which is exacerbated by low firing thresholds of motoneurons, resembles the clonus seen in spasticity (Hidler & Rymer, 1999). Of course, problems of stabilization in the presence of phase lags arise in engineering control systems as well; in those systems, careful signal processing (filtering) within the controller can often solve the problem. But the price paid is a limitation on the range and type of loads that can be controlled while maintaining stability.

An ingenious way to investigate the problem of stabilization faced by the motor control system is to substitute an artificial—and therefore readily manipulated—controller for the real one while still relying on real muscles as the actuators. Jacks, Prochazka, and Trend (1988) used a transducer to monitor the elbow angle in human participants, and after

processing its output to mimic the spindle primary ending's response properties (using a linear model for the spindle), they used it to modulate the electrical stimuli applied to elbow flexor and extensor muscles so as to oppose any elbow motion. They found that when the effectiveness of the feedback (i.e., loop gain) was increased, spontaneous forearm oscillations developed (mean frequency = 4.4 Hz). The oscillations grew rapidly in magnitude, demonstrating the instability of the system, and the concomitantly increased electrical stimulation became painful. Introduction of a soft-saturation nonlinearity in the spindle model did not prevent the oscillations but restricted their amplitude. Similar instability was observed when tendon vibration instead of electrical stimulation of the muscles was modulated in correspondence with elbow angle (Prochazka & Trend, 1988). Participants were found, however, to differ in the threshold of instability, and some individuals may not have had a large safety margin with respect to forearm instability (see also Stein, Hunter, Lafontaine, & Jones, 1995).

In general, stability of a joint angle demands stiffness, that is, resistance to change in angle. Irrespective of how stiff a muscle may be, the joint stiffness can never exceed the stiffness provided by any elements that are interposed in series between the muscle fibers and the external world, such as the tendon and other deformable tissues. The existence of such compliant elements constrains the ability of the motor control system to resist perturbations. A case in point is the Achilles tendon, whose stiffness is so astonishingly low that when a standing individual leans slightly forward by dorsiflexing at the ankle, which necessarily lengthens the gastrocnemius muscle-plus-tendon complex, the muscle fiber length actually decreases (Loram, Maganaris, & Lakie, 2004). Such low stiffness of a tendon may be beneficial for energy storage and recovery during locomotion, but it is hardly appropriate for stabilizing the joint angle. The measured ankle stiffness does in fact fall short of the minimum required for stability (Hof, 1998; Morasso & Sanguineti, 2002; Morasso & Schieppati, 1999). Yet, thanks to voluntary interventions, to be discussed later, that deficit does not lead to unbounded growth of error and thus to a fall.

In the case of peripheral systems with many kinematic degrees of freedom, stability demands that perturbations in any direction applied to any segment should be resisted adequately, whatever the pattern of previous voluntary activity among the muscles. Calculations by McIntyre, Mussa-Ivaldi, and Bizzi (1996) showed that when the shoulder and elbow are free to move, the stiffness field (and joint stiffnesses) observed when zero force is exerted by the hand would not suffice for stability when the hand exerts a force in, say, the anterior direction. The resulting instability would be manifested in the medial and lateral directions. Restoration of stability necessitates increasing the activity of biarticular muscles, and co-contraction is needed for hand position to be maintained (Franklin & Milner, 2003).

The role of muscles that affect more than one degree of freedom raises certain additional issues. For example,

biceps brachii contraction affects elbow flexion and forearm supination. If a perturbation pronates the forearm, thus stretching the biceps, then any attempt by the motor control system to resist the change in biceps length will not only oppose the pronation but also can result in elbow flexion. Clearly, if the perturbation is to be resisted, the motor system must consider in the response more than simply the biceps stretch; moreover, the response should be routed to more than just the stretched muscles (Gielen, Ramaekers, & van Zuylen, 1988).

Quite independent of the existence of multiarticular muscles, a perturbation applied to one segment of the body will cause motion of the adjacent segments as well, because the perturbed segment applies forces to the adjacent segments via joint contact (Hasan, 1991; Soechting, 1989). The latter segments, in turn, will push their adjacent segments until every segment that is free to move in the chain is perturbed. If the motor control system then acts to resist the perturbation of the first segment, the resulting deceleration of that segment will change the joint-contact forces on adjacent segments, starting another chain of intersegmental interaction effects.

Although the emphasis in the preceding discussion was on the problems of stabilizing a system for controlling position, the stability of the control of force is perhaps equally important for some everyday activities. Contrary to long-established views, findings in cats suggest that the force feedback pathway in certain circumstances may in fact be such as to exacerbate any deviations in force (Pearson & Collins, 1993; Pratt, 1995). The resulting instability, it has been proposed, can drive the muscle to a short enough length at which the force-generating capability of the muscle, and hence the effectiveness of the positive-feedback pathway, is reduced so that the new position can be stable (Prochazka, Gillard, & Bennett, 1997a). In contrast, when a muscle contracts under isometric conditions, or against stiff loads, the instability will not resolve itself (Prochazka, Gillard, & Bennett, 1997b).

In short, stabilization of a joint is a serious challenge when perturbations at the joint are to be resisted substantially. The challenge arises from the properties of peripheral elements: nerves, muscles, and tendons. The motor control system is not in a position to provide significant resistance to perturbations and yet ensure stability over a wide range of external conditions, ranging from isometric to inertial or compliant loading. The challenge is multiplied when several degrees of freedom are involved and many directions of perturbation are considered. Those may not be insurmountable challenges, but they do require among muscles a flexible distribution of responses to perturbation in a manner far cleverer than what is usually contemplated (cf. Wilmink & Nichols, 2003).

### **Does the Motor Control System Ensure Stability?**

Because boundedness cannot be a criterion of stability as defined here, the following question arises: How can one tell

whether a system is stable? The mathematical literature on stability is not much help in that regard because in the tests of stability discussed in that literature, knowledge of the inner workings of the system is assumed. One must rely, then, on experimental observations of how the system responds to sudden perturbations and conclude that if the response is in a direction such as to resist or assist the perturbation, then the system is probably stable or unstable, respectively (McIntyre et al., 1996; Prochazka et al., 1997b). Another possible indicator of stability is a proactive adjustment whereby joint stiffness is increased by co-contraction of antagonist muscles (Franklin & Milner, 2003). In what follows, I give preferential attention to responses that appear to be destabilizing.

#### *Responses to Perturbation in the Context of Maintenance of Position*

Loram and Lakie (2002) studied the spontaneous sway when an individual tried, solely through ankle movements, to hold still an intrinsically unstable, inverted pendulum of the same mass as his body. They found that the ankle stiffness is not sufficient to stabilize the pendulum; instead, the motor control system generates a series of biphasic, ballistic torques, shifting the inverted pendulum in a series of steps “from one momentary rest position of imperfect balance to another” (Loram & Lackie, p. 119). Considering that those shifts occur over a time scale much slower than kinesthetic reaction times, it is presumably the voluntary reactions that prevent a fall. Therefore, even in that one-joint case, the system is not stabilized via continuous feedback; rather, it is allowed to drop unstably to a certain extent but is caught intermittently. Similar results were obtained when the elbow joint controlled a large inertial load through a spring; in that situation, again, the spontaneous sway did not depend on the mass and stiffness characteristics (as it would if joint stiffness stabilized the system); instead, it reflected a series of intermittent, voluntary brakings and reversals of the unstable motion (Lakie, Caplan, & Loram, 2003).

The importance of voluntary responses was also shown in a study in which participants were instructed to maintain constant effort while the investigators imposed constant-velocity rotation on the joint (Burgess et al., 2002). Regions of negative stiffness were found in which the response was opposite to that expected on the basis of the stretch reflex. Burgess and colleagues concluded that whenever a stabilizing positive stiffness is sustained for more than a fraction of a second, it is associated with a change in voluntary effort. Those findings call into serious question the long-standing dominance of the viewpoint that continuously operative, resistive responses are the chief mechanisms for compensation.

Experiments in which only one joint is free to move and the participant attempts to maintain the joint position in the face of unexpected mechanical perturbations have a long history, which gives them a paradigmatic status. The widely accepted understanding based on those experiments is that perturbations are resisted, partly by the intrinsic stiffness of

the muscles and partly by the neurally mediated changes in muscle activation revealed by a sequence of electromyographic (EMG) responses. Both short- and long-latency responses are observed when a muscle is stretched. It is not, however, the short-latency, monosynaptic stretch reflex (whose EMG response latency is around 25 ms for human arm muscles) that is responsible for most of the resistance; rather, it is the responses that occur later. Those include the long-latency reflex responses (commencing at about 40 ms) and a triggered reaction (at about 90-ms kinesthetic reaction time; Crago, Houk, & Hasan, 1976; Marsden, Rothwell, & Day, 1983). The latter is readily modified by the instruction given to the participant, and, notably, it is the prominent response when restoration of position is desired (Bennett, Gorassini, & Prochazka, 1994).

When more than one joint is free to move, a perturbation applied to one segment elicits, in some situations, consistently produced EMG responses that appear to destabilize another segment. For example, Lacquaniti and Soechting (1984, 1986) reported that when a brief (50 ms), posteriorly directed force pulse is applied to the upper arm, it causes the shoulder to extend, and, not surprisingly, an EMG response is seen in the stretched anterior deltoid. The imposed posterior motion of the upper arm causes flexion about the elbow joint through intersegmental interaction. From what is known about the effect of perturbation in the single-joint case, one may expect that the elbow extensors will be activated when intersegmental interaction throws the elbow into flexion, and the activated extensors will resist the elbow flexion and help restore the initial configuration. In fact, what is observed consistently is that the elbow flexor muscles are activated, which is a response that can only aggravate, rather than resist, the effect of the perturbation.

Koshland, Gerilovsky, and Hasan (1991), who studied the effect of elbow perturbation on elbow and wrist muscle EMGs, obtained analogous results. When the wrist is free, a brief force pulse to the forearm in the direction of elbow extension elicits not only elbow extension but also motion at the wrist via intersegmental interaction. In addition to elbow flexor muscles, which resist the elbow extension, those wrist muscles that assist the already occurring wrist motion are activated.<sup>5</sup>

Clearly, the EMG response at the wrist is not simply related to local joint kinematics and cannot be described in terms of increased activation of stretched muscles. That conclusion was also supported by the observations of Latash (2000) in a series of experiments involving the elbow and wrist joints. Consider experiments in which the participant, with a fairly flexed elbow, applies a constant pulling force on a stationary bar by activating the elbow flexors, contacting the bar with either the forearm or the palm. In either case, when the bar suddenly gives way, the initial elbow motion is in the direction of flexion. The initial wrist motion is in the direction of extension if the forearm was in contact, and in the direction of flexion if the palm was in contact. In both cases, however, there is an

increase in wrist extensor EMG and a decrease in wrist flexor EMG. Thus, if the forearm was in contact, the initial EMG response assists the already-occurring wrist motion.

On the basis of those observations on two-joint systems, it appears that even in tasks involving maintenance of position, for which stability at each joint may have been considered essential, motor control beats to a different drummer. The aforementioned destabilizing response at the distal joint does not result in runaway motion, however, partly because of nonlinear damping but also because, at around 100 ms, the destabilizing EMG burst dissipates.

It is difficult to see the benefit at any joint of worsening the effect of perturbation via neurally mediated responses. It has been suggested that the muscle response pattern seen across multiple joints following a perturbation is a pattern used habitually for voluntary movement in the absence of perturbation (Koshland et al., 1991; Latash, 2000). In other words, the pattern is one from a limited repertoire of pre-programmed activation sequences, which accounts well for the intersegmental interactions involved in a coordinated multijoint movement but does not account for the intersegmental interactions for resisting the perturbation. The burden of restoring the position is shifted onto later reaction time responses, thus perhaps allowing more time for taking the intersegmental interactions into account.

#### *Responses to Perturbation When Voluntary Movement Is Impending*

Just before a voluntary movement, the stretch reflex response in agonist muscles is enhanced (Prochazka, 1989), consistent with a stabilizing effect. The early agonist EMG activity for the voluntary movement is increased in magnitude (S. H. Brown & Cooke, 1986) and reduced in latency (Adamovich, Levin, & Feldman, 1997) whether the perturbation stretches the agonist muscle or shortens it. The finding in the case of imposed shortening of the agonist muscle is inconsistent with resistance to perturbation.

Further evidence that the responses are not necessarily resistive comes from the complementary experimental protocol of Koshland and Hasan (2000), who compared responses to the same perturbation, applied in random trials during the reaction time period after the go signal, when the intended movement was either elbow flexion or extension. They found a short-latency EMG response in the muscles stretched by the perturbation that was quite small in comparison with the longer latency response. The later, large response, however, depended on the direction of the intended movement and appeared at reduced latency and increased amplitude in the agonist muscles about to be voluntarily activated, whether or not those muscles were stretched by the perturbation. The response thus rendered the intended movement faster, and even the later activity of the antagonist for braking the movement occurred earlier and was enhanced by the perturbation. Whether the response resisted or assisted the perturbation therefore depended on the direction of the intended movement.

The same conclusion was drawn from experiments involving shoulder and elbow motions for reaching movements of the hand in the horizontal plane to targets in different spatial directions, involving all four combinations of shoulder and elbow flexor and extensor agonists (Koshland & Hasan, 2000). Whether or not the reduced-latency launching of the intended movement on external perturbation can be described as the release of a motor program by a startle (cf. Valls-Sole, Rothwell, Goulart, Cossu, & Munoz, 1999), the finding contradicts, in the context of impending movement, the notion that external perturbations are always resisted. Instead, the response to perturbation is tuned so that the command for the upcoming voluntary movement is augmented, whatever the combination of muscles to which the voluntary command is directed.

Although the emphasis here is on human motor systems, it is noteworthy that remarkably similar findings have been reported in the abdominal muscle system of the lobster. The response to stretching an abdominal receptor organ is resistive or assistive, depending on whether the spontaneously generated motor activity is flexor or extensor, but the response is always such as to augment the spontaneous activity (Sukhdeo & Page, 1992). Assistance reflexes are well established in the literature on invertebrate motor systems; they are found to be associated with states of arousal and movement (e.g., Cattaert & LeRay, 2001; DiCaprio & Clarac, 1981; Knop, Denzer, & Buschges, 2001; Skorupski & Sillar, 1986). Assistance to perturbation appears to be of wide phylogenetic significance.

If the external perturbation is in a direction similar to the direction of the impending movement, then there arguably is little need to oppose the perturbation; instead, it is expedient to let the perturbation contribute to the voluntary movement. In fact, as described earlier, the motor control system in such circumstances does not only not oppose the perturbation, it actually assists it, oblivious of the concept of stability.

#### *Responses to Perturbation During Voluntary Movement*

During a single-joint voluntary movement, the stretch reflex response is attenuated, recovering only toward the later part of the movement (Gottlieb & Agarwal, 1980; Shapiro, Gottlieb, & Corcos, 2004). The joint stiffness is correspondingly reduced (Bennett, Hollerbach, Xu, & Hunter, 1992), which suggests that the neural response is not well poised to resist perturbations. Moreover, owing to the phase lag phenomenon discussed earlier, the higher frequency components of the perturbation are assisted by the stretch reflex response (Bennett, 1994).

Nevertheless, people can achieve the goal of the voluntary movement despite perturbation. Soechting (1988) reported the effect of applying a brief force perturbation to the upper arm during a pointing movement involving the shoulder and elbow joints. The response at the elbow initially assists the perturbation, but soon thereafter the elbow

reverses motion and, even when the duration of the movement is prolonged by the perturbation, the spatial path followed by the hand is restored (cf. Won & Hogan, 1995). It appears that the system may be unstable, in that every point reached on the path may not come close to where the hand would have been at the same instant without the perturbation, but the perturbed path can nevertheless converge on the unperturbed path.

When the external inertia, viscosity, or compliance is altered, participants respond to the alteration by modifying the EMGs and torques (Gottlieb, 1996). The movement time, too, is modified in those conditions, which is not what one would expect if the control system were trying to follow a movement trajectory specified as a function of time. A significant role in those modifications is played by the long-latency response (Smeets, Erkelens, & Denier van der Gon, 1995), which, along with co-contraction, is important for coping with alterations in more exotic force fields (Wang, Dordevic, & Shadmehr, 2001). When the external force field itself is such as to destabilize the arm by exacerbating any veering of the hand perpendicular to the direction of the goal-directed movement, the participant learns to perform the task, not by changing the joint torques but by the proactive technique of increased co-contraction of antagonist muscles to increase the stiffness in the direction of the instability (Franklin, Burdet, Osu, Kawato, & Milner, 2003; Franklin, Osu, Burdet, Kawato, & Milner, 2003).

In short, the immediate, significant response to perturbation in many situations does not oppose the perturbation; boundedness is ensured not by continuous resistance to perturbations but by later events, including voluntary interventions.

### An Overview

Any active muscle opposes, at least initially, perturbations that stretch (or shorten) it, by an increase (or decrease) in the muscle force. The force response to change in length—unlike the case for change in activation—occurs without lag or delay. That certainly contributes to stability, independent of the motor control system's response. The phenomenon that a continuing stretch can cause a transient decrease in muscle force (the yield property of active muscle) is more or less compensated via the stretch reflex (Nichols & Houk, 1976). Those mechanisms, however, do not ensure stability, and the stretch reflex, if sufficiently strong, may indeed contribute to instability because of the lag property of muscle, nerve conduction delays, and tendon compliance, as discussed earlier. If stability is necessary for either maintenance of position or during voluntary movement, the proactive mechanism of co-contraction of antagonist muscles is the one used, because, although metabolically inefficient, it can increase joint stiffness without the necessity for the motor control system to respond to perturbations on a continuous basis. That mechanism, however, is useful only up to a limit if the tendon compliance is high or the peripheral system is unstable. For instance, in maintaining upright stance, no attempt is made to stabilize

the unstable inverted pendulum. Instead, the motor system generates corrections intermittently to prevent the instability from evolving into a fall. The inverted pendulum is not the only instance in everyday life of peripheral instability. Many joints are inherently unstable in a certain part of the range of motion at which an increase in muscle length is concomitant with a large decrease in the muscle's moment arm, which can result in a decrease in muscle torque with increasing muscle length (e.g., see Hasan & Enoka, 1985, for the elbow joint).

### *Long-Latency Responses: A Hypothesis*

As for the longer latency EMG responses to muscle stretch, which are usually more prominent than the short-latency responses, because of the delay those are even less suitable for joint stabilization using continuous feedback. But their presence in muscles not stretched by the perturbation hints at a more global role. When elicited during position maintenance, the response is an assistive one at a distal joint affected indirectly by perturbation at a proximal joint (i.e., via intersegmental interaction). If the indirect effect causes flexion of the distal joint, for example, then what could be the possible utility of a response that activates flexor muscles at that joint? One possibility is that the motor control system anticipates the eventual deceleration of the directly perturbed segment and emits a response to oppose the expected intersegmental consequence of that future event (R. L. Sainburg, personal communication, November, 2002).

A simpler hypothesis is that the pattern of responses to external perturbation seen across muscles at different joints mimics a pattern normally used for an unperturbed voluntary movement, the latter being a part of the accustomed repertoire. More specifically, let *A* represent the joint or joints directly perturbed and *B* the linked joint or joints that are affected via intersegmental interactions. The triggered pattern of muscle activity at the various joints is that which would have been used, in the absence of perturbation, to cause a voluntary movement of *A* while simultaneously preventing motion of *B*, for a movement of *A* in a direction opposite to that of the perturbation. (Note that it would take muscle activity in order for *B* to not move.) Such a rule, when used in response to perturbation, will indeed result in assisting the indirectly transmitted perturbation at the linked joints. For example, if the elbow is perturbed into extension, the response will be seen not only in the elbow flexors but also in those muscles at the wrist joint that are normally activated along with elbow flexors for causing a voluntary elbow flexion without wrist motion. Such is indeed the case. That hypothesis is consistent with the observations described earlier, but its generality remains to be investigated.

When the perturbation occurs just before a voluntary movement, the observations indicate that the responses simply augment that movement. In that case, too, the hypothesis that the pattern of responses mimics a voluntary move-

ment is supported—the voluntary movement being the same as the impending one. As for their effect on the outside world, the responses can be described as assistive or resistive depending on the relative directions of the voluntary movement and the perturbation. The motor control system takes advantage of the perturbation when feasible, incorporating it in the voluntary movement, but opposes it when not feasible. That is a pragmatic strategy that shows disregard for considerations of what we call stability.

### *Less Stringent Meanings of Stability?*

Perhaps the meaning of stability adopted here, which was taken from descriptions of nonbiological systems, is too stringent because it constrains the growth of each of the variables that constitute the state of the system. It is possible that only certain combinations of the variables are important enough to be stabilized. For example, in the case of voluntary point-to-point movement, only the direction and extent of the hand movement may be worthy of stabilization, not the movement duration or the time course of individual joint angles and torques. In that context, it is interesting to note that vertebrate muscle receptors first appeared in the muscles that control the fins of fish and thus affect the direction of motion, not in the large muscles that provide propulsion for swimming (Barker, 1974). Likewise, in driving an automobile, the steering function is separate from power generation, and the stability requirements for the two are of greatly different import. It so happens that in mammals the same muscles provide propulsion as well as steering, but it does not follow that the control of those two functions must be unitary (Hasan, 1992).

My emphasis here has been on responses that assist the initial effects of a perturbation. Despite such destabilizing responses, humans can usually surmount the perturbation and accomplish the desired motor task, thanks to later responses of the motor control system, including voluntary responses. That accomplishment can be considered an indicator of stability of a different, more general kind than the narrowly particular one defined here. In some instances, the achievement of the task may require the abandonment of the (unperturbed) trajectory in favor of a new one—which would be interpreted as instability.

Assuming, then, that the instabilities recited in this article are an artifact of the unwarranted expectation that all the motion variables should resist changes caused by perturbation, the question remains how one can identify which combinations of those variables, if any, are the ones actually stabilized. Even for the maintenance of the position of an inverted pendulum by one joint, the joint angle is not stabilized. Likewise for voluntary movement, the trajectory of the state variables (in its temporal and spatial aspects) is not what is stabilized. Todorov and Jordan (2002) in proposing a theory of motor coordination also argued against a preplanned movement trajectory. In their theory, the task goals are specified, and a cost function that depends on the task error and the effort is minimized. The minimization yields, after con-

siderable computation, different, time-varying feedback rules for different tasks, and the optimal feedback theory can predict many aspects of experimental results. In particular, the trial-to-trial variability observed in task-irrelevant combinations of the variables (Scholz & Schöner, 1999) is encompassed in that global optimization theory.

The simple hypothesis just presented, of triggered responses picked from an accustomed repertoire, is quite different from the hypothesis of tailoring the feedback rules in each task for optimal effort and accuracy. It is not clear, however, to what extent the predictions from the hypotheses actually differ regarding the initial response and whether both are consistent with perturbation findings, especially in cases when destabilizing responses are observed. It is also not clear whether and when the instabilities contribute to improved maneuverability or are simply irrelevant but benign consequences of the motor control system's resort to familiar patterns of motor output when faced with unexpected perturbation. The challenge is to identify in different contexts, without a priori faith in the desirability of conventional notions of stability, those aspects of the effects of a perturbation that the motor control system resists and those that it does not.

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### NOTES

1. A linear system has the property that if an input waveform (i.e., time series) is replaced by another that is a scaled version of the former, then the resulting output waveform is a similarly scaled version of the original output waveform. Note that, in general, the output waveform of a linear system is not a scaled version of the input waveform; the two can have totally different shapes, but they must scale together. In addition, because the scaling factor can be arbitrary, a linear system's output has no inherent ceiling or floor.

2. Similarly, studies of the stability of trunk equilibrium have revealed the requirement of a certain minimum stiffness at the trunk (Crisco & Panjabi, 1990). Granata and Orishimo (2001) provided another postural example of the essential distinction between equilibrium and stability. Those authors reported a change in muscle co-contractions for holding a barbell at different heights but at the same horizontal distance from the body, whereby the stability requirement (in terms of joint stiffnesses) is changed without changing the equilibrium requirement (in terms of joint moments).

3. The way this imprecise statement is turned into a rigorous definition of Lyapunov stability is by reversing it, as follows. If an upper limit is specified, for all times  $t > t_0$ , on the magnitude of the difference between two possible state trajectories, then, no matter how small the specified limit may be, adherence to the limit is ensured if the magnitude of the difference between the two states at time  $t_0$  is smaller than a certain quantity, that quantity being a function of the specified upper limit. (For a mathematical statement of that definition, see, e.g., Jordan & Smith, 1999, or Török, 2000.)

4. For a discussion of the tradeoff between stability and maneuverability in airplane design, see, for example, the National Aeronautics and Space Administration (NASA) Web site, <http://www>.

dfrc.nasa.gov/Education/OnlineEd/Intro2Flight/nasut.html. The history behind the F-16 fighter plane, which was the first to be based on a deliberately unstable design (negative stability in pitch) but which could be stabilized when needed by computer-controlled feedback (fly-by-wire operation), is discussed at the Federation of American Scientists' Web site, <http://www.fas.org/man/dod-101/sys/ac/f-16.htm>

5. Specifically, if the forearm is in a supinated position, the elbow extension causes wrist flexion and the wrist flexors are activated subsequently, whereas if the forearm is pronated, the same elbow extension results in wrist extension and consequent wrist extensor activity.

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