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Research report

# Corticospinal control strategies underlying voluntary and involuntary wrist movements

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## HIGHLIGHTS

- ► The corticospinal system sets spatial thresholds for proprioceptive reflexes.
- ► Voluntary motor actions are produced by resetting the spatial reflex thresholds.
- ► During involuntary actions descending systems maintain invariant values of reflex thresholds.
- ► Resetting of reflex thresholds solves the classical posture-movement problem.
- ► Corticospinal control is done without programming of EMG patterns and kinematics.

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## ABSTRACT

The difference between voluntary and involuntary motor actions has been recognized since ancient times, but the nature of this difference remains unclear. We compared corticospinal influences at wrist positions established before and after voluntary motion with those established before and after involuntary motion elicited by sudden removal of a load (the unloading reflex). To minimize the effect of motoneuronal excitability on the evaluation of corticospinal influences, motor potentials from transcranial magnetic stimulation of the wrist motor cortex area were evoked during an EMG silent period produced by brief muscle shortening. The motoneuronal excitability was thus equalized at different wrist positions. Results showed that the unloading reflex was generated in the presence of a corticospinal drive, rather than autonomously by the spinal cord. Although the tonic EMG levels were substantially different, the corticospinal influences remained the same at the pre- and post-unloading wrist positions. These influences however changed when subjects voluntarily moved the wrist to another position. Previous studies showed that the corticospinal system sets the referent position (R) at which neuromuscular posture-stabilizing mechanisms begin to act. In self-initiated actions, the corticospinal system shifts the R to relay these mechanisms to a new posture, thus converting them from mechanisms resisting to those assisting motion. This solves the classical posture-movement problem. In contrast, by maintaining the R value constant, the corticospinal system relies on these posture-stabilizing mechanisms to allow involuntary responses to occur after unloading. Thus, central control strategies underlying the two types of motor actions are fundamentally different.

## 1. Introduction

The relationship between voluntary and involuntary motor actions has been a topic of public and scientific interest since ancient times [1–4]. Voluntary motor actions are self-initiated by subjects, unlike involuntary actions (usually called reflexes) that represent compulsory responses to unexpected external sensory or mechanical stimuli. A known example of an involuntary action is the unloading reflex demonstrated in a person who holds a heavy book on the palm of the hand by contracting elbow flexors and lets the arm go to another position when the book is suddenly lifted off the palm by a second person. To reproduce the response

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*Abbreviations:* EC, efference copy; EMG, electromyogram; MNs, motoneurons; FCR, flexor carpi radialis; FCU, flexor carpi ulnaris; ECR, extensor carpi radialis; ECU, extensor carpi ulnaris; MEP, motor evoked potential; RMS, root mean square; SD, standard deviation; TMS, transcranial magnetic stimulation.

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in subsequent trials, it is usually sufficient to ask the subject to minimize voluntary interventions to the unloading [4] (for recent review see [5]).

Involuntary motor actions such as the stretch reflex and other proprioceptive reflexes have parameters (gains and thresholds) that are controlled by descending systems [6]. In other words, like voluntary motor actions, involuntary actions involve descending systems, rather than being generated autonomously by the spinal cord. The descending control strategies underlying the two types of actions are likely different but the essence of these strategies and differences between them remain unclear [6].

von Holst [2] emphasized that the control strategies in the two types of actions can be identified by solving the posture-movement problem, i.e. by answering the question of why self-initiated, voluntary movements of body segments from a stable posture are not impeded by posture-stabilizing reflexes [2,7–9]. A posture of one or more body segments is stabilized by intrinsic muscle properties and postural reflexes, including the stretch reflex, that generate position- and velocity-dependent resistance to deviations from this posture. Von Holst assumed that to prevent resistance of postural reflexes to self-initiated deviations from an initial posture, a copy of motor commands to muscle (called efference copy, EC) is used to compensate for the major source of this resistance – motion-related proprioceptive signals (reafference).

The EC notion conforms to the dominant view of pre-programming of motor output for actions, a view shared by several prominent scholars in the field [10–12]. There is, however, growing concern that this view might be incorrect [9,13–16]. In this controversial situation, it is important to re-examine the EC-based solution of the posture-movement problem to verify the physiological feasibility of this view. In von Holst's proposal, EC prevents resistance to self-initiated motion by suppressing reafference and thus postural reactions to deviations from the initial posture. In other words, the system destabilizes the initial posture to prevent resistance to the intentional movement. This proposal does not explain how stability of the final posture is regained. One can suggest that EC suppresses reafference only during motion and restores postural reflexes after that to stabilize the final posture. However, before the movement onset, postural reflexes were tuned to stabilize the initial posture and von Holst's proposal does not explain what prevents them from driving the body segments back to the initial posture.

Another problem of von Holst's proposal is that tonic EMG levels of arm muscles and thus ECs are often similar at different voluntarily established positions in isotonic conditions [7–9,16]. Therefore, in these cases, EC could only temporarily suppress postural reflexes. Again, restored postural reflexes should drive the body segments back to the initial position. This prediction of von Holst's proposal apparently conflicts with the absence of any tendency of body segments to return to the initial position after isotonic or other voluntary movements.

The posture-movement problem has been solved empirically, by identifying the central control strategies underlying the unloading reflex and voluntary changes in the elbow joint angle [4,5]. Specifically, by analyzing the unloading reflex, it has been found that with increasing amount of unloading, the arm displacement from the initial position increased, whereas the EMG activity of pre-loaded muscles decreased–a spring-like behavior described by a non-linear torque-angle characteristic resulting from intrinsic muscle properties and proprioceptive reflexes [4,5,17–20]. Thereby, the active muscle torque was reduced to zero at a specific, referent (R) elbow position. In the absence of co-activation of flexors and extensors, this position corresponds to the joint angle at which flexors and extensors reach their common activation threshold. More often, however, flexor and extensor thresholds are somewhat different being shifted in the opposite directions from R. Say, the flexor threshold is shifted to $R - R_f$ and the extensor threshold to $R + R_e$, thus surrounding the R with a *spatial zone* (between $R_f$ and $R_e$) within which agonist and antagonist muscles are co-activated [5]. The level of muscle co-activation at position R is defined by the width of the spatial zone.

It has also been shown that the R and thus the torque-angle characteristic are shifted when the subject voluntary changes the initial arm position [4,5,17–20]. These shifts are accomplished by changing the sub-threshold state of $\alpha$-motoneurons (MNs) [5,9,21] due to direct or indirect pre- and post-synaptic inputs to these MNs, via spinal interneurons and $\gamma$-MNs that innervate length- and velocity sensitive receptors–muscle spindles [22–24]. These sub-threshold signals that shift the R to elicit voluntary movement result in recruitment of agonist and de-recruitment of antagonist motor units. Therefore, the R is also called the reciprocal command, unlike the co-activation command (C) that specifies the width of the co-activation zone that surrounds the referent position. Thus, experimental data suggest that the nervous system actively controls reflexes in both actions but in involuntary action (unloading reflex), it maintains invariant values of the spatial thresholds at which proprioceptive reflexes are initiated, whereas in voluntary action, it shifts the spatial thresholds of reflexes. These empirical results underlie the equilibrium-point theory for motor actions [5].

Unlike all previous theoretical attempts to solve the posture-movement problem, referent position control represents an empirically-based solution of the problem [5,9]. Specifically, by resetting the R, the nervous system relays ("re-addresses") postural reflexes to a new position. In this case, the *initial arm position becomes deviated from the new R*. As a consequence, the same postural reflexes, instead of resisting motion, drive the arm toward a final posture at which muscle and external forces become balanced again. In other words, by shifting the referent position at which postural reflexes begin to act, the nervous system (1) converts these reflexes from a movement-resisting to a movement-producing mechanism and (2) relays stability to the final posture. The solution of the posture-movement problem remains valid even if a co-activation command is used: since the co-activation zone surrounds the R, this zone is shifted together with the R command when voluntary motion is made. Due to this hierarchy between the R and C commands and the spatial aspect of the latter, arm stiffness and damping responsible for an increase in arm stability due to the C command is relayed from the initial to the final arm posture. This shows that the C command subordinated to the R command in the context of threshold position control is a powerful tool in controlling action dynamics (movement speed in particular [5]) without any posture-movement problem.

The next step in the analysis of the relationship between voluntary and involuntary actions is to answer the question of which neural levels are involved in resetting or maintaining the referent position in the respective motor tasks. It has been shown that the referent position for activation of leg muscles in decerebrated cats can be set or reset by tonic electrical stimulation of different descending systems [23]. However, this method of changing the state of descending systems may not be considered as physiological.

In intact humans, it has recently been found that changes in corticospinal influences during intentional wrist movements are associated with resetting of the referent wrist position at which muscle recruitment is initiated [21,24]. Is it possible that the human motor cortex can also maintain identical corticospinal influences and thus maintain a constant *R*-value when motion to another wrist position is accomplished involuntarily, following unloading? The existing data are not sufficient to answer this question. One can argue that long-loop, transcortical reflexes [25–30] evoked by unloading could alter corticospinal influences when the wrist position changes due to unloading. This would imply that a different area of the brain is responsible for maintaining the same *R* value at