Université de Montréal

Control of adaptation to load in point-to-point arm movements

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Mémoire présenté à la Faculté des études supérieures
en vue de l'obtention du grade de maîtrise
en sciences neurologiques

Février 2004

Université de Montréal

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Université de Montréal
Faculté des études supérieures

Ce mémoire intitulé :

Control of adaptation to load in point-to-point arm movements

Présenté par

Martin Foisy

A été évalué par un jury compose des personnes suivantes :

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Résumé

Les simulations de mouvements d'atteinte du bras utilisant l'hypothèse du contrôle de la force, selon laquelle les niveaux de contrôle du système nerveux spécifient les signaux electromyographiques (EMG) et forces produisant un mouvement volontaire, suggèrent que l'EMG encode la position. Par opposition au modèle λ de contrôle moteur: les mouvements volontaires sont produits en changeant les coordonnées spatiales du seuil d'activation musculaire. La capacité des ces hypothèses à décrire l'activité EMG finale observée aux différentes positions du bras lors d'adaptation de mouvements d'atteinte à des changements de charge est étudiée.

Le sujet assis (n=16) tenait la poignée du manipulandum bi-articulaire et faisait un mouvement rapide du bras de la position initiale à une cible située à 30 cm dans l'espace de travail ipsilatéral. L'adaptation à 2 charges pratiquement perpendiculaires à la trajectoire mais de direction opposées fut évaluée sous 2 instructions: corriger ou ne pas corriger les erreurs de position pendant l'essai (4 expériences). Les 2 conditions de charge (sans et avec) s'alternaient pendant 20 blocs contenant entre 5 et 10 essais. Variables enregistrées: cinématique, torques et EMG de 7 muscles.

L'adaptation à un changement de charge est plus rapide avec l'instruction de corriger le mouvement pendant l'essai. Aucune amélioration fut observée pour l'adaptation à une même charge au cours de l'expérience, indépendamment de l'instruction. Différentes positions finales du bras sont associées aux conditions sans (R-postures) et avec (Q-postures) charge. Aucune relation significative n'a été obtenue entre l'activité EMG des R-postures et leur position, ce qui discorde avec les hypothèses du contrôle de la force mais non avec celles du contrôle du seuil.

Mots clés: contrôle moteur, théorie de contrôle de la force, problème de posture-mouvement, contrôle du seuil, mémoire motrice, théorie du contrôle du seuil d'activation.

Abstract

Simulations of arm reaching movements using the hypothesis that the nervous system's control levels specify the electromyographic signals (EMG) and forces required for voluntary movements suggest that postures are encoded by tonic EMG signals. Such coding is negated in the λ model for motor control, where active movements occur by shifting the spatial coordinates of the muscles' activation threshold. We tested the ability of these alternative hypotheses to describe steady-state EMG of arm muscles at different final postures during adaptation of arm reaching movements to different loads.

Sitting subjects (n=16) grasped the handle of a double-joint manipulandum and made fast hand movements from an initial position to a target 30 cm from the initial position in the ipsilateral arm workspace. Adaptation to 2 loads of opposed directions acting about perpendicularly to the movement trajectory were tested under 2 instructions: correct or do not to correct movement errors in-trial (4 experiments). The 2 load conditions (zero and non-zero) were presented alternatively for 20 blocks containing between 5 and 10 trials. Kinematics, torques and EMG of 7 muscles were recorded.

Subjects adapted significantly faster to a change in load condition when allowed to correct movement errors on-line. For either instruction, adaptation to a given load condition did not occur faster as the experiment progressed. Different steady-state arm configurations belong to zero (R-postures) and non-zero loads (Q-postures). No significant relationship was found between R-posture tonic EMG levels and position, conflicting with the force control hypotheses, but not with the threshold control theories.

Key words: motor control, force control theories, posture-movement problem, threshold control, motor memory.

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Liste des abbréviations utilisées

BB: biceps brachii muscle.

BR: brachioradialis muscle.

C (command): co-activation command.

cm: centimeter(s).

DA: anterior deltoid.

DF(s): degree(s) of freedom.

DP: posterior deltoid.

EMG: electromyographic activity.

Fig(s): figure(s).

FR: frame of reference.

ms: millisecond

PM: pectoralis major muscle.

Q_0 : arm configuration at the target with load.

Q_- : arm configuration on the first trial where the load is added, experiment 1.

Q_+ : arm configuration on the first trial where the load is added, experiement 2.

R_i : referent arm configuration at the initial target.

R_0 : referent arm configuration at the target without load.

R_- : referent arm configuration on the first trial where the load is removed, experiment 2.

R_+ : referent arm configuration on the first trial where the load is removed, experiment 1.

s : second (s)

TB: triceps brachii muscle.

TM: teres major muscle.

λ: lambda.

Contribution des auteurs

Dr Anatol G. Feldman: idée originale du projet, participation à la rédaction et à la correction de l'article et du mémoire.

Philippe Archambault: développement des programmes d'analyse et de visionnement des données avec le programme Labview. Supervision lors de la phase initiale de l'analyse des données. Participation à la correction de l'article.

Martin Foisy: contribution au développement du projet, recrutement des sujets, expérimentateur, développement des programmes d'analyse de données, analyse des données, création des graphiques, rédaction du mémoire et de l'article, création et présentation d'un poster à la rencontre de la Society for Neuroscience à Orlando, Floride en novembre 2002.

Accord des co-auteurs pour l'inclusion de l'article au mémoire

1. **Identification de l'étudiant et du programme**.
Martin Foisy
Maîtrise en Sciences Neurologiques

2. **Identification de l'article**.
Martin Foisy, Philippe Archambault, and Anatol G. Feldman. *Control of adaptation to loads in point-to-point arm movements.*

3. **Déclaration de tous les coauteurs autres que l'étudiant**.
À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Martin Foisy inclue cet article dans son mémoire de maîtrise qui a pour titre : Control of adaptation to loads in point-to-point arm movements.

Anatol G. Feldman	[redacted]	Nov 17/03
Coauteur		Date

1. **Identification de l'étudiant et du programme.**
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Philippe Archambault [redacted] 30/10/2003
Coauteur Date

Remerciements

Je tiens à remercier très sincèrement les personnes suivantes pour la précieuse aide qu'ils m'ont apportée au cours de ma maîtrise.

Dr Anatol G. Feldman, pour avoir cru en moi en m'acceptant dans son laboratoire, ainsi que pour sa patience et son attention qui m'ont permis de me développer en tant que scientifique.

Dr Mindy F. Levin, pour ses précieux conseils et son aide pour l'analyse statistique.

Philippe Archambault, pour avoir été d'une aide indispensable pour le développement de mon expérience ainsi que pour avoir été un modèle pour moi.

Michel Goyette, pour avoir construit le programme informatique gérant mon expérience.

Joanne Payette, pour m'avoir guidé, conseillé et rassuré tout au long de mes études mais surtout pour la grande passion et tout le dévouement dont elle fait preuve envers les étudiants.

Dédicace

J'aimerais dédier le présent travail à mon père, Ronald, et ma mère, Hélène, qui m'ont soutenu et encouragé tout au long de mes études et qui m'ont toujours donné tout le nécessaire (et plus) afin que je développe mon potentiel au maximum de mes capacités.

Je ne pourrais oublier mes frères, David et Alexandre, qui m'ont aussi beaucoup épaulé et qui ont été, et seront toujours, à leur façon et peut-être à leur insu, une grande source d'inspiration et de motivation pour moi.

CHAPTER I

1.0 Introduction, objectives and review of literature

1.1 Introduction

It is generally assumed that control levels of the nervous system directly calculate and program electromyographic (EMG) signals and forces required for the production of voluntary movements. These calculations are based on internal inverse and forward models of the system's dynamics interacting with the environment (Hollerbach 1982; for recent review see Ostry and Feldman 2003). This theory has been successful in explaining the evolution of hand trajectories and velocity profiles in pointing movements during adaptation to different force fields (Lackner and DiZio, 1994; Shadmehr and Mussa-Ivaldi, 1994; Conditt et al., 1997; Gandolfo et al. 1996; Goodbody and Wolpert, 1998) as well as intrinsic loads, e.g. joint interaction torques (Sainburg et al., 1995, 1999; Gribble and Ostry, 1999). However, basic aspects of arm movement production and adaptation to force fields have also been simulated in the λ model for motor control without relying on the idea of force programming and internal models (Gribble et al. 2002). A major feature of this model is the notion of *threshold control*, implying that the nervous system guides active movements by resetting the position of the body or its segments at which muscles reach their activation thresholds (Feldman, 1986).

To resolve the controversy in the understanding of basic principles underlying motor control, one needs to experimentally test predictions resulting, in particular, from the differences in the ways the two theories account for the relationship between posture and movement. Ostry and Feldman (2003) identified that force control models that integrate basic properties of muscles and reflexes (Schweighofer et al., 1998; Bhushan and Shadmehr, 1999) predict that in order to bring the arm to a new posture, control neural levels should compute and specify not only phasic EMG bursts of activity to accelerate and then decelerate the movement but also an additional, tonic component of EMG activity to hold the arm at the final position. A similar combination of EMG signals has been proposed in the pulse-step model of saccadic eye movements during shifts in the gaze (Robinson 1970). In arm movements, an additional, tonic EMG component is necessary to overcome resistance of posture-stabilizing mechanisms to the deviation of the arm from the initial position when the arm moves away from it (described as the Von Holt's posture-movement paradox, described below). Otherwise, posture-stabilizing mechanisms would drive the arm back to the initial position as soon as the generation of phasic EMG bursts and forces has been completed. In other words, the notion of force control implies that arm postures are encoded by tonic levels of EMG signals. This means, more specifically, that the tonic levels of activity of muscles cannot be the same at two different arm positions when the net joint torques are zero at these positions. The analysis (Ostry and Feldman, 2003) of existing models of horizontal point-to-point arm movements simulated using the framework of the force control theory (Bhushan and Shdmehr,1999; Schweighofer et al., 1998) showed that changes in the arm posture is not possible without changing tonic EMG levels, even in the absence of gravitational loads. Experimentally, however, changes in tonic EMG activity of arm muscles can be observed in some, but not all, cases (see Fig. 1).

In contrast, the notion of threshold control implies that control levels are not involved in EMG and force specification. Instead, they elicit movements by shifting the activation thresholds of muscles to a new position of the arm. In this case, the posture-stabilizing mechanisms are re-addressed to the new posture ("postural resetting") so that no resistance to the deviation of the arm from the initial position is generated. Instead, with the resetting of muscle activation thresholds, the initial position of the arm now appears as a deviation from the newly specified threshold position. The same posture-stabilizing mechanisms that would resist the deviation of the arm from the initial position will now generate EMG activity and forces, driving the arm to the new position. In other words, by shifting muscle activation thresholds, the nervous system not only prevents resistance from posture-stabilizing mechanisms to movement from the initial posture, but also takes advantage of these mechanisms to drive the arm to a new posture. The levels of the nervous system involved in threshold control do not need to provide a position-dependent specification of EMG signals, so that the tonic levels of EMG activity at different arm postures could be the same, unless there is a difference in the external torques that muscles should counteract at these postures.

Thus, the two theories of motor control make alternative predictions on how postures are specified: the force control hypothesis suggests that postures are coded by tonic levels of EMG activity, whereas the threshold control hypothesis negates such coding and suggests, instead, that changes in arm posture emerge following shifts in the muscle activation thresholds. The purpose of this study was to evaluate the ability of the threshold control model to explain EMG an kinematic patterns related to transition from one arm posture to another in a physiologically realistic manner. Also, the threshold control theory was additionally challenged by the necessity to explain major characteristics of adaptation of arm point-to-point movements to different load conditions. To meet these objectives, we used the method employed by Weeks et al. (1996) in which the load applied to the arm during reaching movements changed after each block of 5-10 trials. This paradigm was applied not to single-joint movements (as was the case in the study by Weeks et al.), but to double-joint pointing movements and was complemented by the analysis of EMG signals of multiple arm muscles at different steady-state positions. The results have been reported in abstract form (Foisy et al. 2002).

1.2 Objectives

Based on the brief analysis of different theories of motor control (see next section), the present study was designed to meet the following objectives:

1. To further evaluate the threshold control theory of motor control by testing its capacity to explain the major characteristics of arm point-to-point movements and their adaptation to changes in load. These explanations will also be contrasted with those offered in the framework of the force control theory.

2. To make this testing in the context of adaptation of arm point-to-point movements to different load conditions.

3. To examine the effect of different instructions: “do not correct” and “correct” movement errors during the course of the trial on the adaptation rate.

1.3 Review of Literature

In this section, we will review different theories of motor control in relation to two major problems in movement production: The redundancy problem in the control of multiple skeletal muscles and degrees of freedom of the motor apparatus and the problem of the relationship between posture and movement. Since the present project addresses the question of adaptation of arm movements to external forces, we will also review some relevant studies on adaptation.

1.3.1 Hypotheses related to the redundancy problem

The redundancy problem in the control of multiple degrees of freedom of the motor apparatus can be explained in the following way. Bernstein (1967) conducted experiments in which subjects performed different functional motor tasks. He came to the conclusion that higher levels of the nervous system control the spatial aspects of the desired movement and specify which degrees of freedom (DFs) should participate in the movement production. The number of DFs of a biomechanical system (for example an arm) is defined by the minimal number of independent coordinates (e.g. angles along a plane of movement for each joint participating in the movement) fully determining its geometrical configuration in the limits of the existing mechanical constraints. Usually, the motor goal (e.g. a point in space) can be reached using different configurations of the arm (redundancy problem). Bernstein posed the following question: How does the nervous system choose a unique sequence of arm configurations to perform a task-specific movement? This question is associated with the problem of redundancy at the level of DFs. Suppose that the nervous system has already selected the appropriate DFs to perform a task, how does the nervous system select the appropriate muscles to perform the movement? Thus, a similar redundancy problem now arises at the level of muscles, because the number of muscles is much higher than the number of DFs. We consider first different hypotheses that offer a solution to the redundancy problems and then we describe the essence of the posture-movement problem and review its possible solutions.

1.3.2 Synergies

Bernstein assumed that the nervous system creates different, functionally specific groups of DFs (which he called *synergies*) that, when employed in isolation or in combination, can meet the different requirements of any motor task. He also assumed that synergies can be formed in the process of learning. Thus, by selecting a set of synergies that are functionally relevant for reaching the motor goal, the nervous system provides a unique solution to the redundancy problem in each motor task. This hypothesis reduces the redundancy problem to the question of how the nervous system selects synergies in task-specific way.

1.3.3 Coordinative structures

A somewhat different approach to the redundancy problem was developed by Kugler et al. (1980) and Saltzman and Kelso (1987). They assumed that the nervous system employs each DF depending on its capacity to contribute to reaching the motor goal, rather than employing different synergies. This implies that the system organizes functional ensembles of different DFs (which they called "*coordinative structures*"), each time anew, depending on the motor task. With movement repetition, a somewhat different coordinative structure may emerge, explaining the variability of the performance often observed in repetitive movements, although variability might also result from history-dependent muscle (e.g., fatigue) and neural properties.

1.3.4 Controlled and uncontrolled manifolds

Yet another approach to the redundancy problem is based on the idea that the nervous system classifies DFs into two groups: one group includes those DFs that deal with variables that are essential for reaching the motor goal, and the other group includes those DFs that deal with less essential variables (Scholz and Schöner, 1999). It is further assumed that the nervous system relatively strongly coordinates DFs within the first group ("*controlled manifold*") but allows broad variations and less coordination of the DFs within the second group ("*uncontrolled manifold*"). Scholz and Schöner (1999) elaborated an experimental method to find out which degrees of freedom are actually controlled and uncontrolled. Some DFs may belong to the two groups simultaneously so that the changes in these DFs consist of two components, each related to changes in the degrees of freedom in the appropriate group. They associated neural control with the ability of the nervous system to maintain ("stabilize") some variables that are essential for reaching the functional goal, and, conversely, lack of control with reduced stabilization of the variables that are less or non-essential for the task performance. *Stability* is defined as the ability of a system to return to a specific state in response to an intermittent perturbation that has deviated the system from this state. According to the model by Scholz and Schöner, the choice of DFs for the controlled manifold is primarily made based on their potential capacity to stabilize variables that are essential for the task performance. When used in this sense, stability can also be referred to as the set-point or the fixed point of the system. Experiments (Scholz and Kelso 1989; Scholz et al. 1987) have looked at measures of variability of the variables presumably controlled during a particular state as a means to assess their stability. Others, such as Schöner and Kelso (1990) used the reproducibility of a variable from trial to trial to achieve the same purpose. In experiments using specific postures, variability in time can be used to describe the stability of the system, whereas experiments using movements of a limb are designed to analyze the reproducibility of the movement across multiple trials. Scholz and Schöner used a sit-to-stand task. After having tested different possibilities regarding the essential/non-essential variables, they found that the position of the center of mass in the sagittal plane was controlled. They also found that the horizontal head position and the position of the hand are less controlled. Respectively, the controlled manifold was defined as coordinations influencing the position of the center of mass and the uncontrolled manifolds were identified as coordinations that do not influence the position of the center of mass.

For the uncontrolled manifold theory to be feasible, there must be a forward-kinematic model that relates joint angles to a specific essential variable. Here is how the model explains movement control (from Scholz and Schöner 1999). Initially, the system defines all possible configurations of the arm involving all joints participating in a given movement. An hypothesis is then formulated regarding the variables the nervous system should control. Variables may be specific functions of joint angles. Joint space is then divided into two subspaces that are orthogonal to each other. This is done for any given set of values of control variables. One subspace is made up of all the joint configurations leading to identical (invariant) values of the presumed controlled variables. Scholz and Schöner (1999), who used a sit-to-stand task, analyzed joint configuration variability in the uncontrolled subspaces and compared it to that of the subspace perpendicular to it. They tested the prediction that there would be greater variability in the joint configurations in the uncontrolled subspace. Their results were consistent with this prediction. It is claimed that the uncontrolled manifold concept offers a novel theoretical approach to identifying the important control variables for movement tasks.

1.3.5 Memorized postures

Rosenbaum et al. (1993) approached the redundancy problem based on an idea reminiscent of the equilibrium point hypothesis. They assumed that movement results from the specification of a sequence of equilibrium states of the body defined by a weighted combination of postures stored in motor memory. The role of each posture (weight) depends on the motor task. The theory was successful in simulating kinematic patterns of different body movements.

1.3.6 Frames of reference

Saltzman and Kelso (1987) related the redundancy problem to the question: which coordinate frame does the central nervous system use to represent and plan multi-joint movements? Many studies have looked for an answer to this question by analyzing arm reaching movements to different targets (Feldman and Levin 1995; Flash and Hogan 1985; Morasso 1981). Common features of hand movement trajectories have been identified by Morasso (1981). They found that subjects tend to move the hand along a straight line and concluded that the control variable for these movements was the trajectory of the hand in space, implying that movement is controlled in the frame of reference associated with the environment. However, Ghafouri and Feldman (2001) recently demonstrated, based on the analysis of pointing movements to stationary and moving targets, that the nervous system can rapidly switch the motor performance from a frame of reference associated with the environment to one associated with the body.

1.3.7 Kinematic constraints

Another way to look at the degrees of freedom problem was proposed by Gielen et al. (1997). Their idea was based on the assumption that Donder's and Listing's laws (which had been previously described for eye movements) are applicable to arm movements. Donder's law states that when subjects point with their hand to targets, the end-configuration of the arm is reproducible, irrespective of the initial posture of the arm. The explanation to account for this is that the nervous system identifies specific rotation axes which are defined by the initial and final pointing directions. The movement can be completely defined through rotation about these axes. Rotations about the remaining axes, representing the remaining degrees of freedom, are very small. This control strategy results in a reduction in the number of controlled degrees of freedom contributing to the motor task. One can suggest that taken together, all neural and biomechanical constraints leave no room for redundancy. However, our ability to voluntarily modify movement trajectory despite many constraints implies that the redundancy problem cannot be solved solely based on constraints.

1.4 The principle of minimal interaction and the λ model for motor control

In the framework of the λ model (Feldman et al., 1998; Feldman, 1986; Weeks et al. 1996), the principle of minimal interaction is described by the following points.

1. The activity of each component of the neuromuscular system depends on the difference between the actual (physical) and the referent (threshold) values of the appropriate variables. For example, the activity of muscle spindle afferents depends on the muscle length (physical variable) and the "intrafusal" length determined by γ input (referent variable). At the level of motoneurons, their signals are combined with independent control inputs influencing the activation threshold - the length of the muscle at which motoneurons become active. The activation of motoneurons, thus, depends on the difference between the actual and the threshold muscle lengths. This example shows that the value of the physical variable is transmitted by appropriate afferent systems, whereas an independent control signal determines the referent value for the measurement of this variable.

2. Active movements or isometric torques are produced by shifting the referent values of physical variables. In the lambda model, the referent length at which a given muscle will become active (called activation threshold) is considered the control variable for movement production. By shifting this referent length, the actual length of the muscle will fall either into, or out of, the activation range and the appropriate change in activation will follow. An example of experimental evidence that shifting (resetting) of muscle activation thresholds takes place in active movements is shown in section 1.5 discussing the posture-movement problem.

3. The afferent feedback to each element and the interactions between different elements are specifically organized to drive the system to a state in which the difference between the physical and actual variables, and thus the overall activity in the system, becomes minimal, in the limits determined by task constraints.

In the theoretical framework outlined above, pointing movements are produced by shifting the referent values for the position of the involved limb in the following way (we quote this explanation from Lestienne and Feldman 2002). "Control levels shift the referent coordinates of the effector in an external frame of reference (FR), thus producing a referent trajectory. The response of the system is guided by the principle of minimal interaction that imposes changes in the referent configuration of the body and in individual activation thresholds of muscles. As a consequence, the actual configuration of the body will change and the effector will move along an actual trajectory until a final arm configuration associated with a minimum of activity in the system is re-established. The actual and referent trajectories of the effector may not coincide, due to several biomechanical factors. In particular, in movements in a horizontal plane, the weight of the arm segments deviates the actual hand trajectory downward relative to the referent one. Subjects could produce referent trajectories rising at some angle from a horizontal plane to make the resulting, actual trajectory horizontal. In general, if the final position of the effector is different from its desired position with respect to the target, control levels may adjust the referent shifts so that the movement error is nullified. In the same framework, there are different physiological mechanisms, i.e. co-activation commands, that diminish the sensitivity of the actual hand trajectory to mechanical perturbations, arm inertia or velocity-dependent torques acting between adjacent segments (Feldman and Levin, 1995)".

According to this explanation, the principle of minimal interaction in the theoretical framework of the λ model provides non-computational, dynamical solutions to the problems of multi-muscle and multi-joint redundancy. This solution does not reject the notion of synergies, or the recently proposed classification of multi-joint co-ordinations into two groups ("controlled and uncontrolled manifolds") comprised of co-ordinations that are most essential and less essential for reaching the motor goal, respectively. Rather, this solution suggests that synergies or manifolds, like trajectories and forces, may be an emergent property of the neuromuscular behavior resulting from the response of the system to changes in control (referent) parameters in specific environmental conditions.

1.4.1 Referent configuration of the body: a global factor in the control of multiple muscles

The notion of muscle activation threshold has been generalized to multiple muscles of the body to explain how they may be controlled by the nervous system in a coherent and task-specific way, regardless of the number of them involved in the motor task (Feldman and Levin 1995; St-Onge and Feldman, 2003). The generalized threshold is the configuration of the body at which all skeletal muscles may reach their individual recruitment thresholds (Feldman and Levin, 1995). This configuration is described by the set of threshold angles (one threshold angle for each degree of freedom of the body). It may be considered as a referent (R) configuration with which the actual configuration of the body (Q) is compared. Due to the threshold nature of the R configuration, the activity of each muscle depends on the difference between the Q and R postures. In other words, the difference between these configurations is a global factor influencing all muscles of the body, regardless of their biomechanical function. The R configuration is modified by the nervous system to elicit movement, or if the movement is mechanically prevented, to ensure isometric torque generation.

The referent configuration hypothesis implies that the biomechanical, afferent and central interactions between neuromuscular elements tend to minimize the difference between the Q and R postures. Biomechanical factors such as inertia of body segments and external forces may prevent the two configurations from matching and thus establishing a zero global EMG minimum. However, matching is still possible in some cases. For example, when there is no external force applied to the arm during movement. Also, by reversing the changes in the R configuration, the nervous system may reverse the movement direction. Due to inertia, however, body segments may continue to move in the initial direction for a short period of time, before yielding to the change in the direction of the R command. During this period, the actual and the referent configurations may approach and even match each other, resulting in minimization of the EMG activity of all muscles involved, regardless of their biomechanical function. Ideally, in the absence of co-activation (C) commands, no EMG activity should be generated when the matching occurs. In the presence of a C command, this situation changes. The C command results from a modification in the thresholds of activation of motoneurons of antagonistic (opposing) muscle groups creating a zone surrounding the R position in which these groups are co-active. The R position appears to be inside this zone, so co-activation takes place at this position as well. (Feldman 1980; Feldman and Levin 1995; Levin and Dimov 1997). The activation thresholds are specified in such a way as to preserve the referent position, implying that the torques exerted by these groups at position R are equal and opposite (so that the net joint torque remains zero) but the stiffness of the joint increases so that the resistance to deviation from the R position increases. The notion that muscle co-activation is spatially organized has been confirmed by Levin and Dimov (1997). Although the C command does not influence the R position, it may substantially increase the acceleration and deceleration of intentional movements. Since the spatial location of the co-activation zone is determined by the R command, when the latter changes it relocates the C zone accordingly. Thus, the torques generated due to the difference between the initial and referent position of the arm will be amplified in the presence of the C command resulting in greater activation of agonist muscles and an increase in movement acceleration. Therefore, a C command is often employed to improve postural stability and/or to accelerate movement or for isometric torque production (Feldman 1980). For the present study, it is essential to have in mind that when the R and the Q configurations of the arm match each other, the depth of the minimum in the activity of multiple muscle is limited by the level of co-activation.

Minima in the EMG activity of numerous, functionally diverse muscles have been found at each of two reversal phases during horizontal head rotations in monkeys, jaw movements in rabbits, and jumping and walking in place in humans (Lestienne et al., 2000; Weijs et al., 1999; St-Onge and Feldman, 2003). One minimum was found in sit-to-stand movements with reversal and during hammering in humans (Archambault et al., 1998; Feldman et al., 1998). The referent configuration hypothesis suggests that neural rather than mechanical factors are responsible for minimizing the EMG activity of multiple muscles in these and other movements. In other words, EMG minima in the activity of multiple muscles may occur during reversals in the movement direction whether or not they are assisted by external forces (e.g., gravity). This prediction has been confirmed in studies of movements that are essentially influenced by gravity, e.g. jumping and stepping in place (St-Onge and Feldman, 2003).

1.5 The posture-movement problem and its solution

Von Holst and Mittelstaedt (1950/1972) noted that there are powerful neuromuscular mechanisms that generate electromyographic activity (EMG) and forces in order to resist perturbations that would otherwise deflect the body from its initial position. At the same time it is clear that the organism can intentionally adopt different postures. How then is an intentional movement from the initial posture and the achievement of a new posture possible without triggering resistance?

Ostry and Feldman (2003) refer to this problem as Von Holst's posture-movement paradox. They discussed the capacity of the currently dominant force control theory to resolve this paradox. This model is based on the following major assumptions (Bhushan and Shdmehr,1999; Schweighofer et al., 1998): a) control levels compute and directly specify muscle forces (torques) that are required for movement production, b) the values of muscle forces are computed using an inverse dynamics internal model, c) these computations involve a predictive mechanism which is based upon a forward internal model of the system's dynamics. They have analyzed in detail these aspects of the force control formulation and concluded that this formulation, and in particular its more fully developed versions that incorporate muscle properties and feedback mechanisms, are unable to resolve the Von Holst posture-movement paradox. Basically, the problem is that the formulation cannot account for how the body or its segments can voluntarily change position without triggering resistance. The generation of muscle torques required for movement would be perceived by the mechanisms of postural stabilization as a deviation of the body segments from an initial position, and in response, they would generate resistance that would tend to return the segments to their initial position. Control levels might attempt to reinforce the programmed action by generating additional torque to counteract this resistance. However, this strategy would be non-optimal in terms of energy output, since it would require high forces not only for motion, but also for the maintenance of the final posture. The problem is that the force control model, in its actual formulation, has no means to reset the "postural state" in a physiologically plausible way, i.e. without evoking resistance from the posture-stabilizing mechanisms, and therefore the transition between postures remains an unresolved issue in this model. Feldman and Ostry concluded that the inability of the force control strategy to re-establish postures at a new location without self-generated resistance is a basic failing of the formulation, and figure 1 (from Feldman and Ostry, 2003) illustrates that muscle activity can be decreased to a minimum after a change in posture and that the postural state can be reset to the new position following movement, which is arguably evidence that postures cannot be encoded by EMG signals.

To resolve the posture-movement problem, it is necessary to identify a neurophysiological variable(s), the value of which is different for different voluntarily specified positions, even though forces and tonic muscle activity may be the same at these positions (see Figure 1B). The λ model was based on the empirical identification of such a variable. In particular, it can be identified from Figure 1 or similar figures published in the literature (Gottlieb et al. 1989). It may be seen that the EMG activity at the initial position in Figure 1B is practically zero, but muscles actively reacted to passive oscillations of the arm at this position (Figure 1A). This means that motoneurons of arm muscles before movement onset are in a just sub-threshold state. The fact that zero activity and reactions to passive oscillations are also observed at the final position

(Figure 1C) implies that the activation thresholds of motoneurons were reset to this position. The position at which muscles reach their activation thresholds is thus not constant. In other words, the threshold position was reset so that zero muscle activity could be restored, but at another point in the workspace. This phenomenon is referred to as threshold control. The existence of threshold control follows not only from the simple analysis of the elbow flexion in Figure 1, but also from many experimental studies in animals and humans, starting from work by Matthews (1959), and Asatryan and Feldman (1965). The feasibility of threshold control as a major notion underlying the λ model for motor control, has been demonstrated in computer simulations of single- and double-joint arm movements (e.g., Gribble et al. 1998).

Figure 1

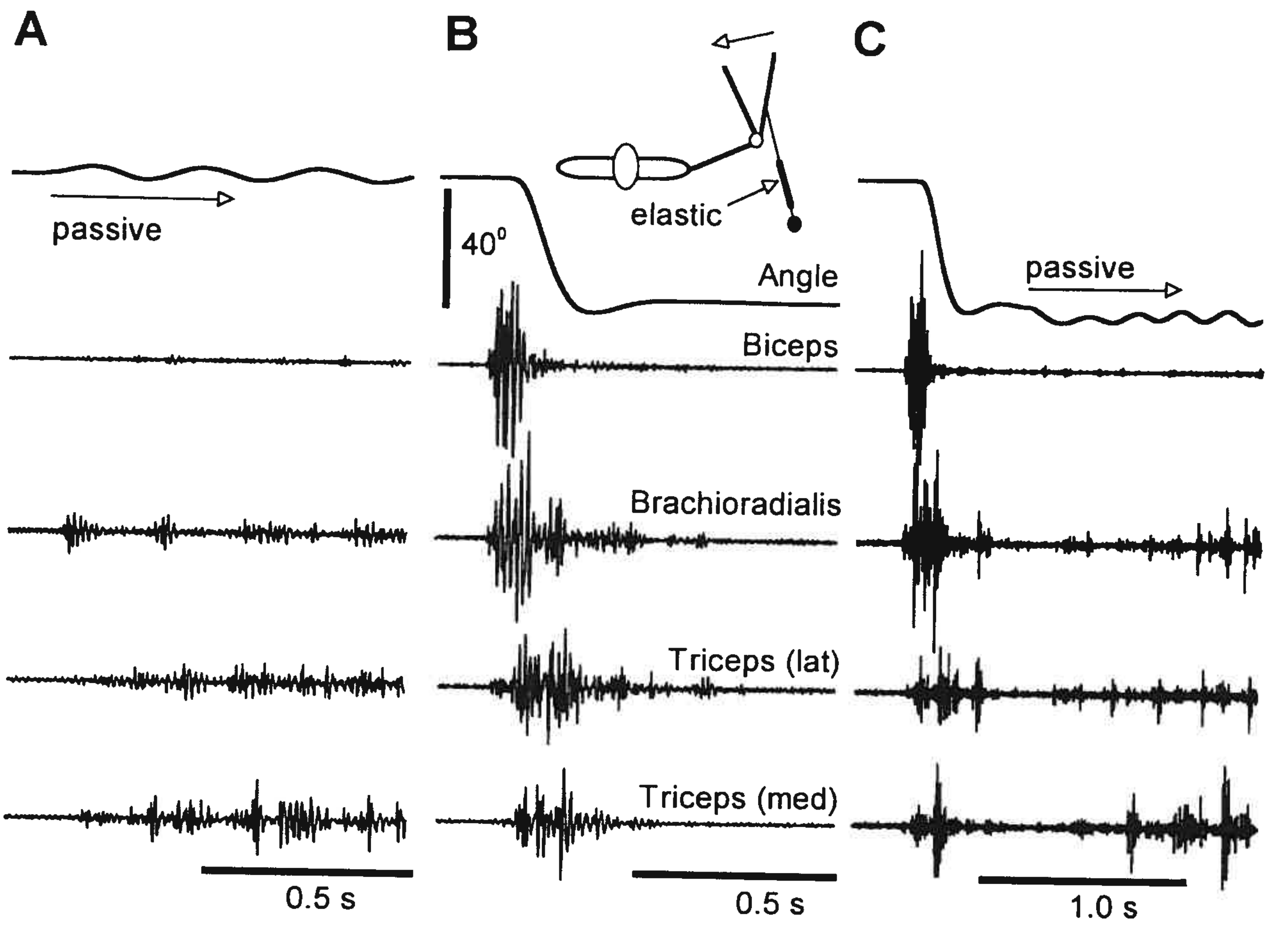

Fig. 1. (from Ostry and Feldman, 2003). Rapid elbow flexion movement (B) and reactions of muscles to passive oscillations at the initial (A) and final (C) positions. Note that the activity of elbow muscles (four lower traces in B) at the initial elbow position is practically zero (background noise level) and, after transient EMG bursts, returns to zero at the final position. Muscles are activated in response to passive oscillations of the arm at the initial (A) and final (C) positions. An elastic connector was used to compensate for the small passive torque of non-active flexor muscles at the initial position of about 140°. The compensation was unnecessary for the final position (about 90°) since it is known that at this position the torque of passive elbow muscles is zero.

1.6 Adaptation of movement to changing external forces (loads)

One of the objectives of the present study is to address the question of how arm movements adapt to different loads. In this connection, we briefly review appropriate studies.

A large number of studies have looked at the effect of changing external load conditions, in both statics and dynamics, to gain further insights on how the neuromuscular system responds to such changes. The authors then tried, with varying degrees of success, to explain these changes in the framework of different models for motor control. Single-joint movements have most often been used to study adaptation of movement to new load conditions because they are comparatively simpler to describe than multi-joint movements. With the advancement of technology came new and efficient tools for recording and analyzing motion, the focus of motor control studies was shifted to multi-joint movements, with the purpose of making the movements used in experimental settings more similar to actual movements performed by people in everyday life. Nevertheless, many conclusions derived from single-joint movements are applicable to multi-joint movements.

Single-joint movements were intensively analyzed by perturbation methods. Weeks et al. (1996) studied single-joint elbow movements that were unexpectedly perturbed by an external spring-like load in order to describe the process of rapid adaptation of elbow movements to changes in load condition. They used two different load conditions in three experiments: no load with opposing or assisting load only (two experiments) and no load with randomly varied opposing or assisting load (one experiment). Subjects were instructed to make corrections of the movement errors within the trial. A sudden change in the load indeed influenced the equilibrium state of the system, thus leading to a positional error. In trials in which a change in the load was made, movements were in error (94% of the first trials in new load conditions) and subjects were forced to make an additional movement to reach the target zone. Subjects quickly adapted to the new load so that the movement error was nullified within one or two trials with the new load. Weeks et al. (1996) explained the basic characteristics of adaptation using the theoretical framework of the λ model for motor control. By analyzing the patterns of movement errors, Weeks et al. concluded that two strategies were used by the nervous system in response to changes in the load. First, subjects might anticipate that the change in the load condition occurred only in the single trials and reproduced control variables that provided a movement without an error if the load condition returned after one trial (the *invariant strategy*). However since the load, once changed, was repeated in several subsequent trials, this strategy resulted in the repetition of the movement error. Second, subjects could anticipate that the new load would remain the same in the subsequent trials and reproduced the control variables that they specified at the end of the first trial with the new load, after they corrected for the movement error (*recurrent strategy*). Since the load was reproduced in several subsequent trials, this strategy was adequate, allowing subjects to make precise movement without corrections in these trials. However, when after several trials with the new load, the change in the load was reversed, the recurrent strategy resulted in a movement error again but in the opposite direction. Weeks et al. hypothesized that the recurrent strategy was predominantly used in the process of rapid adaptation to new load conditions and their results confirmed their explanations: In 63% of the cases, on the second trial of a block in the new load condition, the primary movement accurately reached the target, with no need for a secondary corrective movement.

Another study (Gribble and Ostry 2000) based on the λ model addressed the question of how the nervous system integrates the information about movement error caused by the presence of an external load into the control signals, to try to produce a correct movement in the following trials. These authors assumed that the changes in the control variables (shift in the equilibrium state) are proportional to the positional error. They then used the λ model, in which neither coordinate transformations (of positional error into required corrective forces) nor inverse dynamics calculations of muscle forces are necessary to achieve compensation for an external load during a pointing movement, to make movement simulations. Gribble and Ostry showed that the λ model, with its simple linear adaptation procedure, reproduces the experimental kinematics and changes in movement errors during learning in the presence of velocity-dependent force fields.

The adaptation of arm pointing movements to velocity-dependent, Coriolis force perturbation in a rotating room was analyzed by Lackner and Dizio (1994). Their results show that adaptation occurred within approximately 8 trials. Although these results are often quoted as conflicting with the equilibrium-point hypothesis (Gottlieb 1998), Feldman et al. (1998) reproduced the positional errors using the λ model for motor control and thus demonstrated that the claims of rejection were unfounded.

Shadmehr and Mussa-Ivaldi (1994) studied adaptation of pointing movement to another velocity-dependent force field created by torque motors. They found that adaptation occurred extremely slowly so that subjects restored accuracy after more than 250 trials. Based on their findings, they hypothesized that the nervous system gradually built a model of the force field, which was then used to make predictions and develop compensations for the forces present in the environment.

Conditt et al (1997) used force fields to investigate the learning mechanisms underlying motor adaptation of arm movements. They considered two alternative learning hypotheses, both leading to adaptation of the movement to the new load condition. One hypothesis states that adaptation occurs through learning of a correlation between the various states (positions and velocities) the arm goes through during movement and the forces experienced in these states. The alternative hypothesis explains adaptation to a new load through memorization of the sequence in time of the forces experienced along specific trajectories. In the first learning hypothesis, subjects develop a model of the dynamics of their environment. In the second, adaptation is a form of "rote learning". Their findings support the first hypothesis and do not seem to be compatible with the second. In addition, they observed that adaptation of movement to changes in load seems to occur independently of the movements made during the adaptation process.

Scheidt (2000) and his colleagues had subjects perform two-joint, target-directed movements of the arm while holding a handle linked to a two-joint robotic manipulator, which generated a viscous force perpendicular to the movement trajectory, in order to study the stability of changes in motor performance that are associated with adaptation to new load conditions. Their results show that adaptation requires fewer trials when the information on kinematic errors was available. They concluded that the role of kinematic and dynamic factors should be taken into account in modelling motor adaptation.

Simmons and Richardson (1984) compared the effectiveness of two motor control models, the equilibrium point hypothesis and the mass spring model, to explain positioning accuracy during spring loaded, rapid, bi-articular movements. The mass-spring model predicts that movement positioning is under a direct control system. The equilibrium point hypothesis, on the other hand, explains adaptation of movement to new loads through an interaction between afferent and efferent information. They observed that positioning accuracy and applied force varied with increases in load, and thus suggested that the original efferent commands were modified by afferent information during the movement, which is a prediction of the equilibrium point hypothesis.

The study of Karniel and Mussa-Ivaldi (2002) followed in the footsteps of previous studies which have shown that subjects develop a representation of the relationship between the state of motion of the arm and the force applied to it in the process of adapting to new loads during movement. Their experimental procedure was designed to test the ability of the nervous system to build an internal representation for two different force fields and then to switch between them accordingly during an experiment in which they alternated. Their results show that even after training in both fields separately, subjects failed to show signs of improved performance when presented with the sequence of alternating fields. Based on this observation, they hypothesized that when it has to deal with different perturbations presented in a sequence, the central nervous system shows a tendency to use a single internal model.

In conclusion, we have considered the capacity of different theories of motor control to solve the redundancy problems and the posture-movement paradox as described by Von Holst and Mittelstaedt (1950/1970). We also reviewed literature on adaptation of movements to changing load conditions. The λ model seems the only model able to solve the posture-movement paradox in a physiologically realistic way. However, further testing is necessary to choose between alternative theories of motor control. In addition, although Gribble and Ostry (2000) used the λ model to simulate adaptation of movements to different force fields, additional, preferably empirical testing of the capacity of this model to explain adaptation of arm movements to different load conditions seems necessary. The objectives of the present study (see above) were motivated by the necessity to address these issues.

CHAPTER II

2.0 Methods

2.1 Subjects

Sixteen healthy right-handed subjects (7 males and 9 females, age 24.6 ± 7.4 years) participated in the study after signing an informed consent approved by the Ethics Committee of the Institute of Rehabilitation of Montreal. Subjects were tested in 4 different experiments (see below). Thirteen subjects participated in the basic, first experiment and five subjects in experiment 2 (two from the first group and three new subjects). Five subjects (previously tested in experiments 1 or 2 or both) also participated in experiments 3 and 4.

2.2 Experimental set-up and procedures

Subjects sat in a height-adjustable chair with a back support. The right wrist and the distal 1/3 of the forearm were placed in a plastic cast attached to the vertical handle of a double-joint manipulandum so that the wrist and forearm were in their neutral position. The height of the chair was adjusted so that the handle was at the level of the shoulder. The subject's arm moved in the horizontal plane, and movements were produced by changes in elbow and shoulder angles.

Torques could be produced independently at each joint of the manipulandum by two torque motors. A software program reduced the effects of inertia of the manipulandum on the arm movements. Specifically, positive feedback was introduced in the torque output, based on the instantaneous acceleration (recorded directly with 2 accelerometers) and the moments of inertia of the distal and proximal segments of the manipulandum. The feedback factor was determined by trial and error, in order to reduce the inertia without introducing oscillations of the manipulandum, and was the same for all subjects. The moment of inertia of the manipulandum was measured by computing the changes in the angular velocity of each of its segments in response to a torque pulse. This measurement was made before and after introducing acceleration feedback. The moment of inertia was reduced from 0.209 to 0.120 kg m^2 (reduction of 62%) for the proximal limb of the manipulandum, and from 0.038 to 0.031 kg m^2 (reduction of 18%) for the distal limb.

Subjects were asked to bring the handle to the initial position (about 30 cm in front of their sternum, with about 80° of shoulder abduction, 67° of shoulder horizontal adduction, and 74° of elbow flexion). The initial target position was represented by a filled circle (diameter: 2 cm) on a computer display facing the subject. The handle position was represented by a cursor on the same display. To reach the initial hand position, subjects had to bring the cursor into the target zone. The final target was located at a distance of 30 cm from the initial target in the ipsilateral workspace, at an angle of 22.2° ± 5.02 from the frontal plane of the subject (Fig. 2 A). This angle was chosen to allow comfortable movements for the subjects, while keeping them facing the computer display to see the targets. The acceptable reaching zone was a circle of 3 cm in diameter. Subjects received visual feedback of the handle position (on and off the display) and final target throughout each trial. To minimize the role of fatigue in the experiment, subjects were asked from time to time whether they felt fatigue and could rest for 2 to 5 min upon request.

To initiate a trial, the subject had to bring the cursor representing the handle position into the initial target zone and hold it there for 2 s. Then, the initial target disappeared and the final target appeared, signalling to the subject to move the handle to the latter. In each trial, subjects were instructed to make a fast continuous movement of the handle to the final target. Two instructions were used in 4 experiments. In experiments 1 and 2 (that differed in terms of load directions, see below), subjects were asked to quickly move the handle to the target and keep it motionless until the end of the trial (3 s), even if the movement was in error. In other words, subjects were asked not to correct movement errors within each trial. They thus could only modify control variables between trials to improve movement precision. The same load directions were used in experiments 3 and 4, where subjects were instructed to correct movement errors within each trial as soon as possible.

In terms of load conditions, trials in each experiment were organized in blocks, each consisting of 5-10 trials, with the specific number of trials chosen randomly for each block. The load condition was the same within each block, but changed in sequential blocks from a no load to a load condition and vice-versa, until 10 blocks in each condition were completed (20 blocks in total for each experiment). To discourage subjects from making predictions about the upcoming load condition, they were informed that changes in the load condition would be made in randomly selected trials. The load was generated by the torque motors of the manipulandum and acted on the handle in the sagittal direction, perpendicular to the line joining the initial and the final targets, towards the subject in experiments 1 and 3 and away from the subject in experiments 2 and 4. Thus, the loads acted approximately perpendicular to the movement trajectory and in one of two possible directions (towards or away from the subject) in each experiment. More specifically, the load acted towards the subject in experiments 1 and 3 and away from them in experiments 2 and 4. In the blocks of trials in which the load was applied, the load force was initiated as soon as the handle left the initial target zone and increased linearly with the radial distance from the initial target to the current position of the handle (spring-like load). At the final target position, the force was 30% (range of 19 –59 N) of each subject's maximal voluntary contraction (MVC), measured prior to the experiment (the value of maximal force applied to the handle during 3 s). The subject's position for the performance of the MVC was the same as the initial position in the experiments described above, except that they grasped the handle of a force transducer attached to a wall. The subject produced a maximal isometric contraction by pulling on the handle as hard as possible, as if trying to bring it to a target located on the right, in a direction that was similar to that in the experiments. The load magnitude was chosen because it was used in a previous experiment done with the double-joint manipulandum and was deemed to produce changes in positions that were significant (Archambault, 1999).

Before the experiment began, subjects practised to make movements to the final target, in separate trials with and without the load, i.e., without alternations between the load conditions. Subjects were trained until they were able to make fast (hand speed greater than 1 m/s) uncorrected movements to the final target in 5 consecutive trials (less than 15 trials in total). After that, movements in 10 consecutive trials (control) were recorded.

2.3 Data Recording and Analysis

A PC was used to control the experiments with a customized program developed in LabView software (Version 5.1, National Instruments, Texas). Experimental data were recorded for 3 s, starting 0.5 s before the signal to move. The arm position was recorded with a system for

3D analysis of movement (Optotrak, 3 cameras, sampling rate 200 Hz) that determined the coordinates of 4 infrared-emitting markers placed on the right elbow (lateral epicondyle of the humerus), both shoulders (acromion processes) and handle. Two axial resolvers measured the angular position and velocity of each joint of the manipulandum. Torques were recorded using axial strain gauges. From the basic geometry of the arm-manipulandum system, kinematic and kinetic data were used to calculate the position and velocity of the handle in Cartesian space, as well as the force applied at the level of the handle after the end of movements.

The elbow angle was calculated using the dot product of two vectors, one formed by the handle and elbow markers, and the other by the right shoulder and elbow markers. Shoulder horizontal abduction angle was obtained likewise, using the horizontal components of the vectors composed of the right shoulder and elbow markers, and the left and right shoulder markers. For the elbow, 180° corresponded to full extension, so that the elbow angle decreased with flexion. For the shoulder, 0° indicated the arm position when the upper arm was in line with the two shoulder markers, so that the angle increased with horizontal adduction (Fig. 2 A).

In experiments 1 and 2, trials in which subjects, contrary to instruction, made movement corrections, were visually identified based on the presence of easily recognizable deviations (inflection points) in the velocity-position diagrams (called phase diagrams; Fig. 2 C) and were excluded from further analysis (on average 4 trials/subject or 2.9% of all trials). Phase diagrams were also used in the analysis of experiments 3 and 4, in which the instruction was to correct movement errors, to identify the number of trials needed for adaptation after a change in load occurred. The first trial in which the target was reached by a single movement without corrections was considered as the sign that movements became adapted to the new load condition.

In experiments 1 and 2 (instruction do not correct movement errors) we recorded, in all 16 subjects, EMG activity of 7 muscles of the arm and trunk using silver-plated bipolar surface electrodes (diameter 1 cm; 2-3 cm apart) on the following muscles of the right side of the body: brachioradialis (BR), biceps (BB), triceps (TB), anterior (DA) and posterior (DP) deltoid, clavicular portion of pectoralis major (PM), teres major (TM). Electrodes were placed on the muscle bellies previously cleaned with alcohol to reduce skin resistance and thus maximize the signal-to-noise ratio. EMG signals were amplified using a multi-channel electromyograph (Grass company), filtered at 5-500 Hz and digitized at 1500 Hz. They were then filtered off-line using a 55-500 Hz third-order Butterworth filter to remove motion artefacts. We used a custom-built program with Labview 5.1 software to analyze EMG signals. For analysis, we selected to use the averaged EMG activity over the last 200 ms of the trial to ensure that the movement would be over and hence that the subject would have reached a steady-state posture.

CHAPTER III

3.0 Article (will be submitted to Journal of Physiology (London))

Control of adaptation to load in point-to-point arm movements

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Running head: Adaptation to loads

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Acknowledgements: We thank Mindy Levin and Philippe Archambault for comments. Supported by FRNTQ Quebec, CIHR and NSERC (Canada).

3.1 Abstract

Simulations of arm reaching movements using the hypothesis that the nervous system's control levels specify the electromyographic signals (EMG) and forces required for voluntary movements suggest that postures are encoded by tonic EMG signals. Such coding is negated in the λ model for motor control, where active movements occur by shifting the spatial coordinates of the muscles' activation threshold. We tested the ability of these alternative hypotheses to describe steady-state EMG of arm muscles at different final postures during adaptation of arm reaching movements to different loads.

Sitting subjects (n=16) grasped the handle of a double-joint manipulandum and made fast hand movements from an initial position to a target 30 cm from the initial position in the ipsilateral arm workspace. Adaptation to 2 loads of opposed directions acting about perpendicularly to the movement trajectory was tested under 2 instructions: correct or do not to correct movement errors in-trial (4 experiments). The 2 load conditions (zero and non-zero) were presented alternatively for 20 blocks containing between 5 and 10 trials. Kinematics, torques and EMG of 7 muscles were recorded.

Subjects adapted significantly faster to a change in load condition when allowed to correct movement errors on-line. For either instruction, adaptation to a given load condition did not occur faster as the experiment progressed. Different steady-state arm configurations belong to zero (R-postures) and non-zero loads (Q-postures). No significant relationship was found between R-posture tonic EMG levels and position, conflicting with the force control hypotheses, but not with the threshold control theories.

Key words: motor control, force control theories, posture-movement problem, threshold control, motor memory.

3.2 Introduction

It is often assumed that control levels of the nervous system directly calculate and program EMG signals and forces required for the production of voluntary movements. These calculations are based on neural inverse and forward imitations ("internal models") of the system's dynamics interacting with the environment (Hollerbach 1982; for recent review see Ostry and Feldman 2003). This theory has been successful in explaining the evolution of hand trajectories and velocity profiles in pointing movements during adaptation to different force fields (e.g., Kawato 1999). Basic aspects of arm movement production and adaptation to force fields have also been simulated in the λ model for motor control not relying on the idea of EMG-force programming and internal models (Gribble et al. 1998; Gribble and Ostry 1998, 2000). A major feature of this model is the notion of threshold control, implying that the nervous system guides active movements by resetting the position of the body (or its segments) at which muscles reach their activation thresholds (Feldman and Levin 1995).

To resolve the controversy in the understanding of basic principles underlying motor control, one needs to experimentally test predictions resulting in particular from the differences in the ways the two theories account for the relationship between posture and movement. Ostry and Feldman (2003) identified that force control models that integrate basic properties of muscles and reflexes (Schweighofer et al. 1998; Bhushan and Shadmehr 1999) predict that in order to bring the arm to a new posture, neural control levels should compute and specify not only phasic EMG bursts of activity to accelerate and then decelerate the movement but also an additional, tonic component of EMG activity to hold the arm at the final position. A similar combination of EMG signals has been proposed in the pulse-step model of saccadic eye movements during shifts in the gaze (Robinson 1970). In arm movements, an additional, tonic EMG component is necessary to overcome the resistance of posture-stabilizing mechanisms to the deviation of the arm from the initial position when the arm moves away from it. Otherwise, posture-stabilizing mechanisms would drive the arm back to the initial position as soon as the generation of phasic EMG bursts and forces has been completed. This implies that the tonic levels of activity of muscles cannot be the same at two different arm positions when the net joint torques are zero at these positions.

In contrast, the notion of threshold control implies that control levels are not involved in EMG and force specification. Instead, they elicit movements by shifting the activation thresholds of muscles to a new position of the arm. In this case, the posture-stabilizing mechanisms are re-addressed to the new posture ("postural resetting") so that no resistance to the deviation of the arm from the initial position is generated. Instead, with resetting of muscle activation thresholds, the initial position of the arm appears as a deviation from the newly specified threshold position. The same posture-stabilizing mechanisms that would resist the deviation of the arm from the initial position will now generate the EMG activity and forces driving the arm to the new position. In other words, by shifting muscle activation thresholds, the nervous system not only prevents resistance of posture-stabilizing mechanisms to movement from the initial posture, but also takes advantage of these mechanisms to drive the arm to a new posture. By using threshold control, central levels do not need to provide a position-dependent specification of EMG signals so that the tonic levels of EMG activity at different arm postures may be equal, unless there is a difference in the external torques that muscles have to counteract at these postures.

Thus, the two theories of motor control make conflicting predictions on how postures are specified. The force control hypothesis suggests that postures are coded by tonic levels of EMG activity, whereas the threshold control hypothesis suggests instead that changes in arm posture emerge following shifts in the muscle activation thresholds. The purpose of this study was to resolve this controversy by comparing the tonic activity of arm muscles at different postures specified in a functional task. Testing was accomplished for a set of arm postures specified during adaptation of posture-to-posture arm movements to different load conditions. Thus, the theory that survived the test was additionally challenged by the necessity to explain the major characteristics of adaptation. To meet these objectives, we used the method employed by Weeks et al. (1996) in which the load applied to the arm during reaching movements changed after each block of 5-10 trials. This paradigm was applied not to single-joint movements (as was the case in the study by Weeks et al.), but to double-joint pointing movements and was complemented by the analysis of EMG signals of multiple arm muscles at different steady state postures. The results have been reported in abstract form (Foisy et al. 2002).

3.3 Methods

3.3.1 Subjects

Sixteen healthy right-handed subjects (7 males and 9 females, age 24.6 ± 7.4 years) participated in the study after signing an informed consent approved by the Ethics Committee of the Institute of Rehabilitation of Montreal. Subjects were tested in 4 different experiments (see below). Thirteen subjects participated in the basic, first experiment and five subjects in experiment 2 (two from the first group and three new subjects). Five subjects (previously tested in experiments 1 or 2 or both) also participated in experiments 3 and 4. Because of time constraints, only 6 of the 16 subjects tested in experiments 1 and 2 agreed to return to be tested for experiments 3 and 4.

3.3.2 Experimental set-up and procedures

Subjects sat in a height-adjustable chair with a back support. The right wrist and the distal 1/3 of the forearm were placed in a plastic cast attached to the vertical handle of a double-joint manipulandum so that the wrist and forearm were in their neutral position. The handle was at the level of the shoulder so that the subject's arm moved in the horizontal plane and movements were produced by changes in elbow and shoulder angles.

Torques could be produced independently at each joint of the manipulandum by two torque motors. A software program reduced the effects of inertia of the manipulandum on the arm movements. Specifically, positive feedback was introduced in the torque output, based on the instantaneous acceleration (recorded directly with 2 accelerometers) and the movements of inertia of the distal and proximal segments of the manipulandum. The feedback factor was selected by trial and error, in order to reduce the inertia without introducing oscillations of the manipulandum. The moment of inertia of the manipulandum was measured by computing the changes in the angular velocity of each of its segments in response to a torque pulse. This measurement was made before and after introducing acceleration feedback. The moment of inertia was reduced from 0.209 to 0.120 kg m^2 (reduction of 62%) for the proximal limb of the manipulandum, and from 0.038 to 0.031 kg m^2 (reduction of 18%) for the distal limb.

Subjects were asked to bring the handle to the initial position: about 30 cm in front of their sternum, with about 90° of shoulder abduction, 45° of shoulder horizontal adduction, and 90° of elbow flexion (see figure 2A). A filled circle (diameter 2 cm) on a computer display facing the subject represented the initial target position. The handle position was represented by a cursor on the same display. To reach the initial hand position, subjects had to bring the cursor into the target zone. The final target was located at a distance of 30 cm from the initial target in the ipsilateral workspace, at an angle of $22.2^{\circ} \pm 5.02$ to the frontal plane of the subject (Fig. 2 A). This angle was chosen to make movements comfortable for subjects while keeping them facing the computer display to see the targets. The acceptable reaching zone was a circle of 3 cm in diameter. Subjects received visual feedback of the handle position (on and off the display) and final target throughout each trial. To minimize the role of fatigue in the experiment, subjects were asked from time to time whether they felt fatigue and could rest for 2 to 5 min upon request.

To initiate a trial, the subject had to bring the cursor representing the handle position into the initial target zone and hold it there for 2 s. Then, the initial target disappeared and the final target appeared, signalling to the subject to move the handle to the latter. In each trial, subjects were instructed to make a fast continuous movement of the handle to the new target. Two instructions were used in 4 experiments. In experiments 1 and 2 (that differed in terms of load directions, see below), subjects were asked to quickly move the handle to the target and keep it motionless until the end of the trial (3 s), even if the movement was in error. In other words, subjects were asked not to correct movement errors within each trial. They thus could only modify control variables between trials to improve movement precision. The same load directions were used in experiments 3 and 4, where subjects were instructed to correct movement errors within each trial as soon as possible.

In terms of load conditions, trials in each experiment were organized in blocks, each consisting of 5-10 trials, with the specific number of trials chosen randomly for each block. The load condition was the same within each block, but changed in sequential blocks from a no load to a load condition and vice-versa, until 10 blocks in each condition were completed (20 blocks in total for each experiment). To discourage subjects from making predictions about the upcoming load condition, they were informed that changes in the load condition would be made in randomly selected trials. The load was generated by the torque motors of the manipulandum and acted on the handle in the sagittal direction, perpendicular to the line joining the initial and the final targets, towards the subject in experiments 1 and 3 and away from the subject in experiments 2 and 4. Thus, the loads acted approximately perpendicular to the movement trajectory but in opposite directions in sequential experiments 1 and 2 or 3 and 4. In the blocks of trials in which the load was applied, the load force was initiated as soon as the handle left the

Figure 2

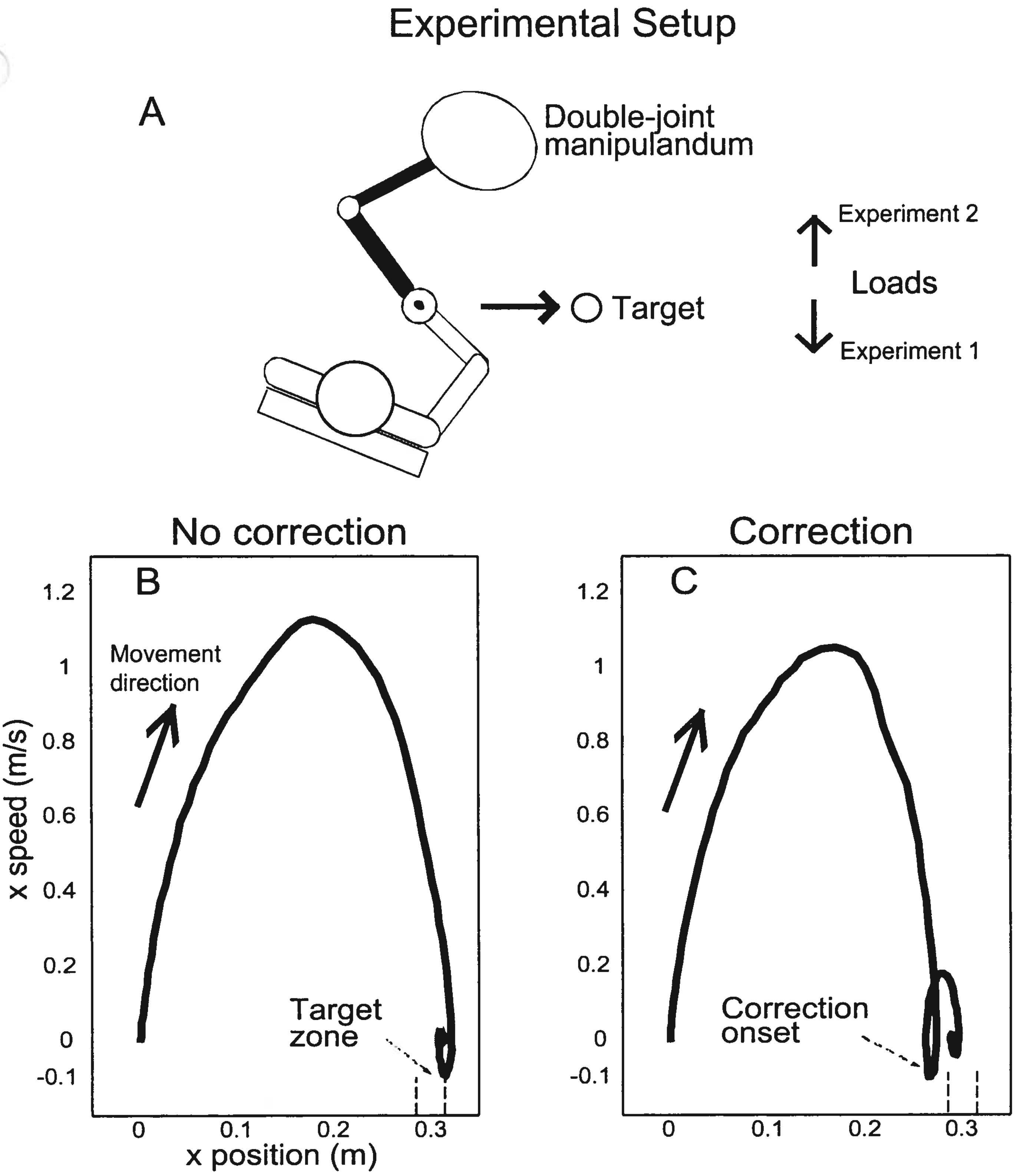


Fig. 1. Experimental setup (A) and typical position-velocity profiles (phase diagrams) from trials in which the rget zone was reached after a single arm movement without corrections (B) or after a small correction that the subject made despite the instruction not to correct errors within trials. No load was applied in B and C.

initial target zone and increased in proportion to the radial distance from the initial target to the current position of the handle (spring-like load). At the final target position, the force was 30% (range of 19 –59 N) of each subject's maximal voluntary contraction (MVC), measured prior to the experiment (the value of maximal force applied to the handle during 3 s). The subject's position for the performance of the MVC was the same as the initial position in the experiments described above, except that they grasped the handle of a force transducer attached to a wall. The subject produced a maximal isometric contraction by pulling on the handle as hard as possible as if trying to bring it to a target located on the right, in a direction that was similar to that in the experiments.

Before the experiment began, subjects practised to make movements to the final target, in separate trials with and without the load, i.e., without alternations between the load conditions. Subjects were trained until they were able to make fast (hand speed greater than 1 m/s) uncorrected movements to the final target in 5 consecutive trials (less than 15 trials in total). After that, movements in 10 consecutive trials (control) were recorded.

3.3.3 Data Recording and Analysis

A PC was used to control the experiments with a customized program developed in LabView software (Version 5.1, National Instruments, Texas). Experimental data were recorded for 3 s, starting 0.5 s before the signal to move. The arm position was recorded with a system for 3D analysis of movement (Optotrak, 3 cameras, sampling rate 200 Hz) that determined the coordinates of 4 infrared emitting markers placed on the right elbow (lateral epicondyle of the humerus), both shoulders (acromion processes) and handle. Two axial resolvers measured the angular position and velocity of each joint of the manipulandum. Torques were recorded using axial strain gauges. From the basic geometry of the arm-manipulandum system, kinematic and kinetic data were used to calculate the position and velocity of the handle in Cartesian space, as well as the force applied at the level of the handle after the end of movements.

The elbow angle was calculated using the dot product of two vectors, one formed by the handle and elbow markers, and the other by the right shoulder and elbow markers. Shoulder horizontal abduction angle was obtained likewise, using the horizontal components of the vectors composed of the right shoulder and elbow markers, and the left and right shoulder markers. For the elbow, 180° corresponded to full extension, so that the elbow angle decreased with flexion. For the shoulder, 0° indicated the arm position when the upper arm was in line with the two shoulder markers, so that the angle increased with horizontal adduction (Fig. 2 A).

In experiments 1 and 2, trials in which subjects, contrary to instruction, made movement corrections were visually identified based on the presence of easily recognizable deviations (inflection points) in the velocity-position diagrams (called phase diagrams; Fig. 2 B and C) and were excluded from further analysis (about 4 trials/subject or 2.9% of all trials). Phase diagrams were also used, in addition to velocity and trajectory graphs, in the analysis of experiments 3 and 4 in which the instruction was to correct movement errors to identify the number of trials needed for adaptation after a change in load occurred. The first trial in which the target was reached by a single movement without corrections was considered as the sign that movements became adapted to the new load condition.

In experiments 1 and 2 (instruction do not correct movement errors) we recorded, in all 16 subjects, EMG activity of 7 muscles of the arm and trunk using silver-plated bipolar surface electrodes (diameter 1 cm; 2-3 cm apart) on the following muscles of the right side of the body: brachioradialis (BR), biceps (BB), triceps (TB), anterior (DA) and posterior (DP) deltoid, clavicular portion of pectoralis major (PM), and teres major (TM). Electrodes were placed on the muscle bellies previously cleaned with alcohol to reduce skin resistance and thus maximize the signal-to-noise ratio. EMG signals were amplified using a multi-channel electromyograph (Grass company), filtered at 5-500 Hz and digitized at 1500 Hz. They were then filtered off-line using a 55-500 Hz third-order Butterworth filter to remove motion artefacts. We used a custom-built program with Labview 5.1 software to analyze EMG signals. For analysis, we selected to use the averaged EMG activity over the last 200 ms of the trial to ensure that the movement would be over and hence that the subject would have reached a steady-state posture. The analysis of tonic EMG activity levels was done for all final steady state postures, separately for each experiment. To determine whether the mean steady-state EMG values for each muscle were different for the different postures observed, we used a statistical analysis software (Statistica v. 5.0) and made paired t-tests for each muscle to determine statistical significance in EMG activity between the postures compared.

3.4 Results

3.4.1 Instruction do not correct positional errors

3.4.1.1 Movement errors and their corrections

The instruction "do not correct" required subjects to abstain from correcting movement errors within each trial but left the possibility of improving the movement precision in the subsequent trials. After adaptation to a specific load condition, subjects were able to produce a single hand movement (peak velocity about 1 m/s) to bring the hand to the target zone, typically after a small terminal overshoot (Fig. 2 B). Occasionally, subjects corrected movements within the same trial when the hand approached or had reached the final position. These corrections were visually identified by the presence of additional loops in the phase diagrams (Fig. 2 C, arrow). Trials in which a corrective movement was made were excluded from further analysis (see Methods).

When the load was changed in a trial, the hand always arrived at a position outside the target zone in all subjects (Figs. 3 and 4). Positional errors sometimes occurred along the x or y axis alone, or in both axes simultaneously (Fig. 3). This occurred whether the load was suddenly added after adaptation of movements to the no-load condition in the preceding block of trials (Fig. 4, pluses) or removed after adaptation to the load in the preceding block of trials (Fig. 4 open circles). Specifically, when the load acting towards the subject was introduced, the final hand position was deviated on average, across all subjects, by 4.4 cm in the x (frontal) direction and by - 4.2 cm in the y (sagittal) direction (total distance –6.1 cm). For clarity and brevity, we determined that the y coordinate of movements ending "below" the target (closer to the subject) would be negative and that those ending "above" it would be positive. For the x axis, final positions to the left of the target were attributed a negative value, and positive values where given to those that were to the right of the target. Upon removal of that load after adaptation, the final hand position deviated on average by –3.5 cm and 2.7 cm in the x and y directions (total distance 4,4 cm), respectively. These data and Fig. 4 show that the two clusters of points identifying the final hand positions in the first trials in the new load condition were located on opposite sides of the target zone in which hand movements adapted to no-load or load conditions terminated. In other words, there were 3 spatially separate clusters of points characterizing final hand positions, as was statistically confirmed for each subject and experiment using 1-way ANOVA fixed effect and the HSD post-hoc test ($p<0.001$). In addition, the points characterizing the final positions grouped along a diagonal line crossing the target zone in a sagittal-frontal direction (Fig. 4 A). Thus, the direction of the deviation of the hand resulting from the changes in the load condition substantially differed from the sagittal direction of the load. When the load direction was reversed, the signs of the positional errors occurring in the first trials were inverted as well (compare final hand positions in Fig. 4, A and B). The final hand position deviated on average by -2.8 cm in the x direction and 2.7 cm in the y direction when the load acting away from the subjects (Fig. 4B) was added (total distance: 3.9 cm) and, respectively, by 4.7 and -4.2 cm when it was removed (total distance: 6.3 cm). Despite the change in the load direction, the final hand positions remained grouped along a diagonal line (Fig. 4, compare A and B).

The final positions of the hand for each of the postures observed experimentally in each of experiments 1 and 2 were statistically (see Results) different (Fig. 4). Joint torque values and the

Table 1

Examples of mean forces (N) applied at the handle and torques (Nm) at the shoulder and elbow joints for Q postures in experiments 1 and 2.

A

		Force at the handle (N)		
	Subject	10	11	12
	Postures			
Load towards subject (experiment 1)	Q-	18.72	20.62	25.05
	Qo	19.06	21.04	22.03
		1	2	5
Load away from subject (experiment 2)	Q+	-15.39	-17.37	-16.50
	Qo	-19.44	-17.86	-18.55

B

		Joint torques (shoulder, elbow)		
	Subject	10	11	12
	Postures			
Load towards subject (experiment 1)	Q-	2.02, -2.67	2.62, -0.09	6.67, -2.81
	Qo	5.65, -2.24	2.39, 0.23	5.71, -1.97
		1	2	5
Load away from subject (experiment 2)	Q+	-4.92, 2.25	-5.04, 1.67	-4.60, 2.55
	Qo	-5.87, 1.76	-5.121, 1.41	-5.32, 3.33

Figure 3

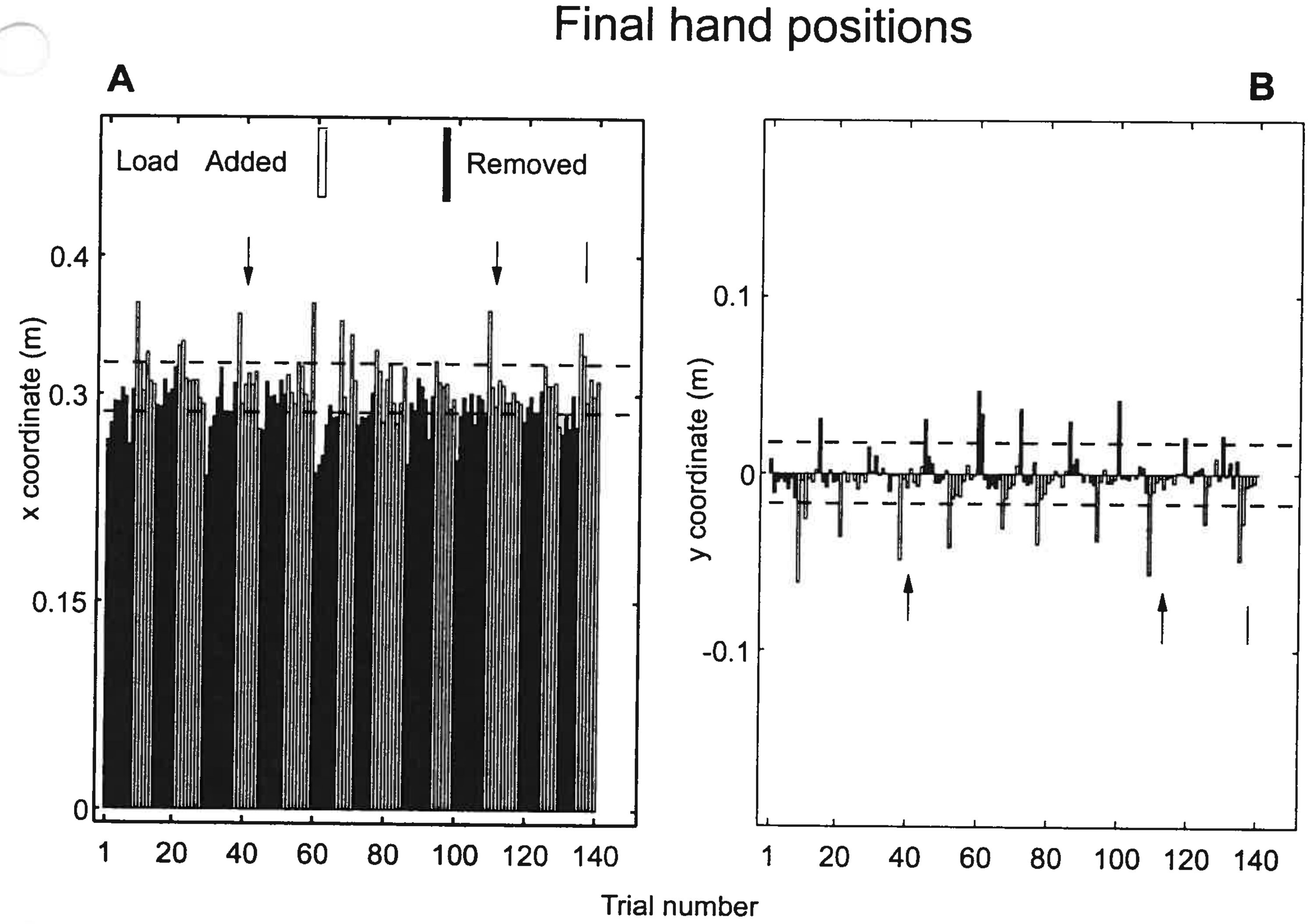


Fig. 3. Final positions of the hand in sequential blocks of trials in which the load was added (open bars) or removed (black bars). Dashed horizontal lines mark the target zone; x - frontal (A) and y - sagittal (B) coordinates of final hand positions. Data are from experiment 1 (the load direction towards the subject; instruction: do not correct errors within trials). The arrows indicate examples of trials where a change in load caused an error in both x and y coordinates. The bars indicate an example of a block of trials in which adaptation occured gradually.

Figure 4

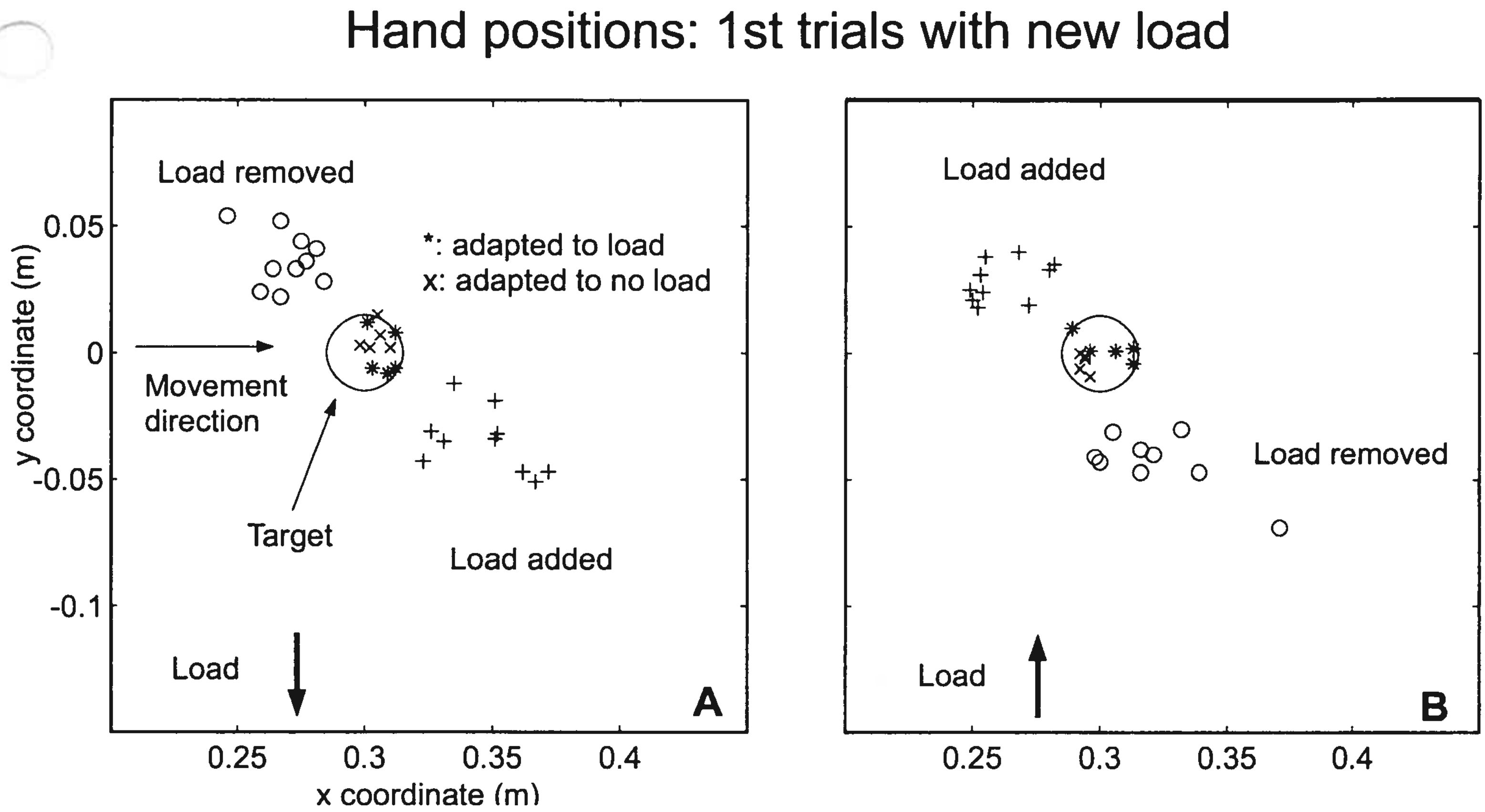


Fig. 4. Final hand positions in the arm workspace in the first trials (symbols + and o) in which a load was introduced after previous adaptation of movements to no-load condition or vice versa. Note that, in these trials, the hand reached a position that was outside of the target zone (movement errors). Movements adapted to a load condition terminated inside the target zone (symbols * and x). Data from experiments 1 (A) and 2 (B) in which the load directions (vertical arrows) were different but the instruction was the same (do not correct movement errors within trials); x, y: frontal and sagittal coordinates of final hand positions, respectively.

force applied at the handle by the subject were also different between the load and no load conditions, but similar amongst the same load condition (Table 1). On the other hand, the velocity profiles of the movements ending at these various postures showed very similar curves, except for the R posture obtained upon removal of the load, which occasionally presented with a slightly lower peak velocity (Fig. 5 B, dashed line).

Once changed in a trial, the load condition was repeated in the 5-10 subsequent trials (see Methods), so subjects had the opportunity to adapt to this condition and thus restore movement accuracy. In the new load condition, subjects could restore accuracy after only one trial (e.g., Fig. 3, arrows) or after several trials (e.g., Fig. 3, line). In most cases, accuracy was restored gradually by diminishing the distance to the target zone in several sequential trials (Fig. 6). The improvement in accuracy was accomplished by a simultaneous modification of the frontal (x) and sagittal (y) coordinates of the hand so that the points representing the final hand positions in sequential trials shifted obliquely towards the target (Fig. 6 A, C, D). Occasionally, only one coordinate was modified (Fig. 6 B, trial 2, and C, trial 3).

The mean numbers of trials required for restoring movement precision after each change in the load condition are shown in Fig. 7 A-F (instruction "do not correct"). When the load acting towards the subject was applied, the subject whose data are shown in Fig. 7 A and B restored movement precision after 1, 2, 3 or more trials with about the same probability: 20-30%. However, this subject adapted to the no-load condition after making movements with the load (B) in fewer trials, (after one trial in 70% of cases). For the group of subjects who had the load acting towards them (n= 13), the adaptation was accomplished after one trial in 41.54% of trials when the load was introduced (Fig. 7 C) and in 58.27% of cases when the load was removed (Fig. 7 D).

Figure 5

Sample end-point trajectory and velocity profile
for each of the 4 conditions in experiment 1.

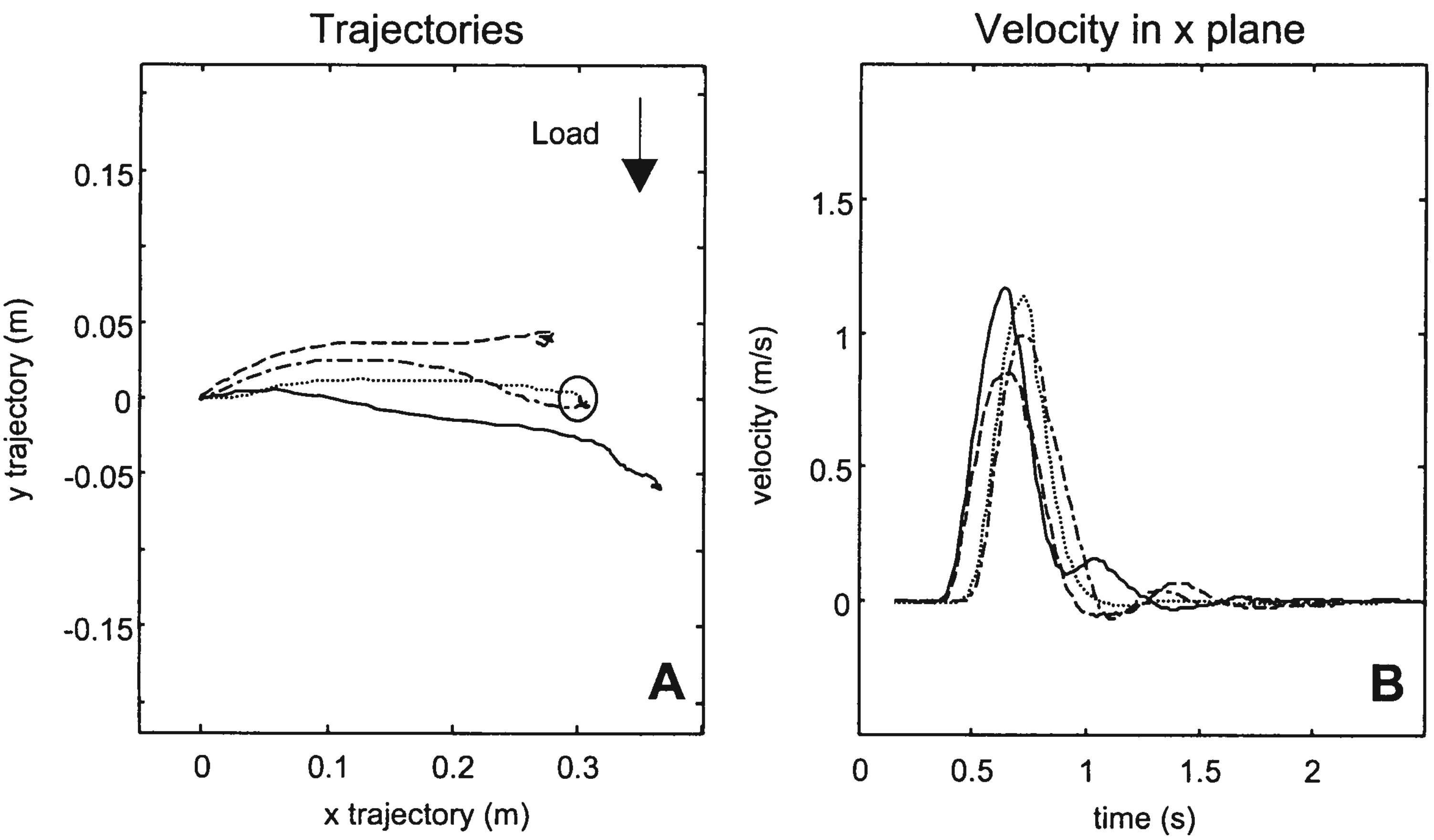


Fig. 5. End-point trajectory (A) and velocity profiles (B) for a sample trial in each of the four conditions for experiment 1 (load towards subject). When the load is added (solid line) the movement ends more towards the subject and slightly past the target. Upon removal of that load, an error in the opposite direction occurs, with the movement ending slightly before the target and farther up from it (dashed line). Adapted movements with (dash-dot line) and without load (dotted line) both end within the target zone, but each has a slightly different trajectory, possibly due to the load condition. The velocity profiles were similar for all conditions, except for the load removed movements which, on occasion, presented a slightly lower peak velocity (B, dashed line).

Figure 6

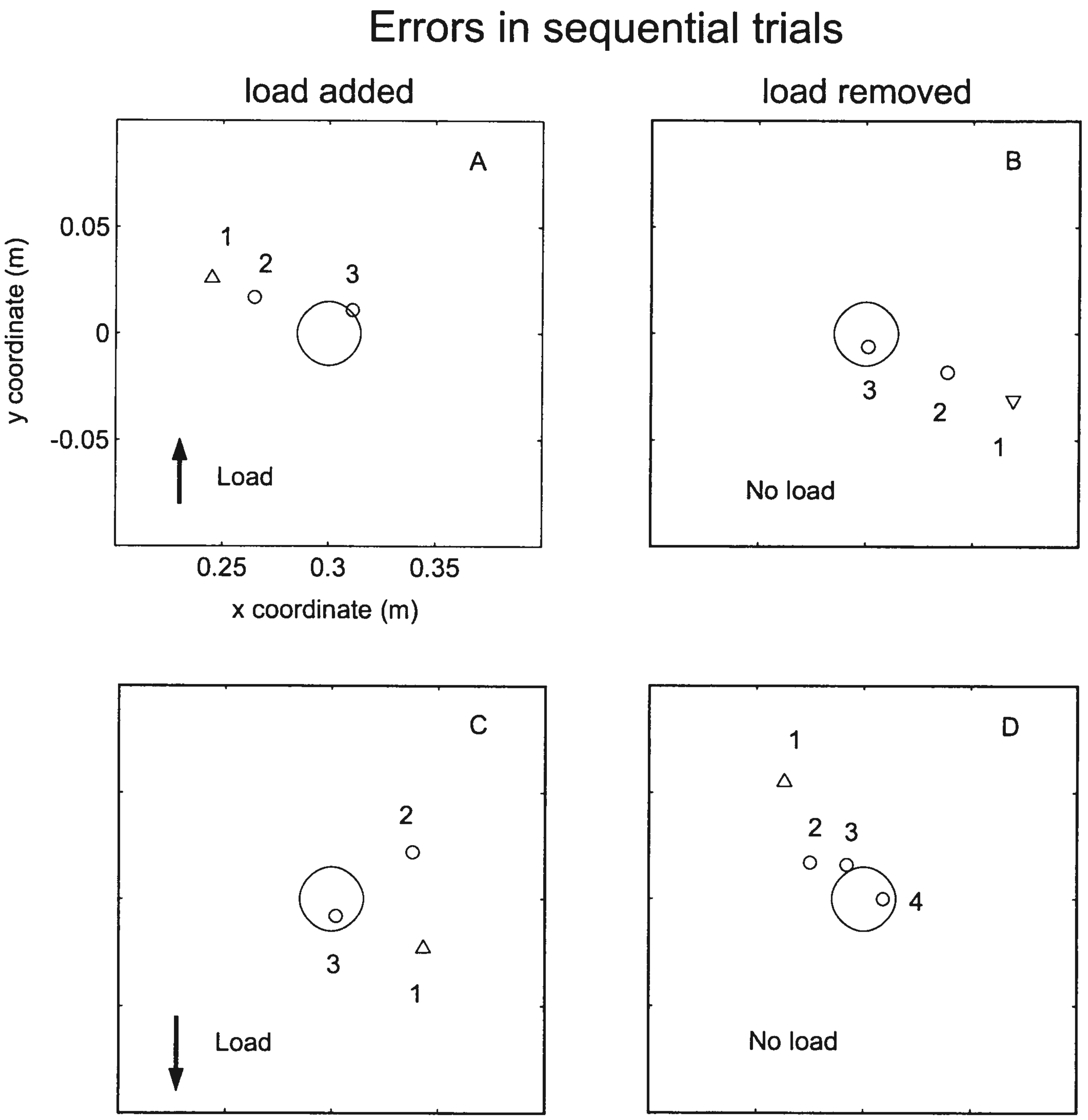


Fig. 6. Rapid adaptation of arm movements to changing load conditions. In several sequential trials (1, 2, 3) in a new load condition, movement accuracy was restored so that with each passing trial the final hand movement ended closer to the target zone. The decrease in movement errors was due to changes in either both (A, B) or only one (C, D) final coordinates of the hand. Data from experiments 1 (A, B) and 2 (C,D).

Figure 7

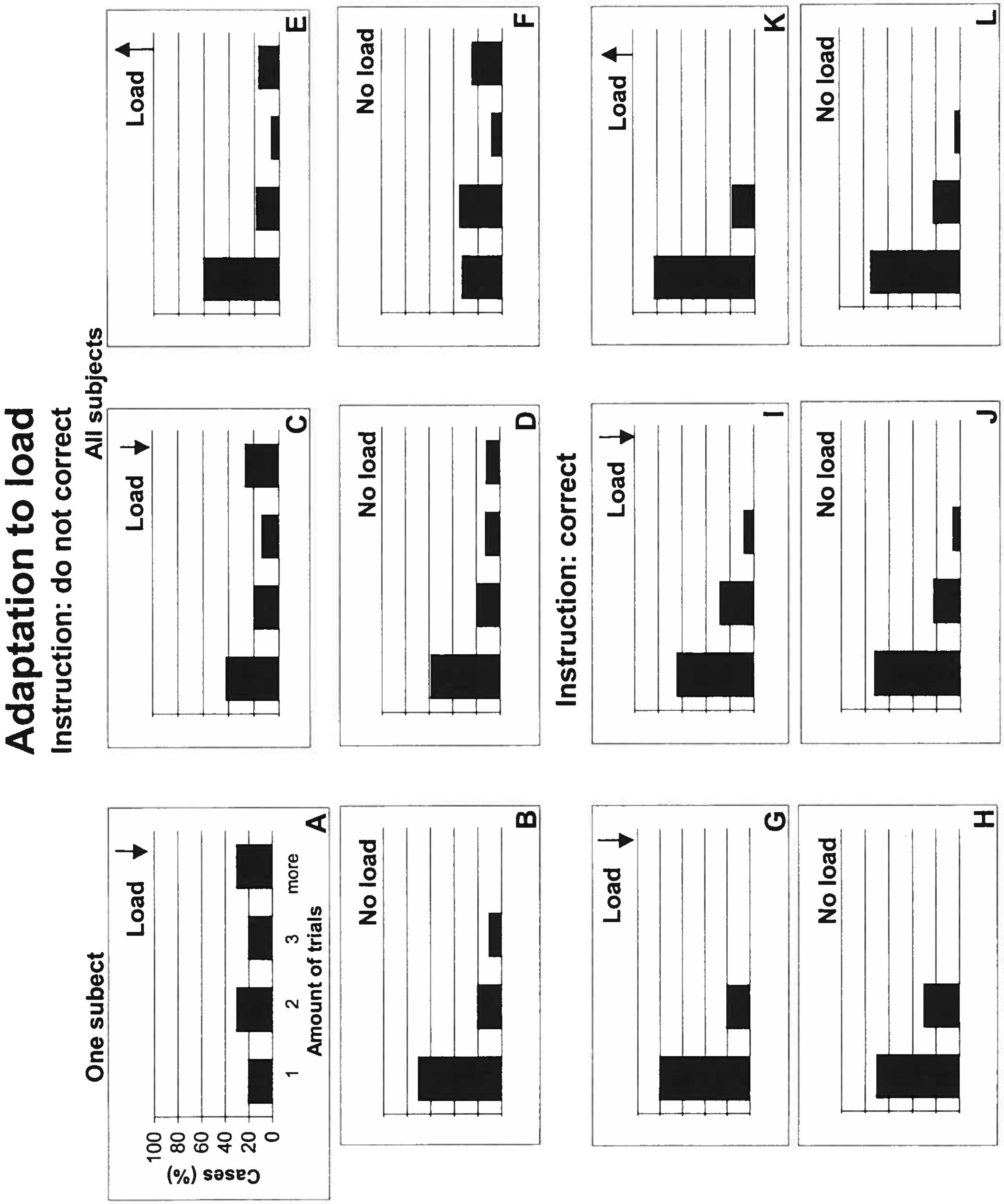

Adaptation to load
Instruction: do not correct
One subject
All subjects
Instruction: correct
Load
No load
Cases (%)
100
80
60
40
20
0
1
2
3
more
Amount of trials
A
B
C
D
E
F
G
H
I
J
K
L

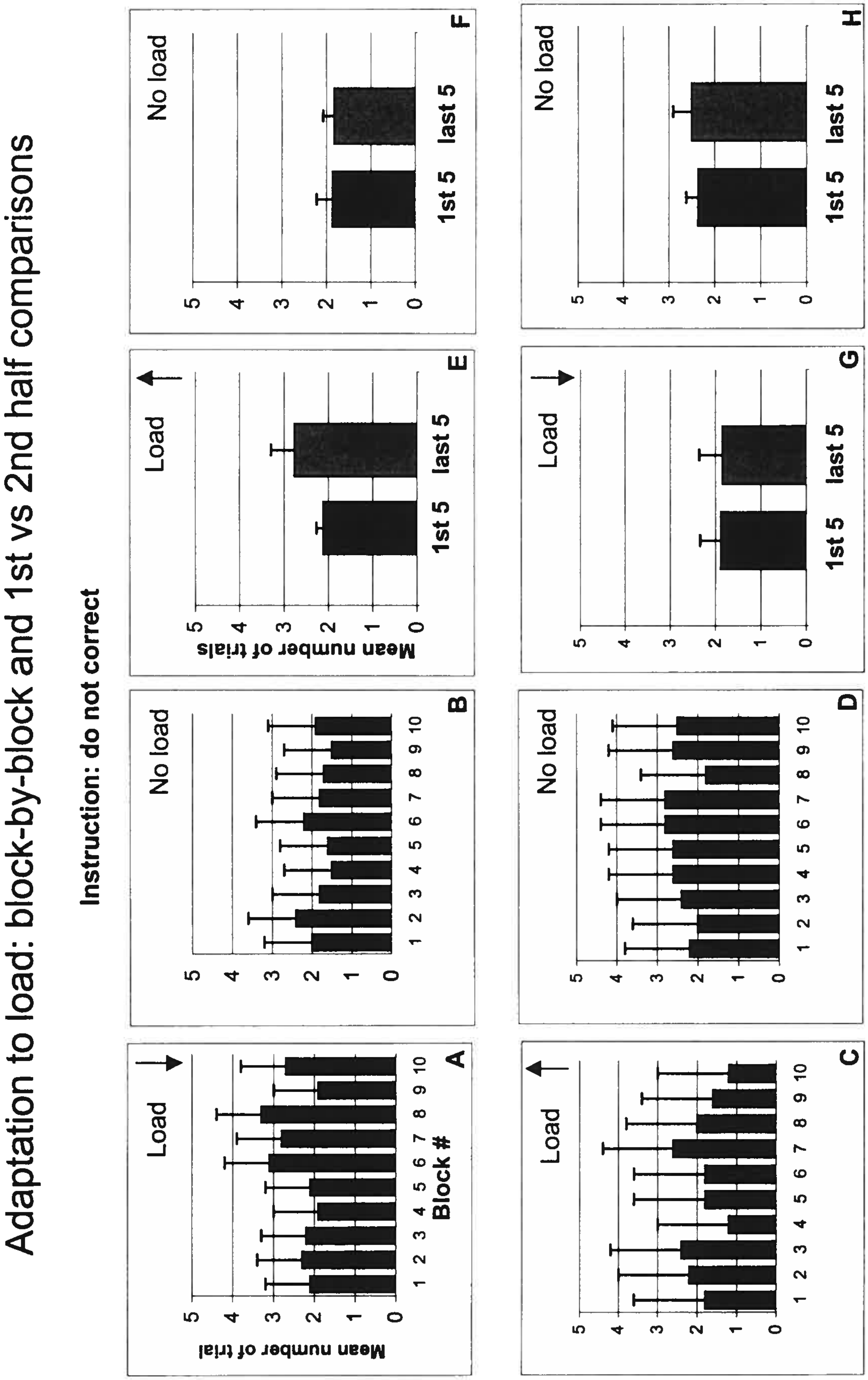
Fig. 7. A decrease in the number of trials required for adaptation of movements to either load condition was observed for the experiments where subjects were instructed to correct movement errors in the course of the trial (G-L), when compared to the number of trials required in the experiments with the instruction “do not correct” (A-F). Each panel shows the number of cases (in %) in which the target was reached after 1, 2, 3 or more trials in a new load condition. We show: individual data for one subject (left column) and averaged data for the group of subjects (middle and right columns); data from experiments 1 (A-D), 2 (E, F), 3(G-J) and 4 (K, L).

The difference was statistically significant ($p < 0.008$, 2-sided test for proportions). Data for the whole group in experiment 1 (Fig. 7 C and D) shows that the adaptation of movements to the no load condition was accomplished after fewer trials than adaptation to the non-zero load condition. However, the opposite was true for experiment 2, in which the load acted in the opposite direction (away from the subject). Adaptation occurred after one trial in 60% of blocks when the load was added (Fig. 7 E) and in only 32.65% of cases when the load was removed (Fig. 7 F; $p < 0.008$). In other words, the ability (in terms of the number of trials) to adapt to a change in load condition was history-dependent, i.e. dependent on the load condition which was used in the previous block of trials (see discussion).

3.4.2 Test of anticipation

For the group, the mean number of trials required for adaptation in each block of trials with the same load condition varied between 1.2 and 3.1 (Fig. 8 A-D). When looking at the data for experiments 1 and 2, we see that for the first 5 blocks of trials in the same load condition, subjects restored movement accuracy on average after 2.06 trials (Fig. 8, E-H). Furthermore, no improvement was observed in the last 5 blocks compared with the first five blocks of trials in the same load condition, for each of the 4 load conditions. Also, in one condition in experiment 1 (Fig. 8 E), the mean number of trials required to restore accuracy actually increased significantly for the group in the last compared to the initial blocks of trials ($p < 0.033$, t-test for independent samples). These findings imply that anticipatory or pre-programmed strategies, if used, as well as the knowledge that the same load conditions are repeated in an alternating way did not improve the subjects' performance in the course of experiment.

Figure 8



Adaptation to load: block-by-block and 1st vs 2nd half comparisons

Instruction: do not correct

Fig. 8. There was no improvement in terms of the number of trials required for adaptation over the course of experiments 1 (A, B and E, F) and 2 (C, D and G, H). The panels show group mean numbers of trials (± sd) after which arm movements were adapted in each of the 10 blocks of trials (A-D) or in the first 5 blocks compared to the last 5 blocks (E-H) with the same load condition.

3.4.3 Steady-state arm configurations and EMG activity

By definition (see Introduction), the arm postures that are established in the absence of an external load are called referent (R) postures, to distinguish them from Q postures, which results from a deviation of the arm from the R configuration due to the load. Of the five different postures observed in experiments 1 and 2, three are R postures (Fig. 9 A and B): the initial referent posture (R_i) specified by the subjects to bring the arm to the initial position, the posture specified in movements adapted to the no-load condition (R_0) when the hand arrived inside the target zone and postures R_+ and R_-. Postures R_+ and R_- were observed in the first trial in which the load was removed. These postures actually represent the referent arm configurations specified to bring the arm to the target with the load present (position Q_0). The previously mentioned R postures were wrongly repeated by the subject to produce movement in the first non-loaded trial of a block, after a block of trials with the load, because the change in load could not be anticipated. The other postures were all observed with the load present and therefore do not match the R configuration specified by the nervous system, and are therefore referred to as Q postures. In the no-load condition, the precision was restored in the subsequent trial(s) by a transition from R_+ or R_- to R_0 in experiments 1 and 2, respectively.

Additionally, non-referent arm configurations were observed in trials in which movements were made in the presence of a load. Q_0 is the arm configuration in movements adapted to the load so that the hand reached the target zone; Q_- and Q_+ are the arm configurations with the hand outside the target zone, established in the first trial in which the load was introduced after the previous block with no load, in experiments 1 and 2, respectively (Fig. 9 C and D). Because of the load, the net joint torques and force applied at the handle at these configurations were not zero (Table 1).

Note that the three R configurations (of each of experiments 1 and 2) substantially differed in terms of observed position even though joint torques at all 3 positions, because the load was absent, were zero. On the other hand, configurations R_0 and Q_0 for which the hand was in the target zone were practically indistinguishable in terms of observed position, although the former was established in the absence of load and the latter in the presence of load, that was compensated for by appropriate joint torques. These findings show that arm postures cannot be encoded by joint torques (see also Discussion).

Figure 9

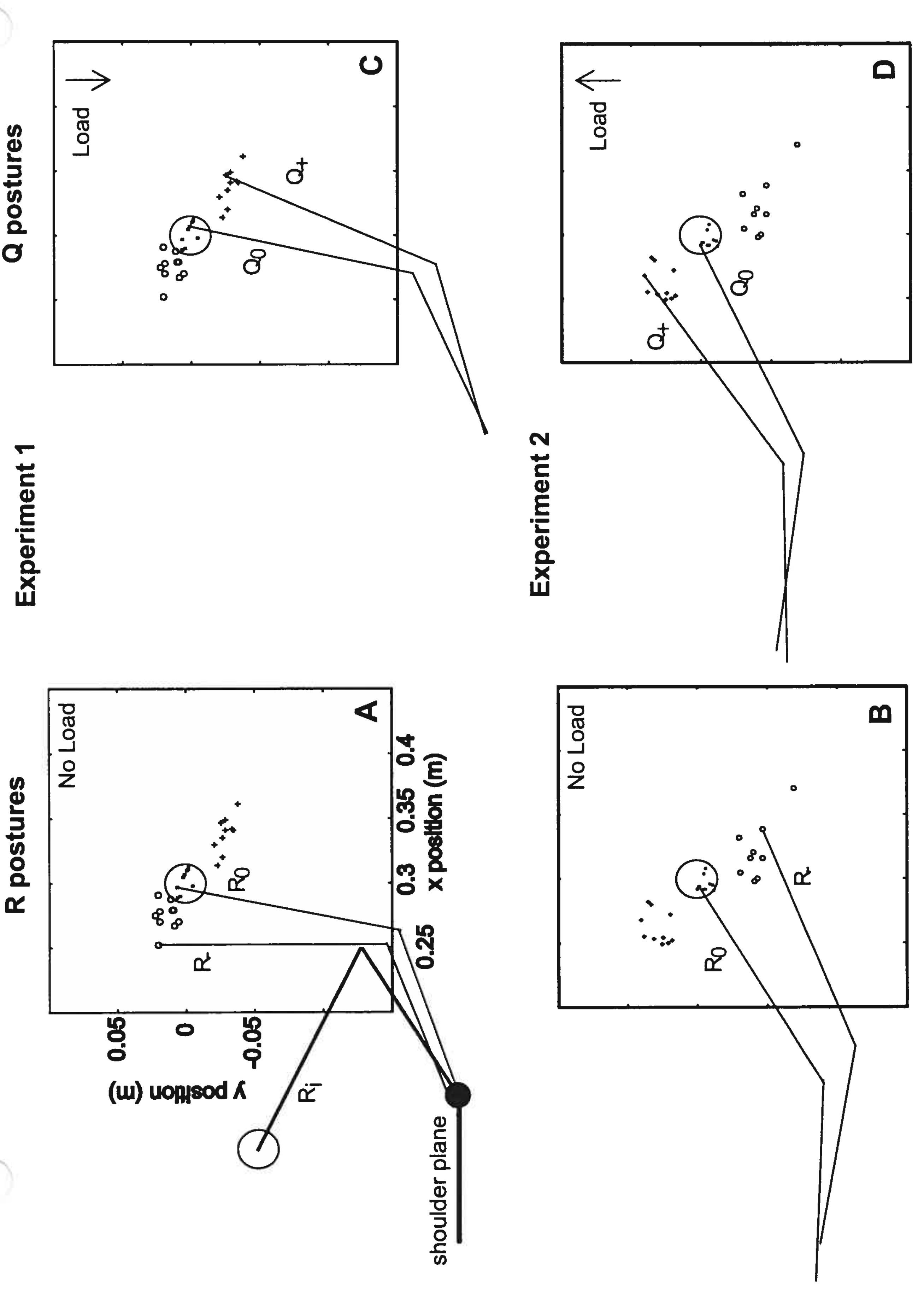

R postures
Q postures
Experiment 1
Experiment 2
No Load
No Load
Load
Load
A
B
C
D
R_0
R_-
R_i
R_0
R_-
Q_0
Q_+
Q_0
Q_+
x position (m)
0.25
0.3
0.35
0.4
y position (m)
0.05
0
-0.05
shoulder plane

Fig. 9. Steady state arm postures observed in experiments 1 and 2. Symbol R refers to postures that subjects specified in the absence of load. R_i: initial posture, R_0: posture adapted to zero load when the hand arrived in the target zone, R_+ and R_-: postures in the first trials in which the load was removed in experiments 1 and 2, respectively. Symbol Q refers to the postures achieved in the presence of load. Q_0: posture adapted to a load with the hand in the target zone, Q_- and Q_+: postures in the first trials when the load was added in experiments 1 and 2, respectively.

To address the question of whether or not arm configurations can be coded by the tonic levels of EMG signals, we compared the tonic EMG levels (see Methods) of multiple muscles for different steady-state postures in the no-load (R_0 and R_- or R_+) and load (Q_0 and Q_- or Q_+) conditions in experiments 1 and 2 (Tables 2 and 3). Examples of EMG patterns for movements in different load conditions are shown in Fig. 10. In these examples, the tonic activity of muscles at the initial arm posture was practically zero (background noise level). The movement phase was associated with transient EMG bursts in all recorded muscles. After the end of movement, muscle co-activation was decreased to close to its initial level for some muscles and it remained slightly above it for others (Fig. 10 A, B). The transitions from the initial to the final postures in movements made in the presence of the load were associated with an increase in the tonic activity of some arm and trunk muscles (Fig. 10 C, D). In 6 out of 13 subjects, the EMG activity of all muscles was indistinguishable for postures R_0 and R_+, or in 5 out of 13 subjects, for postures Q_0 and Q_- (Table 2, experiment 1). In the majority of the remaining cases, only 1 muscle (varying from subject to subject) showed different activity for different R postures (Table 2, experiments 1 and 2). In 10 out of 13 subjects in experiment 1, and in 4 subjects in experiment 2, activity on average 4 muscles was greater for Q_0 postures when compared with R_0 postures (Table 3). This result was expected given the difference in the load at these postures.

In experiment 1, the TB muscle showed significantly greater activation in movements ending inside the target when the load was present (posture Q_0) compared with postures R_0 (in 12 of 13 subjects). This muscle, being an elbow extensor, worked to compensate the deviation of the arm caused by the load (towards the subjects, in the direction of elbow flexion). For experiment 2, DA and DP showed greater activation at Q_0 compared with R_0 postures (4 of 4 subjects), but we suggest that they had more of a co-active, joint-stabilizing role in their activity because they were both active together. The muscle most susceptible to act to resist the load deviation, BB, did show significantly greater activity at Q_0 than at R_0 in 3 of 4 subjects. The subject that did not "use" BB instead used one of its agonist, BR, and also was the only subject to show increased activity for PM and TM muscles, suggesting that this subject might have used the PM muscle to further increase the stiffness of the shoulder joint and used combined movements of elbow flexion (BR) and shoulder internal rotation (TM) to compensate for the load deviation.

3.4.4 Instruction-dependent changes in adaptation

When corrections within each trial were allowed (experiments 3 and 4), subjects made first a large continuous movement and, if this primary movement was in error, produced one or more smaller additional corrective movements, eventually bringing the hand to the target before the end of the trial. Corrections could be initiated when the hand approached or had already reached a steady state position following the primary movement. We determined when adaptation occurred by identifying the number of trials from the trial in which the load condition changed to the trial in which a single movement without additional corrections occurred (see methods). In the majority of cases (64-82%) this was accomplished after a single trial and, in fewer cases, non-corrected movement occurred after 2 trials (18-28%). On substantially fewer occasions, precision was restored after 3 trials (0-8%). It should be noted that subjects never required more than three trials to restore precision (Fig. 7 E-F). Compared to movements made with the instruction "do not correct", the improvements were statistically significant for the group for each of the four cases of changes in the load conditions ($p < 0.01$, 2-sided test for proportions).

Figure 10

EMG activity comparison for one trial for each final arm postures observed in experiment 1.

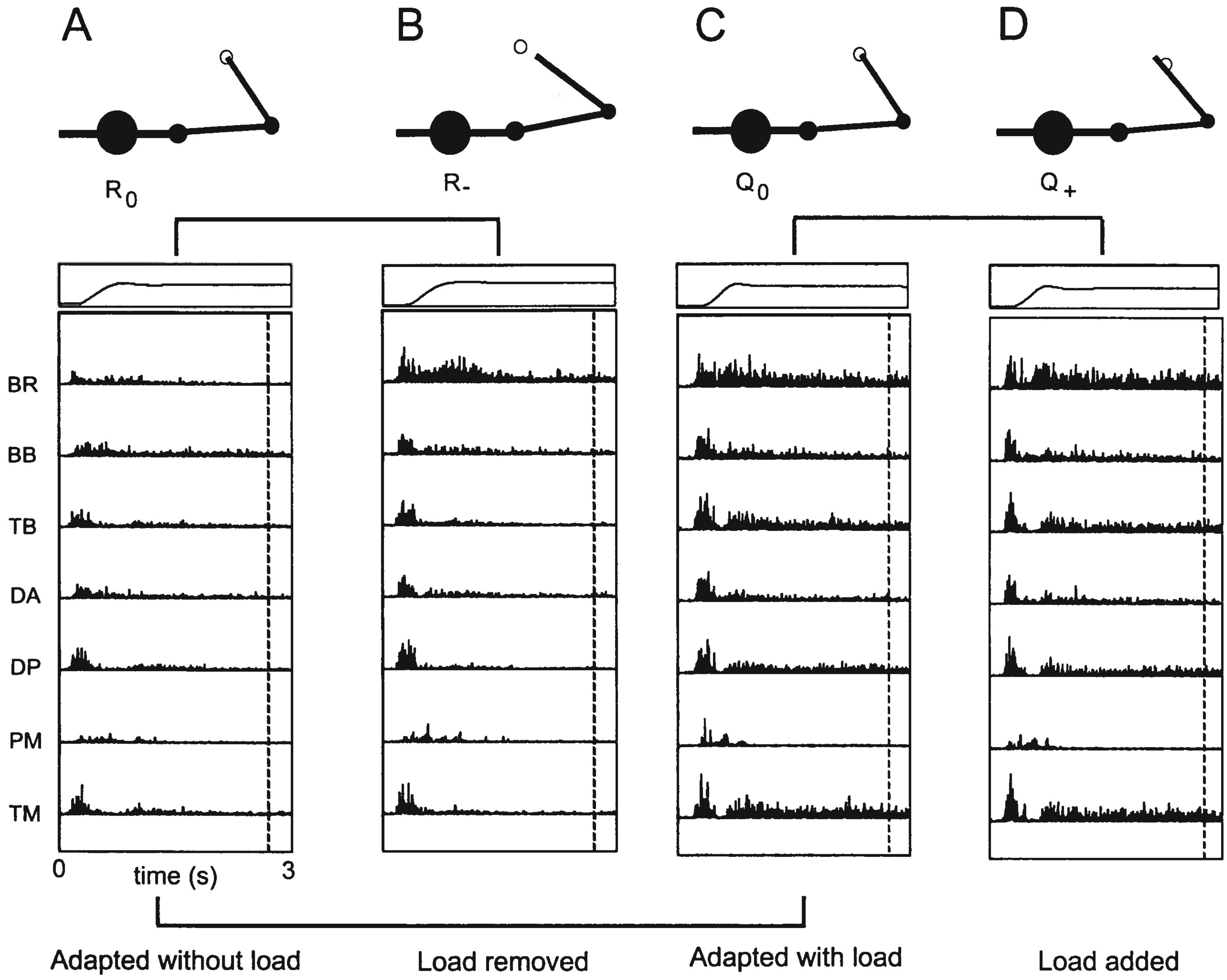


Fig. 10. A typical example of electromyographic (EMG) patterns of 7 arm muscles spanning the arm joints. Data are from experiment 1 (“do not correct” instruction). At an initial position (R_i), activity of all muscles was essentially zero. Movements to a new position were associated with transient EMG bursts in all muscles. After a final posture (R_0, Q_0, R_+ or Q_-, depending on the load condition) was achieved, muscles remained co-active for some time. This co-activation gradually diminished, but except for two cases, remained above zero level. Although postures R_0 and R_+ were significantly different in terms of the hand position and joint angles (Fig. 7), the tonic EMG levels at these postures were indistinguishable, for 6 out of 7 arm muscles; and for all muscles when comparing postures Q_0 and Q_-. Similar results have been obtained for the group of subjects (see text), implying that arm postures cannot be encoded by EMG signals.

Table 2

Significance of EMG activity difference for each muscle for different postures with the same load

Experiment 1 (load towards subject)

Muscle	BR	BB	TB	DA	DP	PM	TM	BR	BB	TB	DA	DP	PM	TM
Postures	Q- vs Qo							R+ vs Ro						
Subject														
1	no	no	no	no	no	no	no	no	no	no	no	no	no	no
2	no	no	no	no	no	no	no	no	p<0.013	no	no	no	p<0.036	no
3	p<0.004	no	no	p<0.022	no	p<0.028	no	no	no	no	no	no	no	no
4	no	no	p<0.037	no	no	no	no	no	no	no	no	no	no	no
5	p<0.008	no	no	no	no	no	p<0.009	no	p<0.002	no	no	no	no	no
6	no	no	no	no	no	no	no	no	no	p<0.049	p<0.013	no	no	no
7	p<0.002	no	p<0.002	p<0.023	no	no	p<0.028	p<0.048	no	no	no	no	no	no
8	no	no	no	no	no	p<0.003	no	no	no	no	no	no	no	no
9	no	p<0.04	p<0.04	no	no	no	no	no	no	p<0.023	no	p<0.012	no	no
10	no	no	no	no	no	no	no	no	no	no	no	no	no	no
11	no	no	no	no	no	no	no	no	no	no	no	no	no	no
12	no	no	p<0.001	no	no	no	no	p<0.042	no	p<0.003	no	no	no	no
13	no	no	no	no	no	p<0.013	no	no	no	no	no	no	p<0.033	no

Experiment 2 (load away from subject)

Muscle	BR	BB	TB	DA	DP	PM	TM	BR	BB	TB	DA	DP	PM	TM
Postures	Q+ vs Qo							R- vs Ro						
Subject														
1	Data for subject could not be read by the EMG analysis software.													
2	no	no	no	no	no	no	no	no	no	no	p<0.005	no	no	no
3	no	no	p<0.028	no	no	no	no	no	no	no	no	p<0.029	no	no
4	no	no	no	p<0.039	no	no	no	no	no	no	no	no	p<0.008	no
5	no	no	no	no	no	no	p<0.019	no	no	no	no	p<0.022	no	no

Table 3

Significance of EMG activity difference for different postures with the same load, for each muscle

Experiment 1 (load towards subject)

Muscle	BR	BB	TB	DA	DP	PM	TM
Posture	Qo vs Ro						
Subject							
1	p<0.001	p<0.001	p<0.001	no	no	p<0.001	p<0.001
2	no	no	p<0.001	p<0.001	no	no	p<0.03
3	p<0.001	p<0.01	p<0.001	p<0.04	no	p<0.04	p<0.01
4	no	no	p<0.001	no	no	p<0.001	p<0.01
5	no	p<0.022	p<0.001	p<0.037	p<0.033	p<0.001	no
6	no	p<0.045	p<0.004	p<0.014	no	no	no
7	p<0.001	p<0.037	p<0.001	no	p<0.011	no	no
8	p<0.008	p<0.02	p<0.001	no	p<0.008	no	p<0.027
9	p<0.008	p<0.043	p<0.003	p<0.001	no	p<0.005	no
10	no	no	p<0.001	no	no	p<0.036	no
11	no	no	p<0.001	p<0.001	p<0.001	no	no
12	no	no	no	no	no	no	no
13	no	no	p<0.002	no	no	no	no

Experiment 2 (load towards subject)

Muscle	BR	BB	TB	DA	DP	PM	TM
Posture	Qo vs Ro						
Subject							
1	Data for subject could not be read by the EMG analysis software.						
2	p<0.001	no	no	p<0.001	p<0.001	p<0.001	p<0.003
3	p<0.017	p<0.015	no	p<0.016	p<0.001	no	no
4	p<0.008	p<0.003	no	p<0.005	p<0.005	no	no
5	no	p<0.027	no	p<0.001	p<0.001	no	no

3.5 Discussion

3.5.1 Basic findings

We have analyzed positional errors elicited by sudden changes in the load and investigated how subjects restored movement precision when the same load was reproduced in a block of 5-10 trials. A load was applied in one block and removed in the subsequent block, and so on, until 10 blocks in each load condition were completed. When present, the load was applied to the handle of the manipulandum by the two torque motors (see Methods) and acted approximately transversally to the hand movement trajectory, either towards or, in a separate experiment, away from the subject.

When subjects were instructed not to correct movement errors within each trial (experiments 1 and 2), the movement was in error in those trials in which the load condition changed so that the final positions of the hand were outside the target zone. The shift in the hand position was in a diagonal, fronto-sagittal direction and thus did not coincide with the sagittal direction of the load action. However, the sagittal component of the hand shift resembled the change in the load in these trials. For example, when a load was introduced after movement adaptation to the no-load condition, the sagittal component of the hand shift was in the direction of the load action, but was in the opposite direction when the load was removed after a previous adaptation of movements to it. Respectively, the clusters of points identifying the final hand positions in these two cases were located on opposite sides of the target zone.

With repetition of the same load condition in several trials, movement precision was restored (adaptation) on average after about two trials. In terms of the number of trials required for adaptation to the same load condition, subjects did not improve their performance as the experiment progressed, for the first two experiments. In contrast, when subjects were instructed to correct movement errors within each trial (experiments 3 and 4), movements were adapted to each new load condition significantly faster – in 62-81% after only one trial.

In experiments 1 and 2, we observed a set of steady state configurations of the arm associated with either zero load (postures R_i, R_0, R_-, R_+) or non-zero load (postures Q_0, Q_-, Q_+). Not only the hand positions (Fig. 4), but also the trajectories (Fig. 5) were different for different R- or Q-postures. For each subject, on average, the tonic levels of EMG activity of muscles at postures R_0, R_- (in experiment 1) or R_0 and R_+ (experiment 2) were indistinguishable for 6 out of the 7 muscles analyzed (Table 2). In one subject in experiment 1, all 7 muscles showed indistinguishable levels of activity for that particular comparison. For similar positions (Q_0 and R_0) the EMG activity was different, on average, in 3 out of 7 muscles per subject (Table 3). There was no systematic relationship between different R (or Q) postures and EMG activity, supporting our claim that postures are not encoded by tonic EMG levels.

3.5.2 Did anticipation and long-term motor memory play a role in adaptation to load conditions?

Consider first the findings in experiments 1 and 2, made with the instruction "do not correct" movement errors. While producing movements, subjects could try to predict the load condition in each forthcoming trial and thus improve their performance. Occasionally, subjects used such a strategy. For example, the subject likely anticipated a change in the load condition in trial 70 (Fig. 3 A) and modified the movement accordingly. However, since the load condition remained the same in this trial, the movement was in error. This example shows that when changes in the load condition are randomized, the anticipatory strategy might not be efficient in improving the overall performance of subjects. There was also a possibility that subjects could realize that the same load condition is reproduced after one block of trials and prepare appropriate central commands for each type of load condition beforehand. To realize such a strategy, it would be necessary to retain the appropriate central commands in long-term motor memory and execute them according to the load condition used in the course of each experiment. Several findings in the present study conflict with the assumption that subjects relied on such a strategy. In particular, if subjects actually used such a strategy, they could generate accurate, non-corrected movements after each trial in which the load condition changed, i.e. movements could be adapted after only one trial. This could be achieved regardless of the instruction given to the subjects (do not correct or correct). Our data shows, however, that the rate of adaptation was instruction-dependent. In addition, although subjects sometimes restored movement accuracy after one trial in several blocks, more often they restored movement accuracy gradually, after several trials in the same load condition (Fig. 6). If subjects could store and recall central commands previously used in several preceding blocks of trials, they could diminish the number of trials required for adaptation in the subsequent blocks of trials, in experiments 1 and 2, when the same load condition is repeated. Our data does not support this assumption: the performance of subjects did not improve in the last half compared with the initial half of blocks of trials in a given load condition (Fig. 8, E-H). Moreover, in one condition, the behavior actually worsened in the last blocks of trials (Fig. 8 E). When corrections within each trial were allowed (experiments 3 and 4), subjects adapted their movements more rapidly, showing that the opportunity to reach the target within the first trial in a new load condition was essential in preparing the movement for the subsequent trial in the same condition.

Taken together, our findings imply that a short-term (working) memory of the movement result in the previous trial, rather than a long-term memory of results in the previous blocks of trials, was most essential for rapid adaptation (see also the next section). In this respect, our study differed from those analyzing adaptation of movement to comparatively more complex force fields; (Lackner and DiZio, 1994; Shadmehr and Mussa-Ivaldi, 1994; Conditt et al., 1997; Gandolfo et al. 1996; Goodbody and Wolpert, 1998). In those studies, subjects had to recognize that the external force was different in different parts of the arm workspace and modify movements accordingly. Even though subjects were allowed to correct movements within each trial in these studies, adaptation to the force field was accomplished after a substantial number (several hundreds) of trials, suggesting the involvement of long-term memory in the process of learning. In contrast, the observation of a much more rapid adaptation in the present study (in most cases after only one trial when subjects were allowed to correct movement errors within each trial) suggests that subjects basically relied on short-term memory.

3.5.3 Explanation of load adaptation in terms of different motor control hypotheses

Note that the ability of force control strategies to move body segments from one posture to another is not in doubt (Ostry and Feldman 2003). The problem is that the programmed generation of muscle activity and torques postulated by the force control models would result in the movement of body segments from an initial position. In response, mechanisms of postural stabilization would generate resistance that would tend to return the segments to their initial position. To reach a new position, the system must thus generate additional muscle activity and forces to overcome this resistance. The tonic activity required to hold the arm at the final position cannot be reduced without eliciting movement of the arm back to the initial position. Additional activity and muscle forces are required at the new position in force control models, even if the movement is not opposed by external forces (e.g., gravity). Thus, the existing formulations of force control models (Schweighofer et al., 1998; Bhushan and Shadmehr, 1999) cannot explain why the system re-establishes zero-level activity at the new (final) position for movements not opposed by load (e.g. Fig. 1). The unopposed shift between postural states is a fundamental characteristic of everyday motor activity and the inability of the force control strategy, in its current form fails to provide a means to re-establish posture at a new location without self-generated resistance, which makes the strategy physiologically unfeasible. The experimentally derived notion of threshold control solves the posture-movement problem. However, this notion may not be integrated in the force control formulation since threshold control suggests that forces and EMG activity are not programmable, but emerge following changes in activation threshold. As a consequence, the notion of threshold control conflicts with the basic idea at the center of the force control formulation that EMG patterns and forces are directly programmed by the nervous system.

The inability of the force control formulation to adequately solve the posture-movement problem results in other inconsistencies with empirical observations. For example, according to this formulation, the tonic EMG activity and the forces that counteract the resistance of posture-stabilizing mechanisms cannot be reduced at a final position without bringing the system back to its initial position. In other words, the formulation predicts that the tonic EMG signals should be different for different arm positions even if the muscle joint torques are zero at these positions.

This prediction of force control models conflicts with empirical data that in identical conditions, tonic muscle activation might be the same (in particular zero) at different arm positions (e.g. Gottlieb et al. 1989; Ostry and Feldman 2003). This prediction of the force control formulation also conflicts with the finding in the present study that tonic EMG levels at postures R_0, R_- and R_+, established in the absence of external forces were indistinguishable for practically all muscles analyzed. This finding also implies that, even though the lengths, moment arms and individual forces of mono- and bi-articular muscles were likely somewhat different at the R positions, the same EMG activity levels could provide net zero joint torques at these positions. In all subjects, for both experiments 1 and 2, tonic EMG levels were indistinguishable for 6 out of 7 muscles on average, for the two different R postures, as well as for the two different Q postures, observed in each experiment. EMG activity was essentially zero at an initial position (R_i) and, after transient EMG bursts and co-activation of muscles, returned to zero at a final posture. This observation also conflicts with the force control hypothesis. In general, by predicting a change in the tonic EMG activity with each transition to a new posture, even if the external forces are zero at both positions, force control models conflict with the known physiological rule that muscle activation and recruitment of motor units are graded according to exerted muscle force rather than position (e.g., Desmedt and Godaux 1977).

One of the main objectives of this study was to analyze the ability of two different models of movement control to explain posture-to-posture transitions in the process of adaptation of movement to changes in load. As is demonstrated by our data, the experimentally derived notion of threshold control can explain this phenomenon as well as solve the posture-movement problem (see introduction), and most importantly does so in a physiologically realistic manner.

Note that our experiments have not been designed to demonstrate the existence of threshold control. Rather, we wanted to see whether our data on movement adaptation could qualitatively be explained based on the notion of threshold control. Consider first data obtained in experiment 1 (instruction "do not correct", load acting towards the subject). In terms of the threshold control, to reach the initial target, subjects shifted the activation thresholds of arm muscles to position R_i. These shifts could have been determined during the short training session and reproduced, with some corrections and variations, in each trial. EMG activity and muscle forces resulting from the difference between the actual arm position (Q) and the threshold position, R_i, elicited motion of the arm towards the initial target. In the absence of external forces, the arm eventually arrived at threshold position R_i with the hand located at the initial target, and the EMG activity of muscles settled to zero.

To move the hand to the final target in the absence of an external load, the system rapidly shifted the activation thresholds of arm muscles towards position R_0. These shifts could also have been learned from the training session. Experimentally, it has been shown that, to produce fast arm movements, such shifts are combined with additional shifts in muscle activation thresholds that provide co-activation of opposing muscle groups without influencing the posture defined by the other shifts in the thresholds (Feldman 1980). Following the combined threshold shifts, the actual arm position became deviated from position R_0, resulting in EMG bursts and muscle forces tending to eliminate this deviation. In the absence of an external load, this process brought the hand to the final position, coinciding with the R_0 posture with the hand located at the final target.

Co-activation of arm muscles is essential in speeding arm movements (Feldman and Levin 1995) but at the final position it can be diminished to a minimum. According to our results, subjects sometimes maintained muscle co-activation at posture R_0 above zero level likely to better stabilize the arm at the final position. In the subsequent trials in the no load condition, subjects reproduced, with some variations, the combined pattern of shifts in thresholds and thus reached the final target by a single, non-corrected movement. However, the same pattern of threshold shifts resulted in a movement error in the trial in which the load was applied - the arm was deviated by the load from position R_0 to a new final position, Q_-, at which muscles generated tonic EMG activity and forces that balanced the load torques, but the hand was outside the target zone. The hand deviated in a direction not coinciding with that of the load action because of the known anisotropy of arm anatomy and muscle intrinsic and reflex properties, together producing direction-dependent stiffness of the arm (Shadmehr and Mussa Ivaldi, 1994).

To eliminate the movement error in the subsequent trials in which the load was reproduced, it was necessary to specify a new threshold configuration (R_-) so that the arm, deviated from it by the load, could establish a posture (Q_0) with the hand at the target zone. After a block of trials in the no-load condition, subjects maybe were unable to recall the appropriate R-configuration they had used during training with the load (see above). Instead, they likely used a trial-and-error approach by making an incremental change in the R posture in each trial to eventually find the required posture, R_-, i.e. a central command that, combined with the action of the load, resulted in accurate reaching of the target. This assumption is consistent with the finding that in experiment 1, the movement error was typically diminished incrementally in a set of sequential trials (Fig. 6). Naturally, when the load was removed after adaptation of the movement, the arm moved to the R_- posture that was observed experimentally. Note that, in the absence of co-activation, the R_0 and R_- are threshold postures. Using the same co-activation command, the system could equalize the levels of tonic EMG activity at different R postures.

This shows that threshold control, in contrast to the force control theory, has no problem with the finding of the same level of EMG activity at different R postures.

A similar trial-and-error strategy was likely used to restore the precision in blocks of trials in which the load was removed after adaptation of movements to it. Subjects made incremental changes in the R configuration in each trial and thus returned to the specification of the posture corresponding to the R_0 configuration instead of R_-. The trial and error strategy was repeated in the remaining blocks of trials in which the load was added or removed. The pattern of errors and adaptation in experiment 2 in which the load direction was reversed can be explained in a similar way, except that in order to make accurate movements in trials in which this load was applied, posture R_+ instead of R_- had to be specified. Note that in the absence of an external load, the difference in R postures is explained by the differences in shifts in the activation of thresholds. The EMG activity level at these postures is determined by the degree of co-activation of the antagonist muscle groups.

Indeed, the adaptation of movement to each load condition could occur faster, if information about the threshold shifts that are required for an accurate movement to the target could be obtained during the first trial in the new load condition. By reproducing these shifts in the subsequent trials, subjects could adapt to each new load condition predominantly after one trial. This hypothesis was confirmed by our observations in experiments 3 and 4, where subjects were allowed to correct movement errors within each trial. By bringing the hand to the target in the first trial in the new load condition, the system could identify an R posture to which the activation threshold should be set to, to bring the hand to the target. This explains why movements were adapted to each new load condition in most cases after one trial. The fact that adaptation to load is instruction dependent is reminiscent of a similar finding in studies that compare implicit and explicit learning of motor sequences (Boyd and Winstein 2001). The explanation, in terms of threshold control in the present study, shows that acceleration of learning can occur when the information about the required shifts in the activation thresholds are available (in our case by giving subjects the opportunity to correct movements within each trial).

In conclusion, the results of this study, more specifically those pertaining to EMG activity at different postures with the same load and similar postures with different loads conflict with the actual formulation of the force control hypothesis, but can be well explained in terms of the threshold control model.

CHAPTER IV

4.0 General discussion

We used sudden changes in load condition in sequential blocks of 5 – 10 trials during hand point-to-point movements to analyse positional errors and to investigate how movement precision was restored by the subjects. Also, we examined the potential of the threshold control theory to explain the observed results, in terms of correction pattern and EMG activity.

Two load directions were used under two different instructions, for a total of four experiments (see methods). Subjects were either instructed not to correct positional errors during the course of a trial or to correct them as soon as possible. One load direction was used per experiment (either towards or away from the subject), and, when present, was applied to the handle of the manipulandum by the two torque motors and reproduced for the whole block of trials.

Movement precision was restored after about two trials after the change in load condition occurred. In spite of the fact that subjects were aware that the two load conditions would be presented to them alternatively and that they were allowed practice with each of them prior to the beginning of the experiment, their adaptation rate to the same load condition did not improve as the experiment progressed. However, the instruction to correct movement errors during a trial lead to a significant reduction in the number of trials subjects required for adaptation (experiments 3 and 4). More specifically, they corrected much more often after only one trial (62 – 81% of cases) and never required more than three trials for adaptation.

Our data shows that the adaptation rate is instruction- rather than history-dependent. Consider the data of the first two experiments, made with the instruction "do not correct" movement errors during the trial. To improve their performance, subjects could use one of two strategies: they could try to guess in which trial the change in load would occur and change their command accordingly, or they could store the commands that lead to a correct movement in each load condition during practice in long-term motor memory and reproduce them at the appropriate time. The data of the final positions for each trial shows that subjects, on occasion, did try to anticipate in which trial the change in load was going to occur. Such a strategy proved useless in improving their overall performance, as the number of trials in each block was chosen at random so that their chances of guessing correctly, let alone predict, in which trial the change in load would occur were minimal. The more intuitive way to improve performance would be to remember the parameters of the motor command that led to a precise movement in either load condition and store them in long-term motor memory to be reproduced when the given load condition would be presented. The use of such a strategy could in theory lead to adaptation to a change in load after only one trial on all occasions, regardless of the instruction given to the subject prior to the experiment. However, our data shows that even though subjects occasionally adapted to a change in load condition after one trial in several blocks, more often their adaptation was done gradually, over the course of several trials (see Figs. 6 and 7) and did not show any improvement as the experiment progressed (Fig. 8). In contrast, when the subjects were allowed to correct movement errors within a trial, they adapted to a change in load condition much more rapidly (experiments 3 and 4). This shows that the opportunity to reach the target, and thus establish a correct configuration to be reproduced in subsequent trials, was a key element in speeding up adaptation of movement to the new load condition.

It can be argued that subjects had the capacity to correct movement errors caused by the change in load after fewer trials on all occasions, but the necessity to overcome the inertia of the manipulandum constrained this ability and, in addition, increased the variability of final positions. To minimize these effects, accelerometers were used to control the torque motors to decrease the inertia. The subjects' position relative to the manipulandum was selected to additionally minimize the inertia of the manipulandum. For some subjects, the necessity to move with their arm attached to the manipulandum's handle, rather than being able to freely move it, might have complicated the reproduction of movement. Also, the position of the target was represented on a computer screen and not in external space. This required subjects to produce an additional sensory transformation, contributing to the variability of final positions. Allowing the subjects to practice with each load condition separately before the test experiments began minimized these effects. Moreover, these complicating factors were present in all experiments. Despite this, in experiments 3 and 4, the subjects were able to diminish the number of trials required for adaptation to almost the absolute minimum (1 trial), implying that the basic behavior was not affected by these methodological complications.

Taken together, our findings imply that a short-term (working) memory of the movement result in the previous trial, rather than a long-term memory of the results in the previous block of trials, was most essential for rapid adaptation of movements to changes in load. In this respect, our study differs from those analyzing adaptation of movement to comparatively more complex force fields (Lackner and DiZio, 1994; Shadmehr and Mussa-Ivaldi, 1994; Conditt et al., 1997;

Gandolfo et al. 1996; Goodbody and Wolpert, 1998). In those studies, subjects had to recognize that the external force was different in different parts of the arm workspace and modify movements accordingly. Even though subjects were allowed to correct movements within each trial in these studies, adaptation to the force field was accomplished after a substantial number (several hundreds) of trials, suggesting the involvement of long-term memory in the process of learning. In contrast, the observation of a much more rapid adaptation in the present study (in most cases after only one trial when subjects were allowed to correct movement errors within each trial) suggests that subjects basically relied on short-term memory.

It is important to note that our experiments were not designed to demonstrate the existence of threshold control, but rather to see whether experimental data on movement adaptation could be explained qualitatively based on the notion of threshold control. We will use the data from experiment 1 (instruction "do not correct"; load acting towards the subject) as an example of how threshold control can explain the adaptation process of reaching movements to changes in load condition. To move the hand to the final target in the absence of an external load, the system rapidly shifted the activation thresholds of arm muscles towards position R_0. These shifts could have been learned from the training session and reproduced with some variations and corrections in each trial (see 2 paragraphs before). Experimentally, it has been shown that, to produce fast arm movements, such shifts are combined with additional shifts in muscle activation thresholds that provide co-activation of the antagonist muscle groups. C command (see Introduction), do not influence the posture defined by the other shifts in the thresholds (Feldman, 1980). Following these combined threshold shifts, the initial arm position (R_i) is now perceived as a deviation from the specified referent position, R_0. In response to this deviation, the posture-stabilizing mechanisms produced EMG bursts and muscle forces tending to eliminate this deviation and thus producing movement towards R_0. In the absence of an external load, this process brought the hand to the final position coinciding with the R_0 posture, with the hand located inside the final target. It has been shown that co-activation of arm muscles is essential in speeding the movement towards the final position (Feldman and Levin 1995). At the final position, it can be diminished to a minimum. However, some level of residual co-activation might be necessary to stabilize the arm after the transition to the final position. Our observation that the tonic activity of muscles at the final position, R_0, exceeded that at the initial position, R_i, is consistent with this explanation.

Now that specification of a posture has been explained, let us continue our explanation by a description of the process of adaptation to changing load conditions. In the subsequent trials in the no load condition (experiment 1), subjects reproduced, with some variations, the combined pattern of shifts in thresholds and thus reached the final target by a single, non-corrected movement. However, the same pattern of threshold shifts resulted in a movement error in the trial in which the load was applied - the arm was deviated by the load from the referent position R_0 to a new final position, Q_-, at which muscles generated tonic EMG activity and forces that balanced the load torques, but the hand was outside the target zone. In order to eliminate the movement error in the subsequent trials in which the load was going to be reproduced, subjects had to specify a new referent configuration (R_-) taking into account the deviation of the arm caused by the load so that the arm would end up at a posture (Q_0), with the hand inside the target zone.

After a set of trials in the no-load condition, subjects for some reason seemed unable to remember the appropriate referent configuration, R_-, they had established during training with the load, and instead likely used a trial-and-error approach by making an incremental change in the R posture in each trial, eventually specifying the required posture, R_-, to accurately reach the target. This assumption is consistent with the finding that, in experiment 1, the movement error was typically diminished incrementally in a set of sequential trials (Fig. 6). Naturally, when the load was removed after adaptation of the movement, it no longer deviated the arm so that it moved to the R_- posture, observed experimentally. The pattern of errors and adaptation in experiment 2, in which the load direction was reversed, can be explained likewise. Except that subjects, in order to make accurate movements in trials in which this load was applied, specified posture R_+ instead of R_-. By appropriately adjusting shifts in the activation thresholds of muscles, the EMG activity level at these postures is determined by the degree of co-activation of the antagonist muscle groups. Note that, in the absence of co-activation, the R_0 and R_- are threshold postures, so that, in principle, the EMG activity of muscles could be zero at both these postures. With a co-activation command, the tonic EMG activity could not be zero, but could be equalized, producing net zero joint torque. This shows that threshold control has no problem with the finding of the same level of EMG activity at different R postures. The existing force control models, as has been noticed (see also Review section), conflict with such observations. Differences in the passive forces of inactive muscles at these postures were likely minimized by our selection of the range of arm configurations used in the present study.

The threshold control model predicts that adaptation of movements to each load condition could occur faster (than in the force field studies cited above or than when the "do not correct" paradigm is used), if information about the threshold shifts that are required for an accurate movement to the target could be obtained during the first trial in the new load condition. By reproducing these shifts in the subsequent trials, subjects should be able to adapt to each change in the load condition predominantly after one trial. Our data confirms this hypothesis. By allowing the subjects to bring the hand to the target in the first trial in the new load condition, the system was able to identify an R posture to which the activation thresholds should be set to, to bring the hand to the target. This explains our observation that movements were adapted to each change in load condition in most cases after one trial in experiments 3 and 4. The fact that adaptation to load is instruction-dependent is reminiscent of a similar finding in a study that compared implicit and explicit learning of motor sequences (Boyd and Winstein 2001). The explanation, in terms of threshold control in the present study, shows that acceleration of learning can occur when the information about the required shifts in the activation thresholds are made available (in our case by giving subjects the opportunity to correct movements within each trial).

A major prediction of the force control model is that different postures are coded by different EMG signals and therefore should, even for R postures, have different steady-state EMG levels. This prediction is inconsistent with our results. For example, in a substantial number of subjects (6 out of 13 for experiment 1) the tonic activity of all muscles at postures R+ and R0 was the same. One can argue that the difference between the postures (4.4 cm for the distance between the hand positions) was too small to elicit noticeably different EMG levels. According to the force control models, the difference would result from internal resistance of stablizing mechanisms resulting from transition from one posture to another. Stiffness of the arm measured at the hand is typically about 4 N/cm (Shadmehr and Mussa-Ivaldi, 1994). In experiment 1, the difference in hand positions for the R postures was about 4.4 cm. Thus, with the transition from one R posture to the other, the internal resistive force to overcome would be about 17.6 N, which is in the range of load forces used in our experiments (Table 1). An obvious increase in EMG activity in response to such loads was observed in our experiments (Table 3). Consequently, if the increase in EMG activity predicted by the force control strategy were used in our experiments, it would have been captured by our analysis. The absence of a difference in EMG levels for R+ and R0 postures points to a problem in the force control strategy.

Note that the ability of the force control model to move body segments from one posture to another is not in doubt, only its ability to solve the posture-movement problem as formulated by Von Holst and Mittelstaedt (1950/1973, see Introduction). Since movement always starts from an initial position, specification of muscle activity and torques for a movement from that position will automatically trigger activity in the posture-stabilization mechanisms to prevent movement from the initial position. Thus, in order to generate movement, the system must generate additional muscle activity and force to overcome the resistance of the posture-stabilization mechanisms, even if the movement is not opposed by external forces (e.g. gravity). The unopposed shift between postural states is a fundamental characteristic of everyday motor activity and the inability of the force control hypothesis to re-establish posture at a new location without self-generated resistance makes the strategy physiologically unfeasible.

The inability of the force control hypothesis to adequately solve the posture-movement problem yields other inconsistencies of the hypothesis with empirical observations. For example, this model predicts that tonic EMG signals should be different for different arm positions, even if the joint torques are zero at these positions. This prediction of the force control model conflicts with empirical data (Gottlieb et al., 1989; Ostry and Feldman, 2003) that show that muscle activation might be the same (in particular zero, see Fig. 1) at different arm positions. Furthermore, in the present, similar tonic EMG levels were observed for different positions with a load. By predicting a change in the tonic EMG activity with each transition to a new posture, even if the external forces are zero at both positions, force control models conflict with the known physiological rule that muscle activation and recruitment of motor units are graded according to exerted muscle force rather than position (e.g. Desmedt and Godaux, 1977).

In conclusion, some of our findings, as well as some findings from the literature conflict with the force control theory. These findings, as well as the basic patterns of adaptation to the load in the present experiments are well accounted for by the threshold control model.

CHAPTER V

5.0 Conclusions

5.1 Basic Findings

a) *A change in the load condition invariably lead to a movement error*

Each time the load was either applied after a block of trials without load or was added after a block with load, there was a positional error in the first trial of the new block, regardless of load direction.

b) *The process of adaptation to a change in load was done sequentially...*

Subjects required a few trials (see next point) before restoring accuracy after a change in the load condition. They gradually decreased the movement error from the first trial until they finally were able to reach the target in a single movement. On some exceptionally rare occasions, subjects were able – maybe through anticipation – to bring the cursor within the target on the first trial of a block.

c) *... and required about 2 trials after the change in load*

Adaptation to a change in the load condition, with the instruction "do not correct" (load towards subject) required on average 2.4 trials when the load was added and 1.8 when it was removed; for the other load direction (away from the subject): 1.9 trials for load added and 2.4 for load removed. More specifically, in experiment 1, subjects adapted after one trial to the introduction of the load in 41.54% of cases, and in 58.27% of cases when to its removal. In experiment 2, subjects corrected after one trial 60% of the time when the load was added and in 32.65% of cases when it was removed.

d) *Despite knowledge of conditions, no improvement was observable for adaptation to the same load condition as the experiment progressed*

Even though subjects were allowed practice prior to the experiment until they were able to make fast discrete movements to the target in each load condition and were aware that the load conditions (zero load and load) were going to be presented to them alternatively, they seemed unable to take advantage of this information and of their practice to decrease the amount of trials required to adapt to a change in load condition as the experiment progressed. This phenomenon may be explained by suggesting the involvement of short- rather than long-term motor memory in the process of adaptation to changing load condition, the subject relying on the information from previous trials to guide his behavior, rather than on information from the previous blocks of trials.

e) The instruction to correct movement errors during a trial led to adaptation to a change in load in significantly less trials, furthermore, subjects never required more than 3 trials for adaptation

When subjects were able to establish the correct arm configuration to bring the handle to the target in the course of the trial where the change in load occurred, data shows that they adapted to the change in load in significantly less trials than when they were not allowed to correct movement errors in-trial, regardless of load direction. For example, adaptation occurred in one trial in 64% (experiment 3, load towards subjects) and 82% (experiment 4, load away from subjects) of cases when the load was added. Also, for experiments 3 and 4, adaptation to removal of the load occurred in one trial in 72 and 74% of cases, respectively and adaptation to introduction of the load in 64 and 82%.

f) *The adaptation process can be explained by the threshold control model in a physiologically feasible way*

Three distinctive R configurations were observed for each experiment (R_i, R_0, R_+ (experiment 1) or R_- (experiment 2)), as well as two Q configurations (Q_0, Q_- (experiment 1) or Q_+ (experiment 2)). Adaptation to a change in the load condition (no load to load or vice-versa) occurred by a gradual transition from either the R_- or Q_+ (e.g. experiment 2) configuration to the R_0 or Q_0 configuration, respectively. Adaptation to a change in load condition occurred as follows: on the first trial of a block, trial in which the subjects, unaware that the load condition was going to change, reproduced the same command as in the previous trial – which had been accurate which now leads to a movement error (configurations R_- or Q_+). Subjects then gradually modified their command in each following trial, taking into account the current load condition, until the specified command allowed them to reach the target again (configurations R_0 or Q_0) and then reproduced this command until the load condition was changed again, where they had to start the adaptation process once more.

g) *EMG-posture relationship can be explained by the threshold control model in a physiologically realistic manner*

Tonic EMG levels of muscles at different steady-state positions with the same load (R_- or R_+ vs. R_0; Q_+ or Q_- vs. Q_0) were analyzed (see methods); as well as similar postures with different loads (R_0 vs. Q_0) in experiments 1 and 2. The results are reported in Table 3. Data shows that the tonic EMG levels for, on average, 6 of the 7 recorded muscles for different positions with the same load condition (R_- or R_+ vs. R_0; Q_+ or Q_- vs. Q_0) were not significantly different. The same analysis done for similar postures with different loads (R_0 vs. Q_0) showed a statistically significant difference in 4 of 7 muscles per subject, on average. This result was to be expected given the load difference between the two conditions. However, the finding of similar levels of EMG for different postures achieved in the same load condition is an experimental finding that the force control model, in its current formulation, cannot explain, whereas it can be explained by the threshold control model and in a physiologically logical manner.

h) The findings of this study, more specifically those pertaining to the analysis of EMG activity for different postures cannot be accounted for by the force control hypothesis in its current form (see Discussion), but are well explained by, and do not prove to be in conflict with, the threshold control theory (λ model for motor control).

CHAPTER VI

6.0 References

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