Endpoint control in fast point-to-point elbow rotations:

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Summary and conclusions

In present literature on the control of movements it is controversial which aspects of our movements are planned and controlled and which information is transferred from the brain to the peripheral motor system (motor commands). When assuming that the brain plans and controls joint angle trajectories a high loan on intelligence is made in the process of calculating the required net joint torques and converting these net joint torques into motor commands. Based on the dynamical properties of the peripheral motor system it has been suggested that the brain plans and controls movement endpoints (Bizzi, et al. 1992; Feldman 1986; Hogan 1984; Kistemaker, et al. 2006). It has been shown that the peripheral motor system behaves like a mass-spring-damper system (Hogan 1985; Mussa-Ivaldi, et al. 1985). Motor commands may prescribe the point at which the peripheral motor system will reach equilibrium. Under this assumption a movement is induced by shifting the equilibrium point (EP) from one set of equilibrium joint angles to another. The dynamical properties of the peripheral motor system then generate the muscle forces that drive the joints to their equilibrium angle. This type of control takes a low loan on intelligence in the process of generating motor commands: a mapping of planned endpoint to EP is sufficient. I would like to find evidence for this type of control by falsifying that the brain plans and controls joint angle trajectories. I investigated if detailed knowledge of the external load is used in the process of generating motor commands. A result indicating that this knowledge is not used would place doubt on the assumption that the brain calculates the required net joint torques to come from planned joint angle trajectories to motor commands.

In Chapter 2, I perturbed point-to-point arm movements with a small (±25%) increase or decrease in inertia of the lower arm. I found that if inertia was changed unexpectedly for a single trial the kinematics of that trial are different from those of the unperturbed trials (peak angular velocity, number of submovements) but the initial overshoot of the movement was not (Fig. 2.2, black symbols). The fact that initial overshoot did not change means that the net joint torques over time were adapted to the new inertia. Since our experiment was set up in such a way that participants had neither the time nor the information to adapt motor commands before the point of initial overshoot this compensation can only be attributed to the dynamical properties of the peripheral motor system. Furthermore, I found that when the changed inertia was kept constant during a series of 11 successive trials, motor commands were customized to the new inertia (Fig 2.4): an increase occurred in early agonistic muscle activity for the increased inertia (HH) compared to the decreased inertia (LL). This result indicates that in the process of controlling movements, the brain does more than minimizing the endpoint error (Todorov and Jordan 2002; Van Beers 2009). This falsifies the simplest form of endpoint control in which the brain only controls the planned endpoint of the movement. Other kinematic parameters are controlled as well. The increased agonistic muscle activity I found when motor commands were customized for the higher inertia can be interpreted in two different ways. Advocates of endpoint control will interpret it as an increase in the level of cocontraction to achieve an increase in joint stiffness; an increase in joint stiffness may lead to an increase in movement acceleration and hence movement velocity (Gribble and Ostry 1998A). Alternatively, advocates of trajectory control would interpret the customization of motor commands as an updating of an internal representation of the inertia of the lower arm. Discriminating between these two interpretations by investigating the customization of motor commands to inertia does not seem possible. For either one of them it can be argued that the customization of motor commands to an increased inertia would lead to both an increase in net joint torque and an increase in joint stiffness due to cocontraction. For the endpoint control hypothesis an increase in joint stiffness would self evidently lead to an increase in net joint torques. Alternatively, for the trajectory control hypothesis it can be argued that an increase in net joint torques would necessitate cocontraction to stabilize the elbow joint (Brookham, et al. 2011; Solomonow, et al. 1988). Therefore I needed an experiment in which the customization of motor commands to external conditions would require an adaptation of net joint torques that could not be achieved by adjusting the joint stiffness. For example a position-dependent external torque perturbation.

In Chapter 3, I perturbed point-to-point arm movements with a position-dependent force field for which the effect on the movement is presumed to be known in the brain: the gravitational field (Papaxanthis, et al. 2002). I reasoned that if the brain plans and controls joint angle trajectories, it would benefit from having an internal model of gravity that predicts gravitational torques for a planned movement trajectory (specific a priori knowledge of the gravitational effects). Participants were first placed in a supine position and practiced to make point-to-point arm movements in a nearly vertical plane of movement relative to gravity. After they were adapted to this unfamiliar orientation in the gravitational field, they were placed in a more familiar orientation: in upright position. The same movement in a body-fixed frame of reference was made; hence the movement now occurred in the horizontal plane relative to gravity. In the case that an internal model of gravity was used to provide specific a priori knowledge of the gravitational effects, motor commands would be customized to the gravitational effects in the new plane of movement from the first trial on. In this case any change in kinematics found for the first trial in the horizontal plane would persist if successive trials in this plane were made. Alternatively, if no specific a priori knowledge of the gravitational effect was used I expected that motor commands were not customized or aspecifically customized to the gravitational effects for the first trial in the horizontal plane of movement. In this case, I expected specific customization to occur if successive trials in this plane were made. I found that for the first trial in the horizontal plane participants adapted their motor commands in an aspecific way: they reduced peak angular velocity and ended movements with less overshoot compared to target centre regardless of the gravitational effects encountered in the preceding movements in the vertical plane (Fig. 3.3). Similar changes in kinematics have been reported for experiments in which information on external conditions was limited (Elliott, et al. 2004; Hansen, et al. 2003). I conclude that for the first trial in a new plane of movement compared to gravity, specific a priori knowledge of the gravitational effects was not used when generating motor commands. This places doubt on the assumption that when planning movements the brain uses an internal model of gravity to calculate gravitational torques for a planned movement and undermines the assumption that the brain calculates required net joint torques for planned joint angle trajectories. When successive trials in the horizontal plane were made the reductions in peak angular velocity and overshoot diminished. This indicates that motor commands were specifically customized when a posteriori knowledge of the gravitational effect in the horizontal plane was available. It is feasible that participants planned and controlled endpoints and used a posteriori knowledge of the gravitational effects to remap planned endpoints to EPs. As I concluded that on the first trial in a new gravitational condition motor commands were not specifically customized to the gravitational effects it still needed explaining why movement errors remained small. To confirm that the dynamics of the peripheral motor system can compensate gravitational effects to a large extent I needed a valid musculoskeletal model of the elbow. I used a previously developed model by Kistemaker et al. (2006) and validated the maximal isometric torques of the elbow muscles with the maximal isometric torque-angle relationships reported in Chapter 4. In Chapter 5, I evaluated to what extend the elastic properties of the peripheral motor system can compensate for gravitational torques working on the lower arm.

In Chapter 4, I measured the maximal isometric torque-angle relationships for the elbow flexors and the elbow extensors. These relationships were used to fine tune the muscle parameters of a previously developed model of the peripheral motor system (Kistemaker, et al. 2006) in such a way that the isometric torque-angle curves obtained with the model fell within the 99% confidence interval of the isometric torque-angle curves as measured and with the additional constraint that values remained within the range reported in previously published research on cadavers (An, et al. 1981; Murray, et al. 1995; Nijhof and Kouwenhoven 2000). A model that has an accurate description of the maximal isometric torque-angle relationship for elbow flexors and extensors will give a realistic representation of the maximal achievable open loop joint stiffness around the elbow and therefore a realistic indication to what extent the nonlinear intrinsic elastic properties of the peripheral motor system help compensate for perturbations in gravitational effects.

Although, the simulations in Chapter 5 were designed to answer a question not directly related to the experiments described in Chapter 3 a limited comparison can be made. I can use the simulated responses to gravitational perturbation in Chapter 5 to illustrate that the peripheral motor system can control movements for the perturbations as used in the experiment described in Chapter 3. The simulation results shown in Fig. 5.3B predict that the intrinsic viscoelastic muscle properties as described by the nonlinear musculoskeletal model (STIM-model) can compensate to a large extend for the position-dependent gravitational torques working on the lower arm and when muscle spindle feedback was added to the model's description of the peripheral motor system (EP-model) compensation for gravitational torques improved substantially (Fig. 5.3B: EP-model predicts only minimal static errors). Although the simulations did not match the conditions of the experiment described in Chapter 3 (the range of motion, the mass of the lower arm and manipulandum, etc.) the gravitational torques simulated (ranging from 0 Nm at elbow angle of 45° till 2.9 Nm at elbow angle of 135°) were comparable to the gravitational torques participants encountered during their movements (Fig. 3.2). Therefore, I conclude that for the gravitational perturbation used in Chapter 3 the peripheral motor system was able to compensate gravitational torques to a large extend. This supports my conclusion that on the first trial in a new plane of movement compared to gravity motor commands are aspecifically customized and a priori knowledge of the gravitational effects was not used when planning elbow rotations.

Not all researchers use a detailed musculoskeletal model to simulate the experimentally observed responses. This can affect the conclusions that are drawn from the kinematic responses observed. If, for instance, I had simulated the gravitational manipulation described in Chapter 3 with a model of the peripheral motor system that does not describe the intrinsic muscle properties and the muscle spindle feedback, this model would have predicted large static errors at the movement's endpoint if motor commands are not specifically customized to the new gravitational effects. This would have led me to draw a completely different conclusion from the kinematic responses I found in my experiment: for the first trial in the horizontal plane motor commands were specifically customized (although not completely) to the gravitational effects. I would then have concluded that participants had used a priori knowledge of the gravitational effects when planning elbow rotations. The simulations described in Chapter 5 were done to see if similar misinterpretations of measured responses can be made for other external load perturbations.

In Chapter 5, I tested several types of models of the peripheral motor system used in the literature for their robustness to perturbation in external load. These models differed in the level of simplification with which the dynamical properties of the peripheral motor system are described. For both a fast 90° flexion and a fast 90° extension of the elbow, I obtained an input signal (motor commands) for each type of model. While keeping the input signal constant, I perturbed the simulated movement using three types of perturbations: position-dependent external torque perturbation (gravity), velocity-dependent external torque perturbation and inertial perturbation. I found that the model in which all dynamical properties of the peripheral motor system were discarded had no robustness to these perturbation types. This type of model would predict that to successfully control movement for a perturbation in external load motor commands need to be accurately customized to the external load condition. For the three models that contain a simple or elaborate description of the dynamical properties of the peripheral motor system the robustness to perturbation differed. This was most clearly present in the position-dependent external torque perturbation (Fig. 5.3, KBI-model, STIM-model and EP-model) and in the destabilizing velocity-dependent torque perturbation (Fig. 5.4, KBI-model, STIM-model and EP-model). These results imply that if in perturbation experiments it is found that participants were successful in controlling the movement for perturbation, the conclusion on how accurate motor commands had been customized to the external load depends on the type of model used to simulate the perturbation. And hence the conclusion made for the involvement of the brain in controlling the movement depends as well on the type of model used.

In summary, my experiments on perturbations in inertia and gravitational effects suggest that detailed information on the external load when making elbow rotations is not essential. In addition, I found that when generating motor commands for elbow rotations specific a priori knowledge of the gravitational effects was not used to customize motor commands to the external load. These findings place doubt on the assumption that the brain calculates net joint torques based on planned joint angle trajectories. I also found that motor commands are customized for a small change in inertia on a trial-to-trial basis. Even though I conclude that the brain does not need detailed knowledge of inertia and the gravitational effects to control movement for external load, it can benefit from a posteriori knowledge of the effect of these loads on the movement to specifically customize motor commands to the external load conditions. This customization can involve an adjustment of mapping endpoints to EPs or an updating of the knowledge available in the brain concerning the external load. I cannot distinguish between these two options using the methodology of mechanically perturbating a point-to-point arm movements.

The perturbations sizes used in the experiments described in this thesis can be qualified as small to moderate. They are comparable to perturbations we encounter frequently in our daily life arm movements, for example when lifting a pack of milk not knowing how full it is. For these experiments, I conclude that to control movement it is feasible that motor commands specified EP's that set both the equilibrium joint angles and the stiffness of the joints. This means that endpoint control can provide an explanation for how the brain controls goal-directed arm movements under the great variety of external conditions as encountered in daily life.