

Grip force adjustments during rapid hand movements suggest that detailed movement kinematics are predicted

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Abstract: The λ model suggests that detailed kinematics arise from changes in control variables and need not be explicitly planned. However, we have shown that when moving a grasped object, grip force is precisely modulated in phase with acceleration-dependent inertial load. This suggests that the motor system can predict detailed kinematics. This prediction may be based on a forward model of the dynamics of the loaded limb.

As outlined in the target article, a central notion of the λ model is that the kinematics of movement arise as a result of changes in control variables (CVs) and need not be explicitly planned. Feldman and Levin (F&L) appear to accept that CVs must be sensitive to parameters such as overall rate, direction, and displacement that define a task but they suggest that the central nervous system (CNS) does not need to be concerned with detailed kinematic features. Thus, for example, the smoothness characteristic of reaching movements is viewed as a natural consequence of dynamic processes rather than a planned feature of the motion trajectory (cf. Hogan & Flash 1987).

Nevertheless, under certain conditions, it may be desirable to predict detailed kinematics accurately. For example, such a prediction would enable the motor system to make precise adjustments for potentially destabilizing loads that depend on kinematics. Recent results related to anticipatory grip force adjustments during rapid arm movements with hand-held loads (Flanagan & Tresilian 1994; Flanagan et al. 1993; Flanagan & Wing 1993) suggest that motion planning may involve the prediction of detailed kinematics. In these studies, subjects held an object in a precision grip with the tips of the index finger and thumb at its sides. In this case, grip force (normal to the object's surface) permits the development of frictional force to counteract gravitational and movement-induced loads. We have shown that when moving an inertial (acceleration-dependent) load, grip force is finely modulated in phase with fluctuations in load force arising from the movement; grip force rises as the load increases and falls as the load decreases. The tight coupling between grip force and load force is observed in vertical and horizontal movements made at varying rates and in different directions (see Fig. 1). Despite marked differences in the form of the load force function across conditions, grip force adjustments anticipate changes in load force in all cases. Moreover, the tight linkage between grip and load is observed within conditions. For example, there are strong correlations between peaks in grip force and load force both in timing and amplitude. Finally, we have demonstrated that changes in grip force parallel fluctuations in inertial load regardless of the articulators subserving the motion of the object.

These results indicate that the motor system is able to predict accurately the time of occurrence of the peaks in the acceleration profile of the hand-held object and the load properties of the object. (On the basis of this information, the load force can be predicted and the grip force adjusted accordingly.) Thus, the results suggest that the motor system is able to predict detailed features of the kinematics. It seems unlikely that detailed kinematics can be directly predicted from changes in CVs underlying the movement. The λ model suggests that the trajectory of the actual hand will, in general, deviate substantially from the trajectory of the equilibrium position of the hand (equilibrium trajectory). Moreover, the extent of deviation will depend on the load and the form of the CVs themselves. At least in the case of rapid movements, the equilibrium trajectory of the hand would appear to be

Another look at redundancy. Redundancy, the ability to solve a problem in more than one way, is a problem that faces actors whenever the number of degrees of freedom (df's) of the effector are in excess of the number specified by the task (i.e., most of the time). Although excess effector df's allow for flexibility in performance, they present the problem of selecting among an often infinite number of possible realizations. One solution is to constrain the effector df's in some fashion to make the task of effector mapping 1:1 (eliminating redundancy). This can be done by introducing a cost function (e.g., minimizing energy or distance) or equations of constraint (Feldman's synergies in sect. 11). However, these solutions violate certain characteristics of biological movement. We illustrate this in the context of a simple, redundant, dynamical system, and then offer a sketch of an alternative solution within the context of the authors' theory (Fikes & Townsend, in preparation).

Consider the system in Figure 1A, a two-joint arm operating in Cartesian two-space with shoulder fixed at the origin. To create a redundant situation, we specify a one-df task, to locate the end effector at a particular value of y . For simplicity, we treat the dynamics in terms of the joints rather than muscles and consider only a first-order system (thus, we can plot the phase space for both joints in a plane). Figure 1B depicts the phase-space of a constraint-based solution, a synergy in which the joints are constrained to equal one another. A goal of $y = 2$ was selected, and a manifold corresponding to the forward kinematics ($y = f(\theta)$, $\theta = \theta_1 = \theta_2$; bold line) plotted. The two stable equilibrium points of the system are at the intersection of $y = 2$ and this manifold. Note that, if unperturbed, the system will move to a new goal slate along this manifold to the nearest fixed point; if perturbed, it moves back onto the manifold and onto one of the same fixed points. Thus, the system exhibits equifinality in both task-space and joint-space (by equifinality, we mean simply that the system comes to the same equilibrium position in spite of perturbations). This violates a characteristic of human movement, namely, that we tend to equifinality in task-space but not effector-space (e.g., see Folkens & Abbs 1975): the system does not seem to care *how* the task is achieved, as long as it is.

As an alternative, consider the strategy depicted in Figures 1C-D. In short, the strategy is to determine a 1-df manifold in joint-space that represents all possible joint configurations that would yield a desired goal (y value), and to define a phase space in which this set is an attractor (specifically, a continuous set of fixed points). In Figure 1C, we represent the collection of such manifolds for $-1 < y < 4$. Specific manifolds (contour lines) are drawn for $y = \{-1, 0, 1, 2, 3\}$ on the three-dimensional structure in Figure 1C. In Figure 1D, we define a vector field (gradient system) that produces trajectories toward the nearest point on the solution manifold for $y = 2$. Note that the vectors along the manifold are zero length - if the system is perturbed along the solution manifold, it will not compensate, but if it is perturbed off the manifold, it will restore onto it. Thus we produce equifinality in task but not effector (joint) space.

We believe this second solution is more reasonable as a model of biological movement, but we would like to emphasize that it is through the use of the language and conventions of dynamics that the two solutions are rigorously distinguishable conceptually. Again, we think the λ model is probably a close approximation to what biological systems actually do, but we await a rigorous, concise, and coherent development of the mathematics, followed by qualitative and quantitative testing of the theory.

NOTE

1. We wish to thank Gregor Schönauer for many helpful discussions on the topic of dynamical systems theory and its application to behavioral research during his stay at Indiana University in the summer of 1994. Many of the ideas presented in this section can be traced, directly or indirectly, to these conversations.

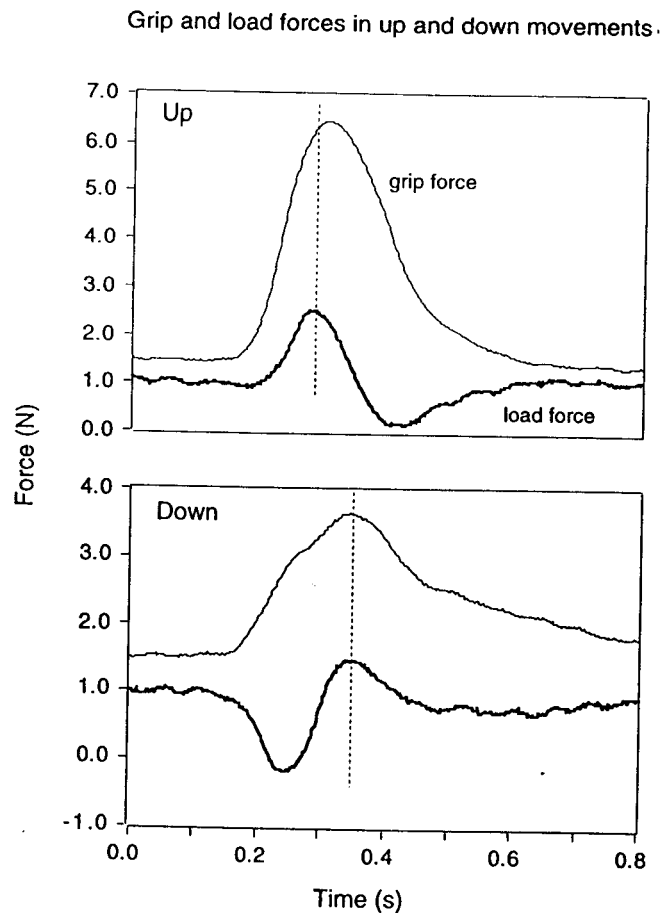


Figure 1 (Flanagan et al.). Grip force (thin) and vertical load force (thick) records from single upward (top panel) and downward (bottom panel) point-to-point movements. The load force represents the sum of the inertial and gravitational loads. The peak load occurs early in the upward movement and late in the downward movement. The peak grip force coincides closely in time with the peak load force (dashed lines). Note that in the downward movement, grip force starts to rise at the start of the movement and there is a "bulge" that coincides with the peak in negative load (shaded area). This prevents slip as the object is accelerated rapidly downward. In slower downward movements, where the load is always positive, grip force does not increase until later in the movement and, in fact, often decreases at the start.

insufficient for predicting kinematics; a fortiori, the equilibrium trajectory is insufficient for control of grip force during transport of grasped objects.

We suggest that the prediction of object acceleration may be based on an internal model of the dynamics of the loaded limb. This is not necessarily inconsistent with the λ model. In particular, the motor system may use an internal forward model of dynamics to predict kinematics from planned CVs. The forward model could thus provide the basis for coordination of arm movement and grip force (and other postural adjustments). Forward models may be distinguished from inverse models, which translate planned kinematics into the forces required to achieve the plan. Thus, whereas inverse models hold that kinematics are planned, forward models suggest that kinematics are predicted. The idea that there is an internal forward model of dynamics preserves the basic idea in the λ model that the motor system plans in terms of CVs rather than kinematics, but, at the same time, provides a way in which grip force can be coupled with load forces that depends on kinematics.

Of course it might be argued that, even though grip force

involves prediction of arm kinematics, such a prediction plays no part in arm movement control in general. That is, control of grip force in moving objects held in a precision grip may be a special case and, if objects are encompassed in a full grasp or if there is no hand-held object, there is no requirement for the CNS to predict kinematics. We believe that this position is not tenable, however, because of findings that there are anticipatory postural adjustments associated with arm movements (Belen'kii et al. 1967; Bouisset & Zattara 1987). These, it has been argued (Friedli et al. 1988), serve to minimise the dynamic consequences of the arm movement for remote body segments. This suggests that an internal model of limb dynamics may serve whole body posture stabilisation just as an internal model might facilitate stabilisation of a hand-held object during arm movement.

Finally, we would point out that the notion that the motor system has an internal representation of limb dynamics is, in some sense, already assumed in the λ model. In particular, to deal with gravitational (or elastic) loads, CVs must be adjusted because the relation between actual positions and equilibrium positions is altered. This adjustment will depend on the position-dependent load properties of the arm. Thus, it seems reasonable to suppose that this information, at least, is used in motion planning.

Reciprocal and coactivation commands are not sufficient to describe muscle activation patterns

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Abstract: Recent results have shown that the relative activation of muscles is different for isometric contractions and for movements. These results exclude an explanation of muscle activation patterns by a combination of reciprocal and coactivation commands. These results also indicate that joint stiffness is not uniquely determined and that it may be different for isometric contractions and movements.

It was one of the attractive features of the λ model that the threshold muscle length λ was the only control variable (CV) necessary and sufficient to characterise the activation of muscle (by the difference between muscle length and λ) and its contribution to stiffness. When several muscles are involved, just as many control parameters are necessary, one for each muscle. With these CVs it was possible, according to the model, to control the position of a limb (by the position at which forces by external loads and those exerted by the limb are in equilibrium), limb velocity during movements (by controlling the rate of change of λ), and EMC patterns.

Recent experiments have provided evidence that nature is more complicated than the simple view described by the λ model. These new studies have shown that the relative amount of EMC activity in human arm muscles is different under conditions in which subjects are instructed to exert an isometric force at the wrist or to move the hand very slowly against the same external force (see Miller et al. 1992; Theeuwens et al. 1994a; 1994b). In terms of the λ model, this implies that the rest-length of these muscles is changing in a different way for each of these instructions. The important point is that the amount of EMC changes in a different way for different muscles: for some muscles the recruitment threshold of motor units decreases (and as a result the corresponding EMC activity increases); for other muscles, the recruitment threshold increases corresponding to a decrease of EMC activity. Further experiments by Theeuwens et al. (1994b) revealed that for movements assisting an external load the relative activation was different from that in isometric contractions and from that observed for movements against an external load. These results demonstrated that the relative activation of muscles is different for various motor tasks.