movement end position (stage 2). This would elicit a large burst of activity in the antagonist muscle, even if the limb does not move at all, as in the blocked trials of Wadman's experiment or if the limb is ischemically deafferented (Sanes & Jennings 1984). Finally, the reflex threshold is set at the final value (stage 3), with a coactivation of agonist and antagonist muscles, generating a large stiffness. Gradually, then, the stiffness decreases to its final value related to the decreasing amount of coactivation (stage 4).

The coactivation observed after fast goal-directed movements (Feldman 1980; Vincken, Gielen & van der Gon 1984) has been shown to reflect the setting of an equilibrium point. Increasing the amount of coactivation results in an increased stiffness, holding the limb close to the equilibrium position. However, if the stretch reflex contributed to stiffness only, system theory explains that coactivation would decrease the damping and therefore the stability of the limb. Recently, it has been shown (Gielen & Houk 1984; Gielen, Houk, Marcus & Miller 1984) that the stretch reflex also contributes to the viscous properties by a nonlinear component. These viscous properties may stabilize the stretch reflex and make it useful, not only to compensate for external disturbances, but also to assist during normal voluntary movements. The role of the stretch reflex as assisting in limb stabilization and in the attainment of desired end position is compatible with the main characteristics of the λ model. However, more experimental data are necessary to obtain conclusive evidence for this hypothesis.

An essential feature of the λ model is that the reflex threshold is set by input to the α motoneurons, γ motoneurons, and interneurons in the reflex pathway. The phenomenon of motor equivalence then requires that the unique solution to the problem of coordination of a system with redundant degrees of freedom be solved in a similar way by the central nervous system and by spinal mechanisms in order to guarantee an effective cooperation between central commands and reflex activity. Berkinblit et al. convincingly show that the coordinate transformations required to explain the phenomenon of motor equivalence have to be attributed to the spinal cord, whether or not similar processes have to be ascribed to higher centers of the central nervous system. In this view the study of the role of interneurons and the input of central command signals to interneurons should be an important field for future research.

What are the building blocks of the frog's wiping reflex?

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A theory of motor control must first and foremost account for observed motor behaviour, so it might be useful to examine some of the descriptive tools used in the target article for the representation and analysis of movement (motor behaviour). By limiting the analysis to movements carried out mainly in the frog's horizontal plane, and by measuring only the projections of joint angles on this plane, movement, which takes place in three-dimensional space, has been reduced to a two-dimensional phenomenon. The main question discussed in this commentary is whether such a reduction is justified in view of the issues being raised. This question is first examined for single-segment movement and then for the movement of the compound limb. The last section examines the chosen scale of measurement.

(a) Single segments. Evidently, the movements of a single axis, of constant length, free to move about one fixed end, are enclosed by a sphere. The curves traced by the axis on its surface are circles or parts of circles, of various sizes and orientations. Every segment of the body can be regarded as such an axis, moving around its joint, which is its fixed end. The path of movement is determined by the angular relation between the stationary axis of movement (around which the circle or its part is traced) and the moving axis. When the angle between the two axes is 90°, the axis traces the largest circle on the surface of the sphere, moving along one plane. When the angle is smaller, the circle is smaller and its curvature steeper (Fig. 1). It follows that any two points on the sphere's surface can be traversed either in the shortest way, that is, through a plane movement (e.g., the interrupted line from E to F in Fig. 2), or through one of many steeper arcs (e.g., the heavy line from E to F in Fig. 2). When the angle equals 0°, the circle is "reduced to a point," and the moving axis rotates around itself (Eshkol & Wachman 1958) (Fig. 1).

The equilibrium point hypothesis suggested by Berkinblit et al.. implies that segments that are free to move around a spherical ball-and-socket joint (e.g., the upper hindleg) would nevertheless always move along the shortest path from one point to the next on the sphere's surface, thus producing only plane movements and excluding controlled steeper arcs between the same points. The elimination of the possibility of steeper arcs allows the exclusive use of the terms flexion and extension. which imply a change of relation between two adjacent segments, disregarding their direction (position) in space. Thus, by ignoring the third dimension, the target article validates the a priori equation between final position and path form, and its results are bound to confirm its initial distinctions. To argue that final positions of a segment's movements are the only variables controlling its movements, it is first necessary to show that the paths of movement are fortuitous, and therefore uncontrolled, but this goal cannot be accomplished in the absence of a system that can represent the different paths.

(b) The compound limb. The limb that performs the wiping may be considered as a mechanical linkage of interdependent segments. This interdependence implies that an active movement of a proximal segment would change the locations and modify the paths of movement of all the segments distal to it. Clearly, a movement of a proximal segment to a fixed position in relation to its base (e.g., if the upper leg had moved in all strokes to the same position in relation to the pelvis) drastically reduces the freedom of movement of the whole linkage. A movement to

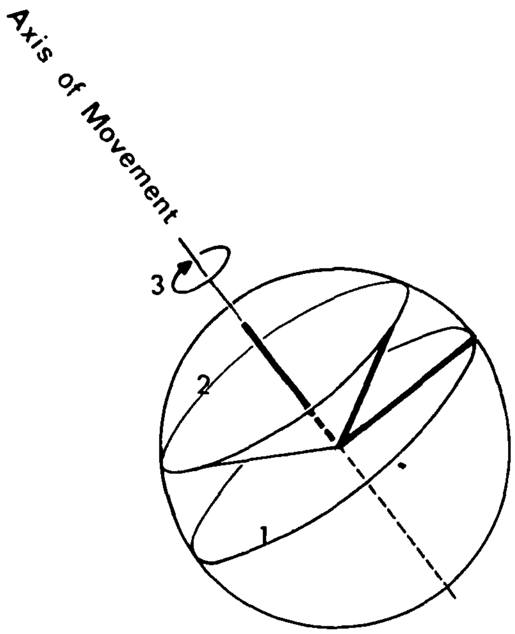

Figure 1. (Golani). Three types of circles produced by movement of an axis about the same stationary axis of movement. The heavy lines describe the moving axis, tracing 1, the largest circle; 2, a smaller circle with a steeper arc, and 3, a rotation.

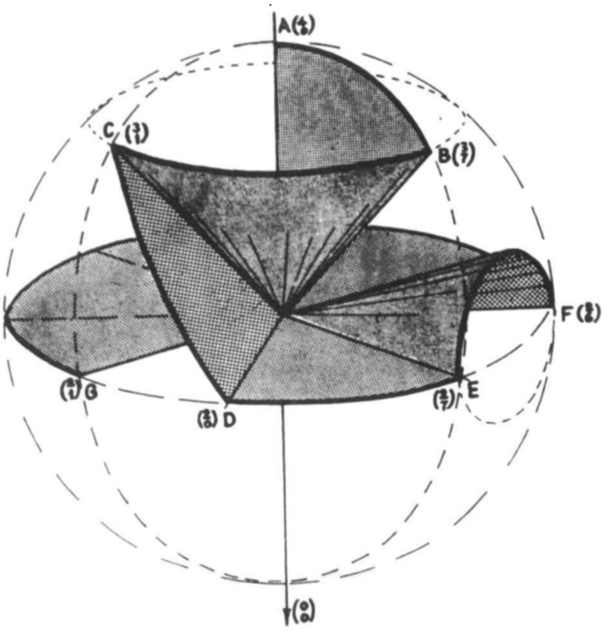

Figure 2. (Golani). A sequence of movement traced within a sphere by an axis. The interrupted line between E and F describes the shortest path between these points. The heavy line from E to F describes one of many steeper and longer possible paths. (Reproduced from Eshkol and Wachman, 1958, with permission of the Movement Notation Society.)

such a position of a distal segment does not reduce the freedom of the segments proximal to it. Therefore, the movement of the metatarsus on the tarsus to a fixed position that allows, anatomically, the next movement of whisking (target article, Fig. 12, Fig. 7) does not tell us anything about the nature of the movements of the more proximal segments. These are expected. and reported, to reach *variable* positions at the end of the same stages of different strokes. The question that lies at the heart of the issue of intersegmental coordination is: What is the computational formula that ties this variability into an organized pattern? Instead of treating this question at the level of observables, the target article relegates it to the function of the spinal cord.

One of the variables presumably controlled in the reflex is suggested by its function – wiping – and is expressed in the relations of contact or near-contact between the tip of the compound limb and specific locations on body surface. Another candidate variable may be the direction (position, viewed proximodistally) of the distal segment – the metatarsus – in relation to the frog's midsagittal plane. This is suggested by the observation that "the frog . . . varies the joint angles . . . to select the 'direction of attack'" on the stimulus (target article, Fig. 7). If indeed these two variables are controlled, then their control is evidently accomplished through spherical movements (see section on single segments) of the individual segments on top of their respective proximal neighbours. For instance, in the aiming phase illustrated in Fig. 7, the relationship between the tip of the toes and body surface is fixated, as the metatarsus changes its position in relation to the midsagittal plane, first by being carried along passively (frames 21–22), and then (frames 22–23) due to its own active movement. Throughout the process, the lower leg moves actively on the upper leg, carrying along the passive tarsus. This process involves a change of position of each of the segments in relation to (a) its posterior segment and (b) the midsagittal plane. Because the computational task exclusively involves relations between the parts of the body, cartesian coordinates and metric transformations are extraneous and irrelevant to the computational task at hand.

(c) The chosen scale. Does variability in and of itself imply motor equivalence? For every scale being used for measurement there is a finer scale that might replace it, and depending on the chosen scale. the movement may appear fixed or variable. One problem in the analysis of the performance of a control system is how to distinguish between variations that reflect (a) different strategies, (b) quantitative variations within strategies, and (c) the system's sensitivity to error. Such a distinction can be exemplified in the analysis of metatarsus movement between aiming and whisking: The strategy is movement to the same position in relation to the tarsus; quantitative variations are reflected in the amount of movement to this position; and the system's sensitivity is disclosed in the range of final positions (130°–150°). But on what grounds are the variations recorded for the more proximal segments interpreted to reflect motor equivalence? The variations in joint angles that are taken to demonstrate motor equivalence in Fig. 9 are smaller than the variations in the final positions of the metatarsus prior to whisking, which are taken to show the opposite, namely, that this position is fixed. It seems that a deliberate choice of a coarser scale would make the organization at the proximal joints of the linkage easier to discern, without refuting the regularity established at the distal end.

The invariant characteristic isn't

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Few theories have a simplicity and elegance that stimulate and inspire an entire discipline. Merton's (1953) servo hypothesis was one. Feldman's invariant characteristic hypothesis (Asatryan & Feldman 1965) is another. It is the nature of such theories to excite not just their creators but many other investigators to challenge them, test them. argue about them, and, of course, as is always the ultimate case with scientific theories, reject parts of them as incorrect or incomplete. This was the case with the reflex servo as the basis for voluntary motor control, and this is also the case for the invariant characteristic.

The invariant characteristic (IC) curve, measured by successive unloadings of a voluntarily contracted limb, is an incomplete observation of the relationship between torque and angle at a joint. A more complete description is shown in Fig. 1. Curve I describes the equilibrium angle of an elbow that is initially supporting a load (T_a) at an angle (X_a) and either unloaded (downward to the left) or loaded (upward to the right).

The S shape of this curve, indicating a softening springlike behavior in both shortening and lengthening, is the most important feature of the muscle–reflex–CNS system. *At rest, the limb always lies at the inflection point of the S-shaped curve.* If we unload from T_a to T_b or T_c we reach equilibrium at X_b or X_c just as predicted by the IC hypothesis. However, if we first unload to T_b, wait a moment, and then further unload to T_c, we do not end at X_c but at $X_{c'}$, which is closer. This is due to the change in muscle state that occurs between the first and second unloadings. The change is a shift in the torque–angle relationship from that described by curve I to that described by curve II. Furthermore, restoring T_a does not restore X_a but falls slightly short. This phenomenon has been described briefly in Gottlieb and Agarwal (1983; 1984).

The plastic change in the joint length–tension description is not an "invariant characteristic." More complex models are required for even this seemingly simple case. These will involve both translation of the torque–angle relation (to keep the inflection point at the "rest" position, wherever it may move to) and a change in its overall steepness. The implications of this are that