Psychophysical approaches to motor control

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A variety of experimental approaches have recently helped identify the reference frames and coordinate systems that describe the control of eye and limb movements. These descriptions apply at the behavioral level and also, despite the distributed nature of neural processing, to the population responses of different neural structures. Studies on the process of adaptation to altered environments have also provided new insights into the controlled variables for movements: although handpaths can be adapted to extrinsic demands, the adaptation is, in some cases, in an intrinsic frame of reference.

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Introduction

The title of this review promises more than it can deliver. Psychophysical approaches to motor control encompass a large variety of studies aimed at resolving many different questions. It would be impossible to review all the work on this topic that has been published in the past two years. Accordingly, in this review we focus on two main issues. Firstly, whether or not the concept of 'frames of reference' is useful to understanding neural processing and, if so, how does one identify the neurally implemented reference frame? Secondly, what insights can be gained by studying the process of movement adaptation to various perturbations? While we have restricted the number of topics, we have tried to unify insights gained from two lines of investigation in motor control: eye and limb movements. At the end of the review, we will briefly mention notable results on related topics.

Reference frames and coordinate systems

The concepts of reference frames and coordinate systems have been used widely in the study of eye and limb movements, especially when these movements are not limited to a single degree of freedom (reviewed in [1,2]). A reference frame is invoked automatically whenever we make a measurement or describe an experimental result: for example, describing the position of the eyes relative to the head (a head-fixed frame of reference), or relative to the trunk (body-fixed frame of reference), or relative to the world (an inertial or gravitational frame of reference). Coordinate systems come into play whenever we use a set of axes fixed to the frame of reference to make our measurements. For example, the superior, anterior and medial directions define a Cartesian coordinate system in a body-fixed frame of reference.

Despite their obvious utility for making measurements and describing data, the question has arisen whether or not these concepts have any biological relevance [3,4]. That is, are they alien ideas from engineering and physics that may actually diminish rather than enhance our understanding of how the nervous system works? The argument is as follows: neural processing is essentially distributed in nature and, therefore, in general, no two neurons will encode the same parameter(s). If that is so, then each neuron would have its own frame of reference and its own coordinate system, implying that there are as many reference frames and coordinate systems as there are neurons. Furthermore, in general, each of these reference frames would be a hybrid: for example, fixed not in space, nor to the body, nor to the head. If that were so, trying to understand neural control of movement in terms of reference frames and transformations between different reference frames would not be a particularly fruitful undertaking and one might be well advised to shift to a different line of inquiry: for example, elucidating the cellular mechanisms by which neural networks manage to organize themselves.

Several investigations, published in the past two years on a wide variety of topics ranging from the vestibulo-ocular reflex to posture control, suggest that reports of the demise of the concept of reference frames in motor systems research may be premature.

Eye movements

Angelaki and Hess [5••] have shown that the vestibulo-ocular reflex (VOR) is organized in a gravitational frame

Abbreviations

INC—interstitial nucleus of Cajal; **OKAN**—optokinetic afternystagmus; **VOR**–vestibulo-ocular reflex.

of reference (i.e. one that is aligned with gravity) and not in a frame of reference that is head centered. They suggest that the transformation from the head-centered reference frame of the semicircular canals to a frame of reference aligned with gravity is accomplished by the 'velocity storage integrator' [6] in the brain stem. This conclusion stems from a series of measurements of the direction of nystagmus following the cessation of head rotation at constant angular velocity, and builds on earlier work [7] concerning the direction of nystagmus after optokinetic stimulation (OKAN) has ceased.

When monkeys are subjected to constant velocity head rotations about different axes in space and the orientation of the monkey's head with respect to gravity is suddenly changed at the end of the constant-velocity rotation, there is a re-orientation (in a head-fixed frame of reference) of the direction of post-rotatory nystagmus [5••]. The axis of eye rotation shifts so that it re-aligns itself with the axis of head rotation (in the inertial frame of reference) that provided the original stimulus. Subsequent work by Angelaki and Hess [8•] has demonstrated that this coordinate transformation involves signals from otolith afferents and deteriorates following lesions of the vestibulo-cerebellum.

The utility of organizing the VOR in a gravitational frame of reference is clear, as the VOR acts to stabilize gaze (i.e. eye position in space). The work reviewed above implicates the velocity storage mechanism and the vestibulo-cerebellum in the spatial transformation from a head-fixed to a spatial frame of reference. Angelaki and Hess [8•,9] suggest that the combination of semicircular canal and otolith signals processed by these structures allow the head angular velocity to be detected within an inertial frame of reference (see also [10,11]). Such a signal may be useful not only for eye movements, but also for controlling posture and limb movements.

Anatomically, there is a segregation of the velocity-to-position integrator into a part dealing with horizontal eye movements (nucleus prepositus hypoglossi) and one dealing with the vertical and torsional components (interstitial nucleus of Cajal [INC]) [12]. Single cells in the INC are tuned to the vertical components of a saccade [13,14]. These cells also exhibit directional tuning during whole body rotations eliciting a VOR. Under these conditions, the directional tuning found in the INC appears typical of a distributed system [15], in that it varies between cells. Some respond similarly to vertical canal afferents, others similarly to motoneurons innervating vertical eye muscles, and some are aligned with neither canals nor muscles, suggesting no particular coordinate frame for this structure [16,17].

An analysis of the result of INC inactivation [18••] leads to a different conclusion. Lesions of the neural integrator lead to a failure to maintain gaze following a saccade [12,19]. When the post-saccadic drift evoked by inactivation of the INC is described in a reference frame that is fixed in space, the post-saccadic drift has horizontal, as well as vertical and torsional, components that are dependent on eye position. However, in the frame of reference defined by Listing's plane, the horizontal component becomes negligible. (Listing's plane is defined behaviorally: eye position at the end of a saccade can be defined mathematically as a rotation of the eye about some axis in space from one initial posture; the rotation axes are found experimentally to be confined to a plane.) Crawford [18••] has taken advantage of the fact that the orientation of Listing's plane may vary from day to day in the same subject, demonstrating an invariance of the post-saccadic drift only when it is defined in that particular frame. His results show a way out of the dilemma posed in the introduction to this section: even though the tuning of individual neurons may vary and not be suitable to define a unique frame of reference, the population response may nevertheless be appropriate to define reference frames and coordinate systems.

In the reference frame defined by Listing's plane, eye positions after saccades have zero torsion (reviewed in [20•,21]). As this is not true for the VOR [22], Listing's law represents a neural constraint. The question of whether or not the same constraint holds for head and arm movements has received considerable attention in recent years [23–25]. The consensus has been that it does not, but that head, trunk and arm movements do obey Donders' law [26•,27•], which states that is there is a unique orientation of the head, trunk or arm for any particular target direction. However, this does not hold true for arm postures when subjects grasp objects [28,29•], and the conclusion has also been challenged for pointing movements [30••].

According to the example described above, inactivation of a neural structure provides one way of deciphering the frame of reference of the population response of that structure. Another means of identifying putative frames of reference is by simulations based on neural network models. Such an approach has been used by Andersen and colleagues [31,32,33••] to show that a neuronal population in posterior parietal cortex could potentially encode the location of a visual stimulus in an inertial frame of reference. Single neurons have responses that are tuned to the retinal location of a spot of light. This tuning does not change when the eye position in the head or the posture of the head relative to the trunk changes (i.e. a stimulus at a particular location in a retinotopic frame of reference always gives the best response). However, the amplitude of the response also depends on the eye position in the head and the head position relative to the trunk. The sensitivity to the latter two parameters is orderly, such that neural discharge depends in a multiplicative fashion on stimulus location in a retinotopic frame of reference and on the gaze direction [33••]. Thus, single neurons do not encode the stimulus location in any intuitively simple reference frame. However, simulations show that the population response has the potential to encode stimulus location in a reference frame that is fixed in space.

Although this approach is less direct than the earlier one, it suffices to at least establish the feasibility of a particular model for neural information processing. Well-designed behavioral paradigms (such as the one described in [5••]) and reversible inactivation studies [18••] provide some of the means for explicit tests of this type of model's predictions.

Posture and arm movements

The past few years have seen considerable progress towards identifying coordinate systems that describe the control of posture. Cat posture exhibits stereotyped behavioral responses under both static and dynamic conditions. When the support surface on which the cat is standing is displaced transiently, the tangential ground reaction forces generated by the limb's musculature are restricted to directions that are approximately ±45° with respect to the midsagittal plane, irrespective of the direction of displacement of the platform [34]. Recent investigations [35•,36,37•] have described the conditions under which this invariant response is maintained by varying the distance between the forelimbs and hindlimbs, and by investigating the effect of previous experience.

Studies on the kinematics (posture) and kinetics (contact forces) under static conditions have identified the coordinate system in which the kinematic aspects of the posture are controlled. In particular, it seems that the length and orientation of each limb are the parameters that represent the limb's geometry [38,39] and that they may be controlled independently. In a recent study, Lacquaniti and Maioli [40••,41••] elaborated on these conclusions by describing cat posture under a wide variety of experimental conditions: varying the tilt of the platform, the interfoot distance, and head orientation, and in the presence of applied loads. They concluded that kinematics and kinetics were regulated independently of each other. They found a large amount of variability in limb posture, as defined by the length and orientation variables, but that the three joint angles of each limb (e.g. hip, knee and ankle for the hindlimb) were linearly dependent on each other (i.e. their values were restricted to one plane). In an analytical *tour de force* they examined several hypotheses that could account for such a linear dependence [41••], and were able to exclude a variety of possible explanations. The biological solution appears to be one that favors motor equivalence, in that different combinations of joint angles are compatible with a single value of length and orientation, and one that permits the independent control of these two variables.

To define the joint angles of a limb, Lacquaniti and Maioli [40••] found it advantageous to use a hybrid coordinate system, in which some joint angles were defined with respect to the vertical (absolute angles), whereas others were defined as the angle between adjacent segments (relative angles). It had previously been suggested, on the basis of psychophysical observation [42], that human arm posture is sensed in terms of the limb's orientation with respect to the vertical direction plane and midsagittal plane (i.e. as absolute angles). Scott and Loeb [43•] have developed an interesting approach to study this problem. Under the assumption that muscle spindles are largely responsible for transducing limb posture, the authors computed the distribution of muscle spindles that would be optimal for encoding limb posture in different coordinate systems, absolute and relative. Each coordinate system gives a different prediction. For example, two-joint muscles are optimal for encoding absolute orientation of the distal limb segment. Comparing the predicted distribution of spindles with data for humans, they found that the actual distribution did not match any of the predicted ones. Their study supports the conclusion that information from muscle spindle afferents may be used for a variety of purposes in a variety of coordinate systems, and that the actual distribution may reflect a compromise between conflicting demands.

Results from several recent studies suggest that the orientation of the hand is defined in a hybrid frame of reference. Subjects are able to orient the hand so that it is aligned with the axis of an elongated object when the hand is at the remembered location of the object. However, they make consistent errors whenever the hand is not at the object's location [28,44•]. The bias in these errors suggests that hand orientation is defined neither in a frame of reference fixed to the arm, nor in one fixed in space. This can also be demonstrated by asking subjects to orient a grasped object either in the inertial frame of reference (e.g. at 45° relative to the vertical) or in the arm's frame of reference (e.g. perpendicularly to the arm) [45•]. In either case, subjects exhibit a bias towards the other frame of reference.

In our review of this topic, we have come full circle. We began with the consideration that the activity of individual neurons is generally defined in a hybrid frame of reference that differs from neuron to neuron, but that the population response will be expressed in a well defined and often intuitively simple reference frame. Accordingly, the behavior should also express itself in such simple frames of reference. We have discussed examples where this is so, but, as we have shown, there are also cases where it is not.

Adaptation

Human subjects can adapt their motor output to compensate for a large variety of perturbations. For example, as Held [46] showed long ago, when subjects view an object through prisms that displace the perceived location of the object, they initially make errors in reaching movements. These errors diminish with practice. If the displacing prisms are then removed, subjects make errors in the opposite direction. Results of such studies demonstrate the remarkable plasticity of the central nervous system, and they can also provide insight about what is controlled and the information that is used in error correction.

Two recent studies [47••,48••] provide illustrative examples. In both studies, subjects made pointing movements in velocity-dependent (viscous) force fields that displaced their arm from the intended trajectory. In one study [47••], a destabilizing perturbation with a fairly complicated dependence on hand location was generated by torque motors. Initially, trajectories on the center-out task popularized by Georgopoulos [15] were severely distorted, but gradually returned to normal, with minimal curvature. As one might expect, subjects showed after-effects on trials in which no forces were applied. The unique aspect of this study is that the authors used this paradigm to identify what aspect of these adapted movements subjects do generalize when they are asked to make movements in a different part of the workspace. The investigators contemplated two alternatives: subjects generalize the forces on the hand, or they generalize the joint torques. To differentiate between these two alternatives, the force fields for movements initiated in a different part of the work space corresponded to the force field used for adaptation in one of two ways: either in Cartesian coordinates or in joint torque coordinates. Only when they were identical in joint torque coordinates was there a transfer of adaptation.

This result leads to the conclusion that adaptation takes place at the level of joint coordinates and not in the extrinsic coordinates of wrist displacement. In this experiment, the elbow angle was the same in both parts of the workspace, and only the shoulder angle was changed. The extent to which subjects are able to generalize when both shoulder and elbow angles change should provide additional insight into the form of the internal dynamic model subjects use, as the equations for torque contain terms that depend explicitly on elbow angle [49,50].

In the second study [48••], no forces were applied directly to the subjects' arms. They were generated indirectly when subjects were instructed to make pointing movements in a room that rotated at a constant angular velocity. In this condition, there is a Coriolis force that is perpendicular to the direction of arm motion and the axis of the room's rotation, and proportional to the speed of the movement. This force led to a lateral displacement of the final steady-state position of the hand. Even in the absence of pressure cues from contact forces on the arm, subjects adapted and also showed the expected after effects. Curiously, adaptation was facilitated if subjects had available tactile cues provided by contact of the fingers with the surface on which the target rested (but not with the target itself, which was a light-emitting diode located below a translucent surface). This study also provides one additional refutation of the equilibrium point hypothesis: according to the hypothesis, viscous forces, because they vanish at zero velocity, should not lead to steady-state errors.

As we have already mentioned, handpaths during pointing movements are generally nearly straight. Wolpert *et al.* [51•,52•] have induced adaptations in the handpath by manipulating visual feedback of the trajectory as displayed on a monitor during the movement. When the visual display of the handpath is distorted, subjects modify the trajectory so that the displayed path becomes straighter, the actual path now being substantially curved. In the second study, the authors showed that the displacement of a cursor along a gently curved path (corresponding to an actual handpath obtained in another experiment) is perceived as being straight. The authors emphasize the role played by visually mediated spatial perception in shaping movement kinematics.

Neural network models have been used to identify the substrates for learning and adaptation. Two notable recent examples [53,54] deal with the topics discussed above: how straight line movements may be learned, and how a body-centered representation of target location can be derived from visual information in a retinotopic frame of reference, incorporating information about eye and head position. A model dealing with transformations between visual and kinesthetic coordinates [55] is also notable for attempting to reconcile the behavior of neurons in motor and pre-motor cortex with psychophysical observations on pointing movements.

We would be remiss not to mention adaptation in the VOR. This has been a long-standing subject for study [56,57], and the question of which neurons in this reflex arc undergo modification has been the subject of considerable controversy. A series of recent publications by Lisberger and colleagues [58–60] has done much to clarify this topic. It has been the subject of a recent review [61••].

Related topics

The past year has seen a continuation in the kinematic analysis of more complex behavior in humans [62–65], monkeys [66] and cats [67]. Errors in pointing movements have also continued to receive considerable attention [68–71]. There is also an increasing trend to use complex behaviors to describe deficits in motor performance following cerebellar lesions [72–74], parietal lobe lesions [75–77], and in patients who are functionally deafferented [78–80].

Conclusions

The concepts of reference frames and coordinate systems, borrowed from classical physics, have contributed to our understanding of motor control both at the behavioral level and in terms of the response of a population of neurons. A variety of experimental approaches have been developed to identify putative coordinate systems. Recently, there has been progress on two fronts: culling out the population response from the widely disparate tuning of single units, and the realization that the reference frames in which behavior manifests itself may be labile. Studies on motor adaptation to altered environments have a long history. Recent studies in this genre have shed light on exactly what is learned during the process of adaptation and what kind of sensory information is used. Results from such studies may generalize to provide an understanding of how skilled movements are normally learned and controlled.

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