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Motor Control: From Joints to Objects and Back

A new study shows that the nervous system has the flexibility to learn dynamics in object-centered coordinates — up to a limit.

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The primary task of the nervous system is to guide action. But in order to move the body gracefully, the brain needs to anticipate the forces and torques that act on the joints. For example, when we move only the lower arm, we need to anticipate and counteract the induced torques that act on the upper, non-moving part of the arm, to ensure stability of the shoulder. This is a complicated problem, as these torques depend on the relative position of the joints, body orientation with respect to gravity, and on the dynamics of tools or other objects we manipulate.

How does the brain solve this problem? One suggestion is that the brain learns an internal model of the body's dynamics by associating the state of the body — it's position, velocity, joint angles, and so on — with forces that arise depending on the state of the limbs. This process has been extensively investigated using dynamic force fields. In a typical experiment, participants move a handle to a target position, while a robotic device generates a position- or velocity-dependent force on the arm. At first, participants make large errors that gradually decrease with further exposure to the force field. If the force field is unexpectedly removed, the hand path deviates in the opposite direction, indicating that the motor control system learned to actively compensate for the expected forces [1].

But what exactly did the brain learn? How we generalize learning from one task to another can help to uncover the structure of the learned representations. In a typical generalization experiment, participants learn to compensate for a force field in one arm position, and then perform similar movements in an unvisited part of the workspace. If participants learned to associate certain movement velocities ($\dot{x}$) with forces (F) in 'extrinsic' coordinates (Figure 1A), then they should expect the same forces in Cartesian space even in a new joint configuration (grey). If, on the other hand, participants learned to associate changes in joint angles (θ) with torques on those joints (τ) — they learned in an 'intrinsic' reference frame — then they should expect forces that are rotated with the joint configuration (Figure 1B). For learning of force fields within a limb, the evidence favours the idea that people learn in an intrinsic coordinate system [1–3].

Thus, learning of force fields can be thought of as the tuning of weights between neuronal populations that code for joint position and velocity, and elements that code for joint torques or muscular forces [4] (Figure 1C). In this

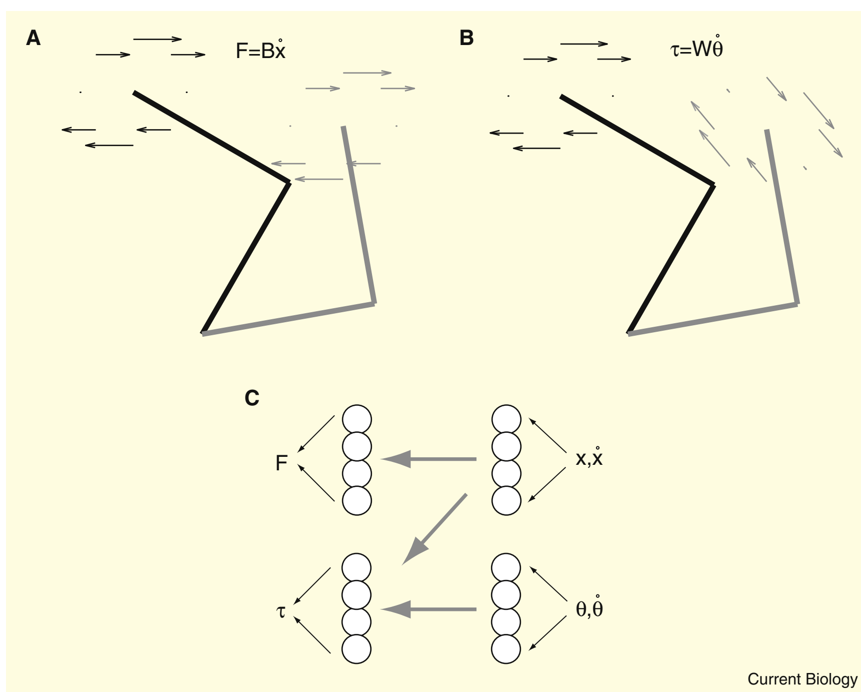

Figure 1. Learning to compensate for force fields.

A force field (black arrows) pushes the hand rightward for upward movements and leftward for downward movements. (A) If participants learn that a force field depends on movement direction in extrinsic space, changes in arm position (grey) do not lead to a directional change of anticipated forces (grey arrows). (B) Conversely, when the forces are learned in terms of joint coordinates, the anticipated forces rotate with the arm configuration. (C) Force fields can be learned as associates between neural elements with preferred directions in external space ($x, \dot{x}$), joint angles ($\theta, \dot{\theta}$), and neural assemblies indicating forces in external space (F) and torques (τ).

theoretical picture, the pattern of generalization is determined by the tuning functions of the neuronal assemblies that are involved in the learning process. Indeed, some characteristics of generalization are elegantly explained by the multiplicatively coding of position and velocity [5], as found in parietal cortex [6].

A paper by Ahmed *et al.* [7], published recently in *Current Biology*, asks how we learn force fields that arise between limbs. Would these force fields also be learned in intrinsic coordinates? From an ecological perspective, one would not suspect this to be the case: force fields experienced between the hands normally arise from objects that are touched with both hands, so the nervous system *should* learn and generalize these forces in extrinsic or object-centred coordinates. This is precisely what the authors found. They trained participants by applying the forces generated by one hand to the other hand, as if they were transmitted through an object. They then tested participants in a different joint configuration and could show that participants learned to associate a leftward push of the left hand with a leftward force on the right hand, independent of joint position. Thus, the nervous system learns and generalizes bimanual force fields as if they arise from objects held between the hands. What the authors do not show — but very reasonably assume — is that the learned forces also rotate with the object. This suggests that populations of neurons might flexibly code dynamics in an object-centred reference frame. Thus far, object-centred representations have only played an important role in theories of hemispatial neglect and visuo-spatial attention [8]; the Ahmed *et al.* paper [7] suggests that they may also have a role in governing motor behaviour.

However, there are two limitations to this flexibility. First, visual information appears to be an important factor. When a visual representation of the object is not displayed, the learning of the inter-manual force dynamics 'degenerates' partly back to a joint-based reference frame. The finding that visual cues influence force field learning is important. Other studies have found that contextual cues, such as serial order [9] or colour information [10], have little influence on the learning of unimanual force fields. In contrast, visual information indicating the presence of an object appears to be an important cue for the learning of inter-manual dynamics.

Secondly, when the object dynamics are made more complicated — a pulley system that rotates the forces exchanged between the hands by 90 degrees — participants learn in joint-based coordinates. This is congruent with a previous study from the same laboratory, in which one hand experienced a force that was proportional to the velocity of the other hand, also rotated by 90 degrees. Forces on the postural arm were learned and generalized in joint coordinates [11]. Interestingly, the forces appeared to be learned as a function of movement direction in external space of the moving hand, but in joint coordinates on the postural hand. This indicates that learning can sometimes occur between neuronal elements in different coordinate frames, such as movement directions in external space and torques in muscle or joint space (Figure 1C).

This more complicated picture may help explain some puzzling findings concerning the inter-manual transfer of force field learning. When trained on a force field with the right hand, participants transfer the learned dynamics to the left hand in external coordinates [12], for example when they experience a leftward force on the right hand, they also expect a leftward force on the left hand. However, small changes in the way the force field is employed may lead to transfer in intrinsic coordinates [13,14]. When the force field is introduced very slowly, no transfer between the hands is observed [15].

The solution to these divergent findings may lie in how the brain solves the 'credit assignment problem': when experiencing unexpected forces, the brain needs to attribute these forces to some state of the environment or body in order to predict these forces accurately the next time. The Ahmed *et al.* [7] study, together with other recent work, shows that forces can be flexibly assigned to dynamics in intrinsic or extrinsic coordinates. An important question for future research is how this credit assignment problem is solved in the nervous system. Do different learning processes compete, such that unexpected forces are only learned in one reference frame? Or does learning occur in parallel for different reference frames, which then compete with each other for control during movement execution?

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