The Nervous System Independently Controls Motion and Force

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When manipulating objects, we must control our hand motion as well as the interaction forces that arise from contact with the environment. At the level of musculoskeletal biomechanics, motions and forces are coupled by intrinsic limb impedance. However, it has yet to be established whether at the neural level the control of motion and force are coupled or independent. Here we provide evidence for the existence of independent neural controllers for arm motion and interaction forces. This evidence is offered by transcranial magnetic stimulation (TMS) of posterior parietal cortex (PPC) resulting in the differential disruption of the control of motion but not of force.

Previous TMS studies have found that stimulation to PPC at the onset of movement disrupts the brain's ability to generate an error signal based on the desired motion of the hand and its actual movement[1]. These findings suggest that PPC may be associated with the neural control of motion and not of force. If control of motion and force were in fact independent, stimulation of PPC would result in a selective disruption of motion without altering the generation of desired contact forces.

To test this prediction, we designed three experimental conditions where force and position control tasks appeared in combination or separately. Accordingly, our experiment consisted of three blocks: Combined, Force, and Motion. During the Combined block subjects ($n = 7$) applied 2 N of force to the handle of the manipulandum in a leftward direction as it was moved to center out positions along a bell shaped velocity profile (Figure 1b). This block required the simultaneous control of motion and force. During the Force block subjects maintained 2 N of force as the manipulandum moved along a very slow constant velocity profile in which intertial effects are negligible(Figure 1b). In this condition, the quality of force control was assessed by quantifying the ability of the subjects to maintain constant force vectors at different arm configurations. In the Motion block subjects were asked to track a predetermined movement trajectory. In order to compare performance in this and in the other tasks, subjects were required to track a predictable motion of the manipulandum while maintaining contact with it. A perfect position controller would result in zero interaction force between the subject and the manipulandum. Thus, deviation from zero force was attributed to errors in the ability of the subject to track the desired trajectory. Single pulse TMS was applied to left PPC during all blocks after learning.

We expressed behavior in each experimental block as fields of force (i.e. $F_{Combined}$, F_{Motion}, F_{Force}). To generate fields, measured force vectors were considered to be samples of a continuous force field describing the action of the controller. The resulting force fields allow us to express the production of motion, force and combined control in common terms of force. Thus we are able to determine if behavior in the Combined block can be attributed to the independent behaviors observed during the Motion and Force blocks (i.e. $F_{Combined}(x(t)) \simeq c_{Motion}F_{Motion}(x(t)) + c_{Force}F_{Force}(x(t)))$. Furthermore, we can establish if TMS disruption of $F_{Combined}(x(t))$ could be attributed solely to TMS disruption during $F_{Motion}(x(t))$.

We found (a) that TMS stimulation results a disruption of performance during the Combined and Motion blocks, but not the Force Block (Figure 2). Furthermore, (b) at the end of learning, a simple summation of forces from F_{Motion} and F_{Force} describes 80-97% of variability for forces applied in block $F_{Combined}$ (Figure 3). F_{Motion} and F_{Force} are responsible for the same amounts of variance of the field summation (Figure 4b). This indicates that each field contributes equally in describing the $F_{Combined}$. F_{Force} is unaffected by TMS stimulation, while increased errors exhibited during stimulation of the $F_{Combined}$ are fully described by the errors resulting from TMS during F_{Motion}. These results are consistent with the presence, after learning, of independent force and motor controllers. They also suggest that PPC is critical to the neural control of hand motion but not of interaction force.

[1]Desmurget et al., Nature Neuroscience 2(6), 1999; Della-Maggiore et al., J Neuroscience 24(44), 2004.

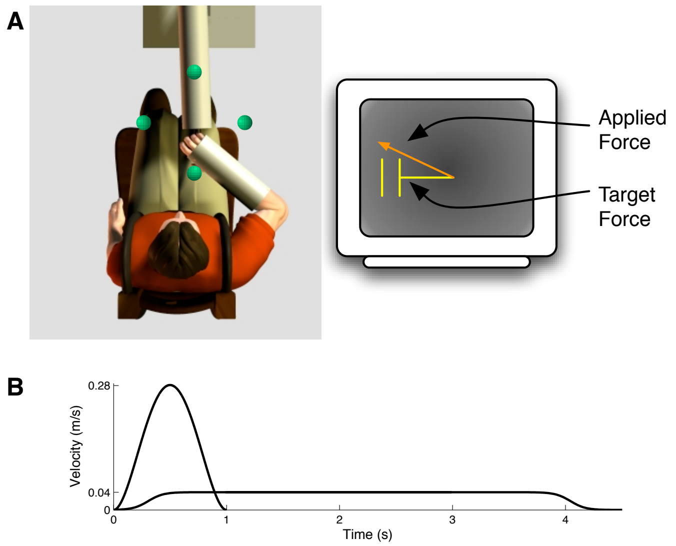

Figure 1: The experimental apparatus and task. **a**. Subjects grasped the handle of the manipulandum as it was servoed to various positions in the workspace. The spheres represent targets in the horizontal plane to which the robot was servoed. As subjects were servoed to the targets they were instructed to generate a constant interaction force. Visual force feedback was provided to subjects throughout the movement. **b**. The manipulandum moved along a 1-sec minimum jerk velocity profile during the Combined and Motion blocks, and a slower constant velocity profile during the force block.

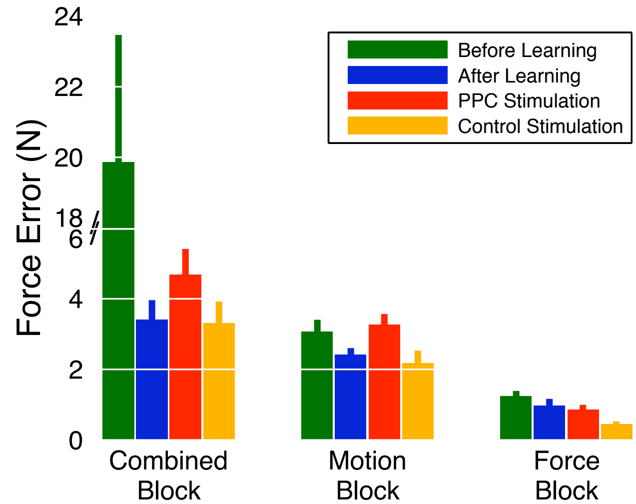

Figure 2: TMS to PPC disrupts the combined task and the control of motion,but not the control of force. Mean force error within each experimental block showed significant differences across each experimental block (Combined block, ANOVA $F_{3,24} = 13.28$; $p < 0.0001$; Motion block, ANOVA $F_{3,24} = 3.20$; $p < 0.05$; Force block, ANOVA $F_{3,24} = 4.78$; $p < 0.01$). Error bars denote s.e.m.

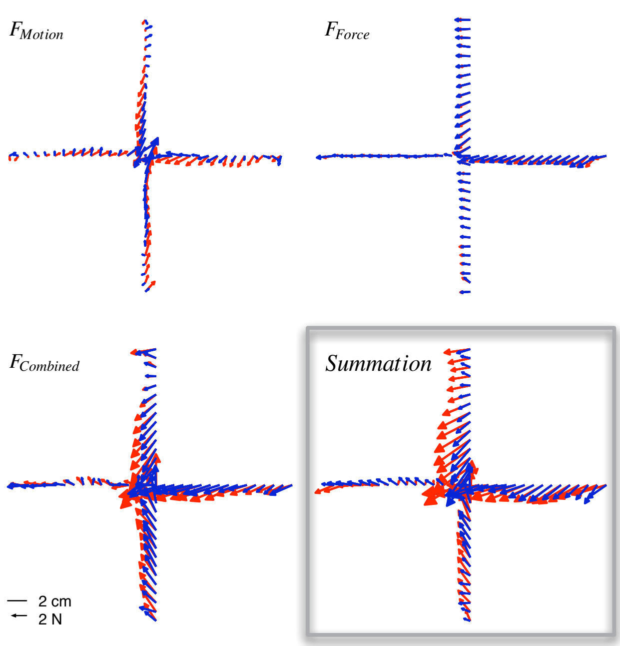

Figure 3: A linear summation of independent motion and force controllers describes the combined task. Fields of force shown are from a typical subject. Fields generated from trials following learning are seen in blue. PPC stimulation fields are seen in red. Force fields generated for trials during learning and stimulation for the Motion (*Upper Left*), Force (*Upper Right*) , and Combined (*Lower Left*) experimental blocks. Vector summation of the Motion and Force fields for trials after learning and during PPC stimulation Fields (*Lower Right*). After learning, $c_{Motion} = 0.89$; $c_{Force} = 1.04$; $R^2 = 0.88$; PPC stimulation, $c_{Motion} = 0.86$; $c_{Force} = 1.20$; $R^2 = 0.90$.

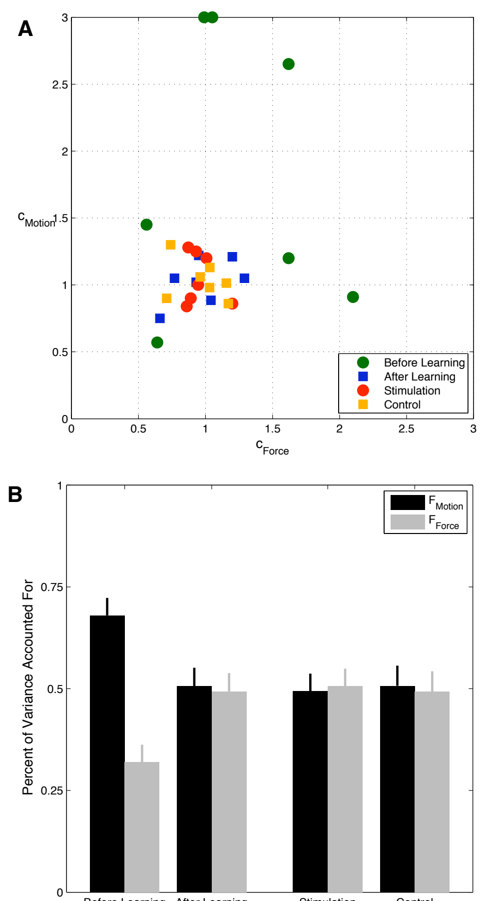

Figure 4. Motion and force controllers equally contribute to the combined behavior. **a**. Regression coefficients for vector summation hypothesis. Vector summation is performed on fields before learning, after learning, during PPC stimulation, and control stimulation. **b**. Variance accounted for by each controller for each vector summation. Error bars denote s.e.m.