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Laterality of Motor Control Specialization is Not Expressed by Long-Latency Stabilizing Reflexes during Posture

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Abstract

Handedness has been proposed as a laterality of motor control specialization: the dominant limb specializes in controlling limb trajectory using feed-forward mechanisms, while the non-dominant limb is specialized for position control, reliant largely upon feedback mechanisms. Experimental motor control research has tended to use the dominant arm, which could bias our understanding of control toward dominant-sided mechanisms. To determine if this is the case for our work on rapid motor responses, we here investigate the effect of laterality on long-latency reflexes, which are a rapid feedback response to perturbations of limb posture. Our results confirm previous work showing a significant effect of environment stability, but we found no significant effect of arm dominance. The dominant and non-dominant arm displayed similar reflex responses during a stabilizing postural task, despite the proposed advantage in the non-dominant hemisphere for position feedback control. This suggests that the lateralized specialization of motor control is confined to different cortical pathways than those involved here.

I. INTRODUCTION

Handedness is colloquially described as more skilled performance with the dominant hand or arm, as compared with the non-dominant one. Indeed, the dominant arm tends to demonstrate superior speed, strength, and dexterity [1]. The idea that the non-dominant arm is simply an inferior counterpart is challenged by the theory that each limb is specialized for a different type of behavior. Sainburg [2] proposed the hypothesis of dynamic-dominance, wherein the dominant arm is specialized for trajectory control, particularly that requiring accurate coordination of interaction forces within the limb. The non-dominant arm, meanwhile, seems to specialize in position control involving load compensation and sensory-feedback corrections [3]. This theory aligns with idea of the non-dominant arm providing a stable frame of reference for the dominant arm in many common bimanual tasks, such as opening a jar [4].

Handed specialization may reflect a lateralization of control systems in the cortical hemispheres. It is well known that each cerebral hemisphere displays functional specializations (e.g. for language or visuospatial abilities). Evidence for motor control lateralization comes from multiple studies comparing motor output from healthy individuals to stroke patients with right or left hemispheric damage [5]. In right-handed individuals, the left hemisphere corresponds to a better-developed trajectory controller reliant on feed-forward mechanisms, while the right hemisphere corresponds to a more developed position controller, relying heavily on feedback mechanisms. This view also agrees with observed upper limb asymmetries in the use of different sensory feedback modalities. The dominant arm of right-handers relies more on visual feedback, useful for trajectory planning, while the non-dominant arm relies more on proprioceptive feedback [6].

Motor control studies tend to have right-handed subjects, and experiments are usually performed with the right (dominant) arm. If each arm is specialized for a different type of control, this may bias our understanding of upper limb motor control towards dominant-sided mechanisms at the expense of non-dominant mechanisms. To determine if this dominance bias affects our own research on rapid motor responses, we compared long-latency reflexes during posture in both arms. Long-latency stretch reflexes in the upper limb provide a mechanism for rapid corrective action in both ballistic trajectory tasks [7] and postural stability tasks [8]. It is commonly believed these long-latency reflexes are at least partially mediated by a feedback loop through the cortex, specifically for the stabilizing component most relevant to postural tasks [9]. Therefore, we hypothesized that the stabilizing component of the long-latency reflex would be differentially expressed in the dominant and non-dominant arms, due to lateralization of motor control in the cerebral hemispheres. Specifically, we expected that the non-dominant limb would exhibit more effective long-latency reflexes during a posture stabilizing task; “more effective” being manifest either by a larger long-latency reflex gain in any environment, or by greater modulation of long-latency reflexes when postural stability is challenged by interactions with an unstable environment.

II. MATERIALS AND METHODS

A. Subjects

Seventeen right-handed, able-bodied individuals (age: 23–51, 8 females, 9 males) with no known neurological disorders volunteered to participate in the experiment. Right-handedness was confirmed using the Edinburgh Handedness Inventory [10]. All protocols were approved by the Northwestern University Institutional Review Board and required informed written consent.

B. Equipment

Participants were seated comfortably with the trunk secured and the experiment arm posture at approximately 90° shoulder abduction, 0° shoulder flexion, and the elbow was at 90° flexion. The upper arm was restrained by an adjustable trough and the wrist was immobilized in a pronated, neutral position using a thermoplastic cast. The cast was attached to a linear motor (Copley ThrustTube TB3806; Copley Controls) instrumented with a force

sensor and linear encoder to track force and position. The linear motor was oriented orthogonal to the forearm, so that displacement of the motor caused forearm rotation about the elbow joint. The linear motor was configured as an admittance servo, allowing us to simulate stable (stiffness = 500 N/m) or unstable (stiffness = -500 N/m) environments. We chose this stiffness magnitude based on a previous study [11] to overcome the intrinsic endpoint stiffness of the arm in the unstable environment. Each environment was further configured as a second-order mechanical system with a mass of 2 kg and a damping of 10 Nm/s.

Surface electromyographic (EMG) activity was recorded from the brachioradialis (BRD), biceps brachii (BIC), and the lateral (TRILAT) and long (TRILNG) heads of the triceps brachii using bipolar Ag/AgCl electrodes (Noraxon). EMGs were amplified and conditioned using a Bortec AMT- 8 (Bortec Biomedical Ltd.), with a band-pass filter of 10–1,000 Hz. The resulting signals were anti-alias filtered using 5th order Bessel filters with a 500-Hz cut-off frequency and sampled at 2,500 Hz using an analog to digital converter (PCI-DAS1602/16). Visual feedback of the current wrist position was provided on a computer monitor placed directly in front of the participant.

C. Protocol

Our experiment was designed to elicit stabilizing long-latency reflexes in the elbow muscles. This was done by perturbing the elbow while subjects were engaged in maintaining a target position in either a stable or unstable environment (Fig. 1). We tested each arm in a separate experiment, with the order of arms randomized for each subject. Before each experiment, we collected a series of isometric maximum voluntary contractions (MVCs). Each muscle contraction lasted for approximately 3 seconds. These data were used to normalize the EMGs recorded from each muscle. We also performed one MVC after the subject's arm was attached to the motor to determine each subject's maximum forces applied at the wrist for the experimental arm posture.

The main experiment for each arm consisted of eight blocks, with two repetitions of each combination of perturbation direction (flexor or extensor stretch) and haptic environment (stable or unstable). The order of these blocks was randomized for each experiment. A bias force of 10% MVC force was applied in the appropriate direction to preload the muscles stretched by the perturbation. This was done in an effort to control the input to the motoneuron pool, thereby reducing variability in the elicited reflex responses.

Each block consisted of 20 trials. In each trial, the subject was instructed to get into the position target (based on arm posture described previously, ± 2 mm). When this target was maintained for 2 seconds, there was a short, variable delay before a ramp-and-hold perturbation was applied. All perturbations were 4 cm at 400 mm/s with duration 100 ms, which is sufficient to activate the long-latency stretch reflex [11]. We matched the perturbations in each environment by transiently switching the linear motor to a position servo mode, as we have done previously [8]. Subjects were told not to react to the perturbation but to maintain the ongoing muscle activity until instructed to relax. The motor then returned to the starting position in servo mode and switched back to the haptic environment, at which point the subject was free to initiate the next trial. Randomly, before

ten percent of trials (2/20 per block), subjects were required to explore the workspace by moving the arm back and forth over the entire range of motion (4 cm). This was done to ensure familiarity with the environment.

D. Data Analysis

We quantified the muscle activity in each recorded muscle during all trials. The mean value was subtracted from the EMG collected in each trial. These were then rectified, and normalized by the maximum mean rectified EMG (0.5 s average) recorded during the MVCs for the same arm. We aligned data so the onset of the perturbation occurred at 0 s. All responses are reported as % MVCs, and changes in EMG amplitude are reported relative to the background activity prior to perturbation onset.

We excluded trials that displayed excessive movement prior to the perturbation or displayed other unwarranted noise; less than 2% of all trials were excluded. The voluntary muscle activation prior to the perturbation, or background activity, was then quantified for all trials. To compare the reflex gain from different conditions, it is necessary to ensure that backgrounds are matched across conditions, since pre-stimulus muscle activity affects the amplitude of stretch reflexes [12]. However, it was particularly challenging to match background activity across both environments and both arms. Therefore, we performed background-matching during data analysis for each subject and each muscle. Depending on the comparison of interest (across arms or environments), we manually selected a subset of trials where background activity overlapped between conditions. If there was insufficient background overlap between conditions, that subject's data was excluded from that analysis.

To quantify the motor response to the perturbation, three main time periods were evaluated: short latency (25–50 ms), early long latency (50–75 ms), late-long latency (75–100 ms). We chose these time bins to be consistent with our previous work. We calculated the average response amplitude during each of these time windows for each trial. For each muscle, only perturbations that stretched the muscle were considered.

E. Statistics

Our primary hypothesis was that arm dominance would have a significant effect on long-latency reflex gain during a postural task. Specifically, we expected the non-dominant, left arm to display larger long-latency reflexes in general, or to show a greater modulation of long-latency reflexes when postural stability is challenged by an unstable environment.

We first tested for a significant effect of environment to corroborate our previous findings [8]. In this analysis, we only included data that was background-matched between environments, considering each arm separately. Next, we tested for a significant effect of arm dominance by including only the data that was background-matched between arms, considering each environment separately. We did not perform an overall analysis with backgrounds matched across both arm and environment because only five to seven subjects had sufficient background overlap between all conditions in each muscle.

For both analyses, statistical comparisons were made separately for each muscle and each time period analyzed. All comparisons were made using a mixed-effect model in which

subjects were treated as a random factor and the factor in question (environment or arm) was treated as a fixed factor. All main effects were included in the model. Analysis of variance was used to assess statistical significance of each factor. Significance for all tests was evaluated against a p -value of 0.05. Post hoc comparisons were used to evaluate the difference between levels of all significant factors. Tukey's Honestly Significant Difference (TukeyHSD) was used to correct for multiple comparisons in these post hoc tests. All statistics were done in MATLAB (2010a, The MathWorks).

III. Results

A. Instability increases long-latency reflex gain

Stabilizing reflexes were consistently elicited by perturbations in both stable and unstable environments for all subjects (Fig. 2). Except for the left TRILNG, there was a significant effect of environment in all muscles analyzed ($p < 0.05$; Fig. 3A, B) with average EMG activity being significantly higher in the unstable environment during the early and/or late long latency period. This is consistent with our previous work showing environment-dependent reflex modulation between 50 and 100 ms post-stimulus [8]. The effect of environment was seen in both the dominant and non-dominant arm.

B. Arm dominance does not affect long-latency reflex gain

We did not find any significant effect of arm dominance on the gain of the long-latency reflex response. Although some subjects did display slightly larger reflexes in one arm or the other, there was not a consistent trend. In both the stable and unstable environment, long-latency reflexes in each arm were not statistically different ($p > 0.05$; Fig. 3C, D).

IV. DISCUSSION

The objective of this study was to determine if long-latency stabilizing reflexes manifest differently in the dominant and non-dominant arm. We hypothesized that the non-dominant specialization for position control would lead to more effective stabilizing reflexes in the non-dominant limb. We found that stabilizing reflexes were robustly present in both arms and environment-dependent modulation did occur. However, there was no significant difference in the gain of these reflexes in the dominant and non-dominant arm. This suggests that the lateralization of motor control specializations does not affect the most rapid, reflexive motor responses, at least during postural tasks.

Some subjects displayed differences in either the timing or amplitude of reflexes between arms. However, there was no consistent pattern found across subjects to support our hypothesis of increased non-dominant reflexes. There may be several reasons for this. One possibility is that our experimental design or statistical power was not sufficient to detect the effect of arm dominance on long-latency reflex amplitude. However, we were able to detect the modulation due to environmental stability, which is a relatively small effect compared to other factors that influence reflexive activity, such as task-instruction [9]. Therefore, we believe that any undetected effect of arm dominance must be of such a small size as to be functionally insignificant.

Previous studies showing the effect of arm dominance on motor output have largely focused on reaching paradigms or movement matching, rather than posture [6,13,14]. It has been shown that posture and movement are controlled distinctly within the primary motor cortex [16]. It may be that motor responses during posture do not rely on lateralized circuitry to the same extent as does reaching control.

It has been shown that the primary motor cortex is involved in the stabilizing long-latency reflex [9], so we expected that cortical lateralization might affect this reflex response. However, the rapidity of this feedback response must severely limit the involvement of many higher order cortical circuits. It may be that lateralized motor differences are only apparent for tasks that require more complex cortical involvement - either for movement planning or for more sophisticated processing of sensory feedback. Many prior studies showing asymmetrical arm performance required subjects to plan specific trajectories [13], coordinate interlimb interaction torques [14], or transfer proprioceptive feedback information between hemispheres [6]. All of these tasks would rely more heavily upon higher computational circuitry of the cortex.

Our results indicate that lateralized specialization of motor control is not present in the cortical circuits involved in stabilizing long-latency reflexes (primary motor cortex). Indeed, in one of his most recent studies in stroke survivors, Sainburg has speculated that parietal cortex in the left (dominant) hemisphere, and inferior frontal and dorsolateral prefrontal cortex in the right (non-dominant) hemisphere, may be key areas for the planning and corrective motor specializations associated with each hemisphere [15]. Thus, motor asymmetries may have more to do with prepared motor actions than rapid feedback responses.

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Figure 1.

Experiment design. We tested two environments in each arm; stable (+500 N/m) and unstable (−500 N/m). For each combination of arm and environment, subjects performed a postural maintenance task until a perturbation stretched either the flexors (orange) or extensors (green).

Figure 2.

EMG responses from a typical subject. Each trace is the average of at least 15 trials, aligned to the onset of muscle stretch. For this subject, BRD could not be bga-matched (dotted traces), but other muscles were bga-matched (solid) and used for statistics. The long-latency reflex period is highlighted. **A** shows EMG from the dominant (dark) and non-dominant (light) arms, for tasks in the stable environment. **B** shows EMG from the unstable environment.

Figure 3.

Average EMG amplitude in each time period, after matching background activity for each comparison. **A** and **B** show the effect of environment in each arm separately. As expected, both arms display higher long latency reflex activity in the unstable environment. **C** and **D** show the effect of arm in each environment separately. Other than a slight difference instable TRILAT short-latency, there were no significant differences between arms. Statistical differences at the level of 0.05 are shown (*), and error bars represent standard error.