Rapid Motor Responses Are Appropriately Tuned to the Metrics of a Visuospatial Task

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Pruszynski JA, Kurtzer I, Scott SH. Rapid motor responses are appropriately tuned to the metrics of a visuospatial task. J Neurophysiol 100: 224–238, 2008. First published May 7, 2008; doi:10.1152/jn.90262.2008. Considerable research has established that rapid motor responses (traditionally called reflexes), can be modified by a subject’s voluntary goals. Here, we expand on past observations using verbal instructions by defining the voluntary goal via visual target position. This approach allowed us to objectively enforce task adherence and explore a richer set of variables, such as target direction and distance, metrics that modify voluntary control and that—according to our hypothesis—will influence rapid motor responses. Our first experiment tested whether upper-limb responses are categorically modulated by target direction by placing targets such that the same perturbation could push the hand into one target and out of the other, a spatial analogue to “resist/yield” verbal instructions. Consistent with these classical results, we found that the short-latency rapid response (R1, 20–45 ms) was not modulated by target direction, whereas long-latency rapid responses (R2/R3, 45–105 ms) were modified in a manner approaching the voluntary response (VOL, 120–180 ms). Our second experiment tested whether upper-limb responses are continuously modulated by target distance by distributing five targets along one axis centered on the hand. Here, the long-latency and voluntary response mirrored the task demands by increasing activity in a graded fashion with increasing target distance. Our final experiment explored how upper-limb responses incorporate two-dimensional spatial information by placing targets radially around the hand. Notably, long-latency responses exhibited smooth tuning functions to target direction that were similar to those observed for the voluntary response. Taken together, these results illustrate the flexibility of long-latency rapid responses and emphasize their similarity to later voluntary responses.

INTRODUCTION

Rapidly adjusting motor actions to account for changing conditions is a critical component of successful movement. Consider a waitress holding a tray of drinks and navigating a crowded restaurant. Although she can plan her path to avoid potential obstacles she must also respond to unexpected events such as a bump of the arm. Clearly, the correct response is sensitive to context. If there is a busy table to the left and an empty area on the right, corrective responses should be biased to the right. In contrast, if the area to the right is filled with children it may be preferable to respond to the left.

Many researchers have examined the flexibility of such rapid responses, traditionally called reflexes, in the upper limb by noting how they are altered by voluntary goals (Capaday et al. 1994; Colebatch et al. 1979; Crago et al. 1976; Evarts and Granit 1976; Hagbarth 1967; Hammond 1956; Jaeger et al. 1982a; Lee and Tatton 1982; Lewis et al. 2006; Rothwell et al. 1980). These studies typically issued a verbal instruction such as “resist/let go” (Colebatch et al. 1979; Hammond 1956; Rothwell et al. 1980), “flex/extend” (Hagbarth 1967), or “compensate/do not intervene” (Crago et al. 1976) that indicated how a subject was to respond to a mechanical perturbation. Indeed, many of these studies have shown that long-latency reflexes are substantially modulated by voluntary goals. Although these pioneering studies revealed that long-latency reflexes are modifiable by subject intent, the use of verbal instructions severely limited the breadth of conditions that could be explored to the subset of behaviors where verbal cues have a reliable interpretation.

The limited range of reflex sophistication that can be explored via verbal instructions is an impediment to testing recent theories of motor control. Specifically, optimal feedback control posits that the extensive repertoire of behavior exhibited by the volitional motor system is accomplished via intelligent manipulation of sensory feedback (Todorov 2004; Todorov and Jordan 2002). We have previously suggested that one neurophysiological implication of such manipulation is that long-latency reflexes, like volitional movement, should be capable of a rich assortment of behaviors because reflexive and volitional control are intimately linked (Kurtzer et al. 2008; Scott 2004); effectively, they are part of the same ongoing control process. Such a close link between reflexive and voluntary responses makes many experimental predictions but belies the traditional distinctions made between reflexive and voluntary responses (see DISCUSSION). Therefore we have discarded the term reflex in favor of a simple empirical separation between slow (voluntary) and rapid motor responses that fits better within our framework (see METHODS).

Our general hypothesis is that these rapid motor responses are capable of all the sophistication attributed to voluntary control within the constraints of their limited processing time. To test for such extensive sophistication, we created a paradigm that can examine these responses under a wide range of behaviors akin to the prevalent methodology used to study the volitional motor system (Shadmehr and Wise 2005). Briefly, subjects are shown a target while they maintain posture at the start position and are trained to respond to an unpredictable perturbation by quickly placing their hand inside the target, thus allowing us to quantify how rapid responses change when targets are placed at various locations. Unlike the ambiguity of the costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

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verbal instructions, target metrics such as position, size, and shape, along with timing constraints, explicitly define the goal of the task and can be monitored and controlled. In the present study, we tested whether rapid responses of muscles spanning the shoulder and elbow were sensitive to the direction and distance of spatial targets in both one and two dimensions. These factors are known to modify voluntary control and we hypothesized the same metrics would modify rapid responses.

In our first experiment we placed targets such that the same perturbation pushed the arm toward one of the targets and away from the other, thus allowing us to establish whether rapid responses are categorically sensitive to target direction, analogous to previous studies using verbal instructions. In the second experiment we placed targets at five positions along one axis to determine whether rapid responses scale continuously with target distance. Last, we placed targets radially around the hand to establish how rapid responses are spatially tuned to target direction. Our results indicate that there is a clear distinction between short-latency and long-latency rapid responses for all the muscles we examined, including shoulder flexors, shoulder extensors, elbow flexors, and elbow extensors. Short-latency rapid responses were never modulated by target position even in conditions of relatively high stimulus predictability. In contrast, long-latency rapid responses were robustly modified in all three experiments even in conditions of relatively low stimulus predictability and the changes they expressed progressively approached the voluntary response. This work was previously presented in abstract form (Pruszynski et al. 2007).

METHODS

Subjects

A total of 18 subjects (11 males and 7 females, aged 21–35 yr, 17 right-handed) participated in 37 experimental sessions. All subjects were neurologically unimpaired, had normal or corrected-to-normal vision, and gave informed consent according to a protocol approved by the Queen’s University Research Ethics Board.

Apparatus and experimental paradigm

Subjects performed the experiments with a robotic exoskeleton (KINARM, BKIN Technologies, Kingston, Ontario, Canada) that permits combined flexion and extension movements of the shoulder and elbow to move the hand in the horizontal plane (Scott 1999). Furthermore, KINARM can independently apply mechanical loads to the shoulder and/or elbow and record kinematic variables of the joints and hand. Target lights and simulated hand feedback were presented to the subject in the horizontal plane via a heads-up display composed of an overhead projector and semitransparent mirror. Throughout the experiment, direct vision of the entire arm and hand was occluded and hand feedback was removed prior to perturbation onset so that responses were guided only by proprioception.

EXPERIMENT 1: CATEGORICAL MODULATION BY TARGET DIRECTION. Subjects (n = 11) maintained their hand in a small central area (radius = 0.3 cm) against a background load (±2 Nm) that activated either the elbow flexors or extensors. The central area was positioned such the shoulder and elbow angles were 45 and 90°, respectively. Subjects were then presented with a peripheral target (PT, radius = 20 cm) located on either the left or right side of their hand and thus requiring predominantly elbow flexion or extension movements (Fig. 1A). After a random hold (1–4 s) at the central area, a rapid torque perturbation (±2 Nm at elbow) displaced the hand either toward (IN condition) or away from (OUT condition) the center of the displayed PT (Fig. 1B). Subjects were instructed not to anticipate the perturbation and to place their hand in the PT as quickly as possible after perturbation onset. On completing the trial, subjects were given feedback to indicate success (PT, filled green) or failure (PT, filled red and an auditory tone) based on preset speed and accuracy criteria (hand within PT for 1,000 of the 1,300 ms after perturbation onset). A detailed timeline of each trial is presented in Fig. 1C. Fifteen repeats of each condition (2 muscle groups and 2 targets) were performed in a blocked sequence, randomized across subjects, for a total of 60 trials.

In addition to the above-described experiment, a subset of the subjects (n = 8) performed the same task (during the same session) except that trials were presented in random order so that subjects could not anticipate either perturbation onset or direction. This was accomplished by adding trials such that the background load was not predictive of the perturbation direction (Fig. 1C, dashed lines). Spatial target location was also randomly chosen for each trial. Subjects

FIG. 1. Task apparatus and experimental paradigm. A: in experiment 1, subjects were presented with one of 2 large peripheral targets (PTs, radius = 20 cm) located on the left or right side of their hand’s starting position (CT, radius = 5 cm). B: the targets in experiment 1 were chosen such that flexion/extension perturbations of the elbow pushed that hand into (IN) or out of (OUT) the target. Applied background loads, perturbations, and locations of the IN and OUT targets were different for flexors and extensors. C: timeline for an exemplar trial. a: subjects shown the CT and PT while the background load was introduced that primed the muscle of interest. b: hand feedback was extinguished while subjects maintained posture at the CT. c and d: after a random 1- to 4-s period, a rapid step perturbation was applied that stretched/lengthened the muscle of interest. e: after 1,300 ms, the load was removed while performance feedback was given to the subject. Note that for the random condition, trials were added (dashed lines) to ensure that subjects could not predict the direction of perturbation based on the background load. D: in experiment 2, subjects were presented with one of 5 PTs (radius = 5 cm) centered 0, 3, or 6 cm to the left or right of their hand requiring predominantly flexion or extension of the elbow. E: in experiment 3, 4 potential PTs (radius = 5 cm) were presented at locations to the left, right, in front, and behind the hand such that obtaining the targets required various degrees of shoulder and elbow motion.

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performed 15 repeats of each condition (2 muscle groups, 2 targets, 2 perturbation directions) for a total of 120 trials.

**EXPERIMENT 2: GRADED MODULATION BY TARGET DISTANCE.** The experimental protocol is similar to experiment 1 with the exception of PT placement and size. Subjects (n = 9) were presented with one of five potential PTs (radius = 5 cm) located at 0, 3, and 6 cm to the left and right of the hand and thus requiring predominantly elbow flexion or extension (Fig. 1D). Twenty-five repeats of each condition (2 muscle groups and 5 targets) were performed in a blocked sequence, randomized across subjects, for a total of 250 trials.

**EXPERIMENT 3: SPATIAL TUNING OF RAPID RESPONSES.** The experimental protocol is similar to experiment 1. Subjects (n = 6) were shown one of four potential PTs (radius = 5 cm) that were equally distributed around the hand’s starting position (CT) at a constant distance of 6 cm and placed at locations requiring predominantly elbow flexion, elbow extension, shoulder flexion, or shoulder extension (Fig. 1E). Twenty repeats were collected in each condition (4 muscle groups and 4 targets) in a blocked sequence, randomized across subjects, for a total of 320 trials.

**CONTROL EXPERIMENT: DETERMINING VOLUNTARY ONSET.** A common problem in previous experiments that investigate reflexes is deciding what components of muscular activity are reflexive. In fact, the philosophical and semantic legacy of the term has made it unclear what responses (if any) qualify (see DISCUSSION). Further, recent theoretical advances suggest that the distinction between reflex and voluntary is obsolete because the underlying processes are inherently linked (Scott 2004). We sought to explicitly avoid these historical considerations so we chose a simple operational definition based on a control experiment that empirically determined voluntary muscle onset; any muscle activity occurring prior to voluntary muscle onset is then termed a rapid motor response.

Voluntary muscle onset was determined by applying perturbations that did not engage significant early phasic responses (Evarts and Vaughn 1978; Hammond 1956; Jaeger et al. 1982b). In the absence of these early phasic responses, we could clearly identify the large and prolonged burst activity typically associated with voluntary muscle activity (compare traces in Fig. 2A). Subjects (n = 9) performed the same protocol as in experiment 1 with perturbations reduced to ≥0.5 Nm and delivered at the shoulder joint. Importantly, although the perturbation was applied at the shoulder, background loads were applied at the elbow (±2 Nm) as in experiment 1 to tonically activate the muscle of interest. We applied the perturbation at the shoulder since it allowed us to generate a perceptually robust perturbation without evoking substantial responses at the elbow. Unlike our other experiments, no formal speed and accuracy criteria were used. Rather, subjects were encouraged to move to the PT as quickly as possible after perturbation onset. Twenty-five repeats were completed in each condition for a total of 50 trials.

We determined muscle onset on a trial-by-trial basis as the point where electromyographic (EMG) activity first exceeded 3SDs from baseline for five consecutive samples (5 ms). The resulting distributions were right-skewed and represented the median onset times of 161, 157, 136, and 143 ms for brachioradialis, biceps, triceps lateral, and triceps long, respectively (Fig. 2, B–E). Based on these distributions and our own qualitative observations we defined the end of the rapid response window at 105 ms, overlapping with only about 8% of all collected voluntary muscle onset times and consistent with many previous reports of voluntary onset (Calancie and Bawa 1985; Hammond 1956; Jaeger et al. 1982b; Kimura et al. 2006; Lee and Tatton 1975; Matthews 1986; Rothwell et al. 1980; Tatton and Lee 1975).

**Muscle activity**

Surface EMG recordings were obtained from six upper-limb muscles involved with flexion or extension at the elbow and/or shoulder: brachioradialis (Br, monoarticular elbow flexor), biceps long (Bi, biarticular flexor), triceps lateral (TLat, monoarticular elbow extensor), triceps long (TLo, biarticular extensor), deltoit posterior (DP, monoarticular shoulder extensor), and pectoralis major (PM, monoarticular shoulder flexor). Prior to electrode placement, the skin was cleaned and abraded with rubbing alcohol and the electrode contacts were covered with conductive gel. Electrodes (DE-2.1, Delsys, Boston, MA) were placed on the belly of the muscle oriented along the muscle fiber and the reference electrode (Dermatrode, American Imex, Irvine, CA) was attached to the ankle. To assess the quality of each EMG signal, we performed a set of maneuvers found to elicit high levels of activation for each muscle in the plane of the task. EMG signals were amplified (gain = 10^3 or 10^4) and band-pass filtered...
(20–450 Hz) by a commercially available system (Bagnoli, Delsys) then digitally sampled at 1,000 Hz.

Rapid response epochs

We were primarily interested in comparing different epochs of muscle activity occurring before our operationally defined voluntary muscle onset (see Control experiment); such responses are referred to as rapid motor responses. Taking into account previous reports (Bonn et al. 1983; Crago et al. 1976; Lee and Tatton 1975; Mortimer et al. 1981; Nakazawa et al. 1997; Rothwell et al. 1980) and our own observations of reliably timed phasic events across subjects and muscles, we defined three distinct epochs of activity in temporal order: Response 1 (R1, 20–45 ms), classically referred to as the short-latency or spinal stretch reflex (Pierrot-Deseilligny and Burke 2005); Response 2 (R2, 45–75 ms), often referred to as the long-latency reflex (Hammond 1954; Matthews 1986); and Response 3 (R3, 75–105 ms), sometimes referred to as long-latency reflex or triggered response (Crago et al. 1976; Rothwell et al. 1980). Note that the timing of our epochs most closely mirror M1, M2, and M3 as proposed by Lee and Tatton (1975) and our choice of R1, R2, and R3 is largely to avoid confusion with the common abbreviation for primary motor cortex (M1). For some analyses, we included time epochs between −100–0 and 120–180 ms, which were defined as baseline (PRE) and voluntary (VOL), respectively. Note that our results were not qualitatively changed by modestly altering epoch onset or duration.

Data analysis

FILTERING AND NORMALIZATION. The combined compliance of the robot and the subject’s arm introduces a shift between the commanded perturbation by the motors and the corresponding start of limb motion. We determined this delay by tightly coupling an accelerometer (EGA Series, Entran, Montreal, Canada) to the arm of several subjects while they performed a perturbation task in the KINARM robotic system. The time between issuing the perturbation command and the onset of arm acceleration was about 10 ms and was similar across several subjects and load conditions. Thus all data were aligned on perturbation onset as determined by the KINARM and then shifted by a fixed delay of 10 ms. Joint and hand position were obtained directly from the KINARM and then low-pass filtered (20 Hz, two-pass, sixth-order Butterworth). EMG signals were band-pass filtered (25–250 Hz, two-pass, sixth-order Butterworth), full-wave rectified, and normalized by their mean activity for a 2-Nm load.

BEHAVIOR AND KINEMATICS. We were most interested in comparing kinematic and muscle responses for the same imposed perturbation but different target positions. To quantify the static changes in behavior as a function of target position, we analyzed the hand’s final position (350 ms after perturbation onset). To quantify the static changes in behavior as a function of target position, we analyzed the hand’s final position (350 ms after perturbation onset). We used principal component analysis to generate 95% confidence ellipses of final hand position (350 ms after perturbation onset). We used principal component analysis to generate 95% confidence ellipses of final hand position (350 ms after perturbation onset). We determined this delay by tightly coupling an accelerometer (EGA Series, Entran, Montreal, Canada) to the arm of several subjects while they performed a perturbation task in the KINARM robotic system. The time between issuing the perturbation command and the onset of arm acceleration was about 10 ms and was similar across several subjects and load conditions. Thus all data were aligned on perturbation onset as determined by the KINARM and then shifted by a fixed delay of 10 ms. Joint and hand position were obtained directly from the KINARM and then low-pass filtered (20 Hz, two-pass, sixth-order Butterworth). EMG signals were band-pass filtered (25–250 Hz, two-pass, sixth-order Butterworth), full-wave rectified, and normalized by their mean activity for a 2-Nm load.

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MUSCLE ACTIVITY. When comparing responses across predefined epochs of muscle activity (PRE, R1, R2, R3, VOL), we calculated the mean level of activity for each muscle in that epoch on a trial-by-trial basis. For each muscle, we used the Wilcoxon rank-sum test (also known as a Mann–Whitney U test), a nonparametric comparison of medians, to evaluate the hypothesis that the median muscle activity differed with target position. Similar results were found using a t-test.

To identify when responses differed across target conditions without a priori assumptions about epochs, we generated an ROC curve for every 1-ms sample to calculate the probability that an ideal observer could discriminate the target position based on the EMG response for the same perturbation but different PTs (ROC < 0.25 or >0.75). We also calculated the point when the ROC curve began to deviate from chance (Thompson et al. 1996), termed the “knee,” by regressing the ROC values located 15 ms around the discrimination point then calculating the time when this line intersected the preperturbation ROC results. Note that calculating the ROC knee is a formalized method of determining when two signals initially diverge and replaces previous attempts to identify this point by visual inspection (Crago et al. 1976; Evarts and Vaughn 1978; Marsden et al. 1976).

In experiment 3, we determined how responses were tuned to two-dimensional target positions by fitting the data with a plane (Kurtzer et al. 2005, 2006). The resulting plane coefficients (X, Y) describe how the EMG activity is related to spatial target position and can be used to calculate the preferred target direction (PD), where PD = atan2( Y, X) and 0, 90, 180, and 270° represent right, ahead, left, and behind in external space. A Rayleigh test was applied across the population of PDs (for a particular muscle and epoch) to determine whether the net tuning was unimodally distributed (Batschelet 1981).

AKAIKE’S INFORMATION CRITERIA. For experiment 2, we used Akaike’s Information Criterion (AIC) to judge the merits of potential models relating muscle activity within our predefined epochs to target position. AIC is a principled technique for choosing a parsimonious model from a set of candidates by providing a metric of model quality that balances fit and complexity (Burnham and Anderson 2002). In AIC, model quality is proportional to the likelihood (L) of a candidate model (θ′), given the experimental data (x), and complexity is accounted for by K, the number of free parameters in the candidate model, expressed as

\[ \text{AIC} = -2 \log \{ L(\theta' | x) \} + 2K \]  

By making an assumption of Gaussian error of equal variance, finding the likelihood was reduced to calculating the square root of the sum of squares (RSS), which was done via either linear regression or constrained nonlinear optimization (minicon in Matlab, The MathWorks, Boston, MA). Note that when nonlinear optimization was used, the procedure was restarted 10,000 times from random locations in an attempt to locate the global best fit. We compared the potential models in two ways. First, we found the model that resulted in the smallest AIC score, which was deemed the best candidate. Second, we found how often a potential candidate was acceptable for explaining the data by calculating the difference between its AIC score and that of the best model \[ \Delta \text{AIC} = \text{AIC} - \text{min} (\text{AIC}) \]. If this difference was less than an arbitrarily chosen threshold (ΔAIC < 2), the model was deemed acceptable (Burnham and Anderson 2002).

We compared four possible models relating EMG activity to target position (for each muscle sample and epoch). 1) A constant function that had one free variable, f(p) = b, where p is the target position (defined as 1 to 5) and b is a positive constant. 2) A step function defined as two piecewise continuous constant functions with three free variables, two constant levels, and the switch point, f(p) = b, if P ≤ x and f(p) = c, otherwise, and constrained such that c > a and that x was within the range of tested positions. 3) A linear function; f(p) = ap + b, where a is a positive constant and b is unconstrained. 4) A sigmoid that had four free variables, f(p) = a/[1 + exp{-(p − x)/c}] + d and constrained such that a > 0, x was within the range of positions. Note that as c approaches 0, a sigmoid approaches a step function; to avoid this we constrained the sigmoid to rise over a
minimum of three consecutive target positions \( (c > 0.34) \). In some analyses the constant function is referred to as “no modulation,” the step function is referred to as “discrete modulation,” and the grouping of linear and sigmoidal functions is termed “graded modulation.” Although our candidates for constant and discrete representation are fundamentally limited to a constant and step function, in principle, any smooth and monotonically increasing function could have been included to describe graded modulation. We included both linear and sigmoidal functions to permit the possibility of no saturation, or saturation at either or both target extremes.

**RESULTS**

**Experiment 1: categorical modulation by target direction**

**FEATURES OF BEHAVIOR.** This experiment examined whether subjects categorically modify their rapid motor responses as a function of spatial target direction when subjects are presented target and load conditions in blocked order. Subjects learned the task quickly and had little difficulty reaching the goal target within the imposed speed and accuracy constraints, performing with a mean success rate of 99% (SD 1). Figure 3A shows the mean hand trajectories and endpoint variability for the IN (gray) and OUT (black) conditions from a representative subject. Note that the IN and OUT correspond to those conditions where the perturbation displaces the hand into or out of the presented target, respectively. The initial segments of the IN and OUT conditions were overlapping, as expected, because they were generated by the same perturbation. However, hand paths rapidly deviated toward the PT (Fig. 3A), which resulted in significant differences in final hand position. We used ROC analysis (see METHODS) to determine when elbow and shoulder

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**FIG. 3.** Exemplar hand kinematics and EMG for experiment 1. A: spatial hand position for a representative subject. Traces correspond to the mean response from the IN (gray) and OUT (black) conditions for both the flexor (dashed) and extensor (solid) muscle groups. Endpoint ellipses represent the SD of hand position 350 ms after perturbation onset. The arrows point to the approximate separation of the kinematic responses as a function of target location. B and C: temporal joint kinematics for the elbow and shoulder. The horizontal axes represent time after perturbation onset and the vertical axes represent the joint angle that is initially 45° and 90° for the shoulder and elbow, respectively. D and E: temporal receiver-operator characteristic (ROC) analysis of elbow and shoulder kinematics (see METHODS) between target locations. Vertical axes represent the ROC area that indicates the probability that an ideal observer can identify the target position based on the kinematics. The horizontal lines at 0.25 and 0.75 are arbitrary significance levels where an ideal observer could discriminate between conditions in 3 out of 4 trials. F and G: traces represent mean muscle activity from the IN and OUT conditions for an exemplar muscle. G: a zoomed-in version of F, focusing on the rapid motor response epochs. H: each bar represents the EMG responses (mean ± SE) of the exemplar muscle within the given epoch for the IN (gray) and OUT (black) targets. Symbols indicate significant increase from the baseline epoch (Wilcoxon rank-sum, ††P < 0.01) and differences as a function of target position within an epoch (*P < 0.01).
kinematics (Fig. 3, B and C) were modified by target position. For this subject, target-dependent differences in elbow and shoulder kinematics were significant 130 and 121 ms after perturbation onset, respectively (see where traces cross 0.75 or 0.25 in Fig. 3, D and E). These results were typical across the population with target-dependent effects becoming significantly different at 139 ms (SD 24) for the elbow and 136 ms (SD 22) for the shoulder.

MUSCLE ACTIVITY. We applied background loads to activate the relevant muscle prior to perturbation onset, thus allowing us to observe both increases and decreases in response to the applied perturbation. When a muscle was stretched by the mechanical perturbation, we consistently observed a robust multipeaked EMG response for all subjects even on single-trial recordings. A typical mean response is shown in Fig. 3, F and G for a single muscle sample.

The mean response exhibits increasing sensitivity to target position, that is, the difference between IN and OUT conditions increased with time after perturbation onset. The earliest rapid response (R1, 20–45 ms) was indistinguishable for the two target positions; medium-latency rapid responses (R2, 45–75 ms) were excited by the perturbation and additionally scaled by target position and late rapid responses (R3, 75–105 ms) were mostly evoked or suppressed by target position. For the exemplar muscle, binned analysis reveals that whereas all epochs are significantly elevated from baseline (Wilcoxon rank-sum, \(P < 0.01\)) there are no target-dependent differences in either the baseline [rank-sum statistic, \(R_s(15,15) = 240, P = 0.77\)] or R1 epochs \([R_s(15,15) = 226, P = 0.81\]). In contrast, target-dependent modulation of muscle activity was significant in the R2 \([R_s(15,15) = 173, P = 0.01\], R3 \([R_s(15,15) = 120, P < 10^{-6}\], and VOL epochs \([R_s(15,15) = 120, P < 10^{-6}\], Fig. 3H). As in the exemplar muscle, target-dependent modulation across the population of muscle samples was rare for early periods and typical to universal for later periods (Wilcoxon rank-sum, \(P < 0.01\)): PRE (2 of 44 muscle samples, 5%), R1 (5%), R2 (32%), R3 (86%), and VOL (100%). Across the population of collected muscles, only the R2, R3, and VOL epochs show a significant change in activity as a function of target position (paired t-test, \(P < 0.01\)). Similar results were found in an analysis of the individual muscles (Table 1).

ROC analysis, which does not assume any underlying epochs, also reveals increasing target dependence. For the exemplar muscle, significant differences were found 79 ms after perturbation onset and a trend toward significance (knee) began at 58 ms (Fig. 4A). This result is visually evident when looking at the ROC response for each muscle collapsed across subjects; the ROC curves begin to deviate from chance about 60 ms postperturbation and cross the threshold at about 85 ms after perturbation onset (Fig. 4B). Across the population, significant target-dependent differences were present at 87 ms (SD 16, Fig. 4C, black) with trends beginning 61 ms (SD 18) after perturbation onset (Fig. 4C, red).

EFFECT OF STIMULUS PREDICTABILITY. The analysis in the previous sections focused exclusively on data collected when the perturbation direction was predictable based on the background load (blocked). Here, we examine data collected when perturbation direction was unpredictable and spatial target position was chosen randomly from trial to trial. Subject behavior was

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<th>Muscle</th>
<th>t-Statistic/P-Value (df = 10)</th>
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<td>R1</td>
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<tr>
<td>Brachioradialis (Br)</td>
<td>-2.1/0.06</td>
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<tr>
<td>Biceps (Bi)</td>
<td>-0.13/0.90</td>
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<td>Triceps lateral (TLat)</td>
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<td>Triceps long (TLo)</td>
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<td>Population (df = 43)</td>
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very similar between blocked and random conditions. Although subjects reported that the random condition was more difficult, they performed extremely well with a mean success rate of 98% (SD 1). We noted only a marginal increase in subject variability, which was quantified by the area of the confidence ellipse for their hand position 350 ms after perturbation onset (paired t-test, $t_{31} = 2.35, P = 0.03$). In addition, only two subjects showed increased variability in all random conditions (IN and OUT, Flexors and Extensors), suggesting that changes in variability with predictability were not particularly strong.

As in the blocked conditions, upper-limb muscle responses exhibited an increasing sensitivity to target position. Figure 5, A and B presents the same exemplar muscle as in Fig. 3, F and G; again, there is little difference in R1 and an increasing difference in the R2, R3, and VOL epochs. Across the population of muscle samples only the R2, R3, and VOL epochs show a significant change in activity as a function of target position (paired t-test, $P < 0.01$). ROC analysis reveals that the knee of the curve for random conditions, which occurs at 64 ms (SD 18), is not significantly different from the blocked condition ($t_{59} = 1.7, P = 0.1$). In contrast, there was a significant delay in the time of significance, which was pushed back to 95 ms ($t_{59} = 3.6, P < 10^{-5}$).

Random and blocked conditions were more directly compared by plotting the amount of target dependence (OUT/IN) for each muscle sample and epoch of activity (Fig. 6). In this plot, points in the top-right quadrant represent muscle samples that showed target dependence in the correct direction (OUT > IN) for both random and blocked conditions; samples located along the line of unity had equal levels of target-dependent modulation. The R1 response shows no target-dependent modulation in either blocked or random trial orders. In contrast, there is a clear similarity between the random and blocked responses for the later epochs, in that nearly all muscles exhibit target dependence in both random and blocked conditions. Although the responses are similar, across the population blocked order responses exhibit significantly more target dependence for each of the R2 (paired t-test, $t_{31} = 3.6, P < 10^{-5}$), R3 ($t_{31} = 4.0, P < 10^{-5}$), and VOL ($t_{31} = 5.78, P < 10^{-5}$) epochs, as seen by the systematic bias away from the line of unity toward the horizontal axis. On average, the amount of task dependence in the random condition was 44, 75, and 80% of the size of the blocked condition in the R2, R3, and VOL epochs, respectively. Thus randomly presenting the perturbations resulted in subtle changes, including a reduction in the amount of target dependence but no significant change in its onset.

Finally, we compared the effect of repeating the same perturbation condition by subdividing the blocked experiment into the first and last five trials of each block. If the target dependence we observed in the blocked condition was the result of scaling with repeated performance we should observe a systematic increase in target dependence for the last five trials. In fact, no epochs exhibited such a systematic increase in target dependence (one-sided t-test, $P > 0.3$).

**Experiment 2: graded modulation by target distance**

**FEATURES OF BEHAVIOR.** Here, we assessed whether rapid motor responses are modulated in a graded fashion as a function of target distance or whether they are limited to categorical

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**Figure 5.** Analysis of EMG under random trial order. A and B: same format as Fig. 3, F and G. C: same format as Fig. 4B. D: same format as Fig. 4C.
changes according to target direction (as shown in experiment 1). Subjects had no difficulty learning the task and were extremely successful with a success rate of 96% (SD 3).

Population mean hand trajectories for each target position in both flexor and extensor conditions are shown in Fig. 7, A and B, respectively. All subjects showed systematic differences in final hand position for the five target conditions and temporal differences in elbow kinematics between the extreme targets were significant 135 ms (SD 30) after perturbation onset (Fig. 7C). Similar temporal trends are found at the shoulder (Fig. 7D). Furthermore, these trajectories reveal a visible rank-order trend according to target position as early as any separation.

MUSCLE ACTIVITY. Figure 7, E and F presents the pooled response to the same perturbation and targets located at five distances; note that target order is reversed for flexors and extensors. Qualitatively (and in agreement with experiment 1), the earliest response (R1) was not scaled by target distance and thus exhibited a constant relationship with target position. In contrast, the R2, R3, and VOL epochs show a monotonic/graded increase in activity as a function of target distance.

Since the qualitative observation of graded modulation across muscles and subjects may simply reflect the temporal smearing of discrete responses, we used Akaike’s Information Criterion (AIC; see METHODS) to determine the best candidate model for each collected muscle sample (Fig. 8A). In the R1 epoch, almost all muscles (29 of 34, 85%) were best described by a constant function, indicating no modulation as a function of target position. The R2 epoch was generally best described by a constant function (59%) with some muscles exhibiting discrete (18%) or graded (linear or sigmoidal) modulation by target position (24%). R3 was most commonly described by a linear function (53%) with a total of 21 muscles that exhibited graded modulation by target position. Last, the VOL epoch was best described by graded modulation (74%) with most muscles exhibiting a sigmoidal (50%) or linear (24%) relationship. A similar progression from constant to graded modulation was found when inspecting individual muscles (Table 2).

Similar trends were found when we calculated relative AIC scores (ΔAIC) to assess the adequacy of the candidate models (Fig. 8B). Based on this analysis, R1 activity was adequately explained by the constant function for 31 of 34 (91%) muscles. Furthermore, activity in the R2, R3, and VOL epochs was adequately explained by a linear or sigmoidal function (graded

FIG. 6. Task dependence under different trial orders as a function of epoch. The horizontal and vertical axes represent the mean difference in activity (OUT − IN) for each muscle sample under blocked and random trial orders, respectively. Samples in the top right quadrant indicate the predicted target-dependent modulation (OUT > IN). Samples that lie close to the diagonal exhibit a similar amount of target dependence for both blocked and random trial orders. Note the different scales for each epoch.

FIG. 7. Behavioral performance and EMG in experiment 2. A and B: each plot represents exemplar hand kinematics for extensor (A) and flexor (B) trials as a function of target position. Subjects began each trial at the filled black circle and the black diamond indicates the hand position 350 ms after perturbation onset. Small arrows indicate the approximate direction of movement caused by the perturbation. Note that the extrinsic target positions requiring the greatest agonist activity (green traces) are reversed for the elbow flexors and extensors. C: temporal kinematics for the elbow joint aligned on perturbation onset. Color and line style represent, respectively, the target position and perturbation conditions shown in A and B. D: temporal kinematics for the shoulder joint; same format as B. E and F: pooled EMG showing graded modulation of activity with target position. Data are collapsed across all available muscle samples and targets reversed for the flexors and extensors. F: a zoomed-in version of G, focusing on the rapid motor response epochs.
modulation) for 59, 82, and 88% of muscle samples, respectively. Taken together, these results suggest a progression of target selectivity, with R1 exhibiting constant or no modulation by target position, whereas R2, R3, and VOL epochs were modulated by target position in a graded, rather than discrete, fashion.

**Experiment 3: spatial tuning of rapid responses**

**FEATURES OF BEHAVIOR.** We distributed four targets radially around the central area to determine whether rapid motor responses could be spatially modulated as a function of two-dimensional target position. As in previous experiments, subjects had little difficulty performing the task, with an average success rate of 93% (SD 8), and no substantive differences in performance across the targets or load conditions. Figure 9, A–D shows hand kinematics for an exemplar subject in all four load conditions. Note that the target locations are identical for all the load conditions and that the only difference was the background and perturbation loads chosen for each muscle group (elbow flexor, elbow extensor, shoulder flexor, shoulder extensor). As in previous experiments, spatial analysis of hand position reveals that every subject achieved significantly different hand endpoints for all targets under all load conditions. Temporal analysis of shoulder and elbow angles revealed rapid target-dependent changes (Fig. 9, E–H). ROC analysis between IN and OUT targets reveals significant differences between elbow and shoulder kinematics at 143 ms (SD 21) and 129 ms (SD 19) after perturbation onset, respectively.

**MUSCLE ACTIVITY.** Figure 10A shows pooled EMG responses that demonstrate how muscle responses change for the same perturbation but different target positions well before the voluntary epoch. To summarize these differences, we calculated tuning functions (EMG vs. the four target positions) by a plane fit for each epoch of activity. Note that for all analyses we used only the background load and perturbation condition that tonically activated and stretched the muscle of interest. Across all collected muscle samples, plane fits for the R1 epoch were universally insignificant (plane fit, \( P < 0.01 \) for 0 of 36 muscle samples) and highly variable with resulting PDs showing no consistent trend (Fig. 10B, R1). R2 responses also typically resulted in insignificant plane fits for individual muscle samples (\( P < 0.01 \) for 3 of 36) but the calculated PDs exhibited trends that qualitatively match results in later periods (Fig. 10B, R2). Last, both R3 (29 of 36) and VOL (35 of 36) epochs exhibited significant fits and showed consistent trends in their preferred directions (Fig. 10B, R3 and Voluntary). The similarity of preferred directions was tested by using a Rayleigh test to determine whether the data were unimodally tuned. In fact, we noted a progression of similarity, with 0, 3, 6, and 6 of 6 muscles exhibiting unimodally tuned preferred directions in the R1, R2, R3, and VOL epochs (Rayleigh test, \( P < 0.05 \)).

The progression of target dependence found in the tuning functions is similar to the increasing levels of task dependence we found in experiments 1 and 2. To summarize how the directionality of rapid responses tends toward the voluntary response, we calculated the angular difference between preferred directions calculated in each rapid response epoch and the voluntary response (\( \text{R1-VOL, R2-VOL, R3-VOL; Fig. 11} \)). There is a clear progression of directionality, with \( \text{R1-VOL} \) being randomly assigned and \( \text{R2-VOL} \) and \( \text{R3-VOL} \) clustering around 0°, indicating more similarity with the voluntary response. This trend was quantified by calculating the mean absolute angular difference, which can range from 0 to 180°, with a random distribution resulting in 90° and perfect correspondence resulting in 0°. In our data set, the mean absolute difference between R1, R2, and R3 was 93° (SD 47), 45° (SD 40), and 19° (SD 20), respectively.

In experiment 1 we compared rapid responses between IN and OUT targets for muscles that span the elbow. Here, we extend this analysis to shoulder muscles because IN/OUT targets are a subset of conditions in this experiment (compare Fig. 3 and Fig. 9). In general we found similar results at the shoulder for R1 with no muscle samples (0 of 12) differentially modulated by IN/OUT conditions (Wilcoxon rank-sum, \( P > 0.2 \)) and for R3 and VOL epochs where nearly all muscle samples (R3: 12 of 12; VOL: 11 of 12) exhibited significant differences (\( P < 0.05 \)). A potential difference may exist in the R2 epoch where one of 12 shoulder muscle samples exhibited significant target-dependent differences (compared with 14 of

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**TABLE 2. Results of model selection by muscle**

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Candidate Model (R1/R2/R3/Vol)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Constant</td>
</tr>
<tr>
<td>Brachioradialis (Br)</td>
<td>9/8/1/1</td>
</tr>
<tr>
<td>Biceps (Bi)</td>
<td>5/4/1/0</td>
</tr>
<tr>
<td>Triceps lateral (Tlat)</td>
<td>8/5/2/0</td>
</tr>
<tr>
<td>Triceps long (Tlo)</td>
<td>7/3/2/0</td>
</tr>
</tbody>
</table>

Values represent the number of times the given candidate model was chosen as best by AIC.
progression of motor sophistication whereby earliest responses showed little or no sensitivity to the spatial goal, whereas the later responses progressively approached the voluntary response. In experiment 1 we showed that long-latency rapid responses (R2: 45–75, R3: 75–105 ms postperturbation) were categorically scaled up and down by the direction to the spatial target. This pattern of scaling was robust across both subjects and muscles with 86% of muscle samples showing significant target-dependent modulation. In contrast, only 5% of samples were modulated within the short-latency rapid response epoch (R1: 20–45 ms). Comparable results were found when load and targets were presented in random order, although the effect size was reduced, suggesting that R2 and R3 epochs incorporate both prior information and current sensory evidence in generating their response. In experiment 2, we established that modulation of long-latency rapid responses, particularly R3, is not merely a categorical switch that is turned “on” for distant targets and “off” for close ones. Rather, the response is graded based on the distance to the spatial target. Last, in experiment 3, we showed that the R2/R3 responses are spatially tuned to two-dimensional target position, indicating that they incorporate the multijoint requirements of the task in their response.

Although many studies have investigated whether rapid motor responses can be modulated by subject intent at the elbow (Colebatch et al. 1979; Crago et al. 1976; Evarts and Granit 1976; Hagbarth 1967; Hammond 1956; Rothwell et al. 1980), wrist (Calancie and Bawa 1985; Jaeger et al. 1982a; Lee and Tatton 1982), finger (Capaday et al. 1994; Marsden et al. 1981; Rothwell et al. 1980), ankle (Gottlieb and Agarwal 1979, 1980; Ludvig et al. 2007), and jaw (Pearce et al. 2003), most of these have focused on individual muscles at that joint. An important feature of the present study is that our experiments were designed to test a large subset of muscles acting to move the arm in the plane of the task including monoarticulars, biarticulars, flexors, and extensors of the shoulder and elbow. Accordingly, our results demonstrate that although muscles exhibit some differences in detail, they all showed the same general pattern of modulation as a function of spatial goal, suggesting that modulation of rapid motor responses is a common feature for upper-limb muscles.

Advantages of our visuospatial perturbation paradigm

Our paradigm builds on a prominent methodology that uses verbal instructions to instruct a subject how to respond to an imposed perturbation (Capaday et al. 1994; Colebatch et al. 1979; Crago et al. 1976; Hagbarth 1967; Hammond 1956; Lewis et al. 2006; Rothwell et al. 1980). Although verbal instructions have varied widely across researchers and experiments, including “resist/let go” (Colebatch et al. 1979; Hammond 1956; Rothwell et al. 1980), “flex/extend” (Hagbarth 1967), and “compensate/do not intervene” (Crago et al. 1976), they are inherently categorical and restricted to the ambiguities of natural language. They are also not amenable to animal models that could explore the neural substrates of sophisticated rapid motor responses. In the present study we minimized the dependence on verbal instructions by specifying and enforcing an explicit spatial goal. In our first experiment we replaced the above-cited categorical verbal instructions with two potential targets placed such that the perturbation displaced the hand directly into one target and directly out of the other. Such an
approach is advantageous because the task is explicitly defined and performance can be directly measured, allowing us to explore the flexibility of rapid motor responses under conditions that would be difficult with verbal cues. For example, we established that the modulation is graded by simply distributing visual targets at various distances from the start position. Furthermore, we showed that rapid responses could be adjusted to varying multijoint requirements at the shoulder and elbow by distributing targets in two dimensions. The analogous verbal cues for these experiments, perhaps “increase/decrease resistance by 25, 50, and 75%” for the gradation experiment, and “respond to the elbow perturbation by flexing your shoulder and elbow” for the multijoint experiment, would be difficult for subjects to adhere to and likely impossible to monitor or enforce.

It is important to note that a few researchers have used spatial targets to study the modulation of rapid motor responses (Brown and Cooke 1986; Day et al. 1983; Koshland and Hasan 2000). However, these studies differ from the present experiments because they provided precise information about when to generate a specific movement and thus tested how rapid motor responses change during the initiation of a reach. For example, Koshland and Hasan (2000) reported that R2 and R3 responses depend on the impending direction of arm movement. In that study, subjects were instructed to reach a target in response to either a “small” or “large” perturbation in the same
However, the demarcation of complexity is inherently subjective when the pathway is complex, the response is voluntary. Conversely, when the mapping is simple and well defined, the response is a reflex and changes with time as pathways become better characterized.

In the present experiment we wanted to avoid the philosophical and semantic debate surrounding the term reflex because it is unclear that such a debate is fruitful in furthering our understanding about the underlying neurophysiological processes. In fact, our own experience suggests that the term is a substantial obstacle. Therefore we turned to an operational definition whereby we empirically defined a set of rapid muscular responses because they appear prior to the earliest muscle activity in a control experiment designed to determine kinesthetic reaction time (Evarts and Vaught 1978; Hammond 1956; Jaeger et al. 1982b). Our reaction time manipulation eliminated the earliest phasic muscle responses by reducing perturbation magnitude, leaving only a large and maintained pattern of muscle activity commonly attributed to a voluntary response. The earliest of these responses occurred about 100 ms after perturbation onset, a result that is consistent with many other studies (Calancie and Bawa 1985; Hammond 1956; Jaeger et al. 1982b; Kimura et al. 2006; Lee and Tatton 1975; Matthews 1986; Rothwell et al. 1980; Tatton and Lee 1975) and corresponds to a similarly timed volley of activity in our main experimental tasks (Figs. 3, 5, 7, and 10). It should be noted that although we labeled this maintained volley of activity as voluntary, we could just as well have chosen R4. In summary, we specifically avoided the term reflex and replaced it with rapid motor response, which refers only to a temporal window of events occurring prior to kinesthetic muscle onset as determined empirically.

Short-latency (R1) rapid responses are not modulated by target position

In agreement with many previous studies, our results demonstrate that R1 responses of the upper limb during postural control are not quickly modified by subject intent (Crago et al. 1976; Hammond 1956; Marsden et al. 1972b; Rothwell et al. 1980). Such inflexibility is surprising given that spinal interneurons receive descending input from cortical areas and exhibit task-specific preparatory activity (Prut and Fetz 1999). However, in that study the muscles were silent in the preparatory period that may have allowed subthreshold changes in muscle activity that would not be visible in the recorded EMG (Capaday and Stein 1987). Because such changes are known to modify R1 responses (Capaday et al. 1994; Marsden et al. 1972a; Matthews 1986) it would be informative to establish whether changes in preparatory activity are present without changes in EMG when the muscles are above threshold.

The lack of R1 modulation within our postural task is contrasted by changes observed across behaviors such as the profound modulation of all rapid motor responses in the upper limb between posture and movement (Mortimer et al. 1981) or in the lower limb between stance and walking (Komiyama et al. 2000) or running (Duyens et al. 1993). In fact, rapid responses of both upper and lower limbs have been shown to change over the course of a cyclical movement such as gait (Akazawa et al. 1982; Capaday and Stein 1986; Forssberg et al. 1975; Zehr et al. 2003), sinusoidal tracking (Dufresne et al. 1980; Johnson et al. 1993), or hand cycling (Zehr and Chua 2000), illustrating that spinal circuitry can generate sophisticated and flexible responses under certain conditions.

**What is a reflex?**

Reflexes are broadly defined as a stereotyped transformation from a sensory stimulus to a motor event (Kandel et al. 2000). However, past research in physiology, psychology, and philosophy has yielded little agreement about what specifically constitutes a reflex response (Prochazka et al. 2000). One class of definitions offered by Prochazka and colleagues (2000) is that reflexes are those responses that are automatic, that is, they are transformations that cannot be consciously modified or suppressed. However, given that even the monosynaptic stretch reflex is modifiable under certain conditions (Stein and Capaday 1988), it is unclear that any muscular responses can be characterized as a reflex by this definition. A second class of definitions is based on the anatomical or physiological nature of the mapping between the input and output. When the mapping is simple and well defined, the response is a reflex and when the pathway is complex, the response is voluntary. However, the demarcation of complexity is inherently subjective and changes with time as pathways become better characterized.
In addition to changes across tasks, several studies have shown systematic changes in R1 responses over long training periods in a single task (Christakos et al. 1983), particularly when R1 magnitude is directly reinforced (Wolf and Segal 1996; Wolpaw 1983; Wolpaw et al. 1983). Although our experiments could have reasonably elicited modulation of the R1 response we did not find such modulation. In fact, two of the authors (AP and IK) have performed the task over several thousands of trials and neither shows modulation of R1 responses. This does not imply that R1 is completely immutable; rather, it is consistent with past observations that changes require extensive practice within a consistent training regime. We suspect that we could have observed R1 target dependence by providing subjects with a very long set of trials under the same perturbation and target conditions. In contrast, naive subjects were able to modify their R2 and R3 responses within seconds of the instruction and with minimal practice (Colebatch et al. 1979; Soechting et al. 1981).

Effect of stimulus predictability on long-latency (R2 and R3) rapid responses

Our three main experiments demonstrate that R2 and R3 responses are modulated in a sophisticated fashion as a function of spatial target position even when perturbation onset is unpredictable. However, in these experiments the perturbation direction was known in advance and it is possible that our observed modulation was due to the release of preplanned motor output in response to the perturbation such as that observed under startle conditions (Carlsen et al. 2004; Valls-Sole et al. 1999). We tested this possibility by having subjects perform experiment 1 in random order such that both the perturbation direction and onset were unpredictable. If the responses merely reflected a preplanned output then we would observe no mean target dependence and highly variable kinematic behavior because on half the trials subjects would release the inappropriate plan for the current perturbation. In fact, subjects showed only a small and inconsistent increase in variability when perturbation direction was unpredictable and never responded with the wrong movement. That said, there were subtle differences in the R2 and R3 responses that exhibited similarly timed but systematically smaller target dependence. These results are consistent with previous findings demonstrating that task dependence of R2/R3 responses is decreased but not eliminated by reducing the predictability of perturbation onset (Rothwell et al. 1980) or direction (Crago et al. 1976; Evarts and Vaughan 1978; Gottlieb and Agarwal 1980; Oriain et al. 1979). However, unlike the reports of some previous authors (Crago et al. 1976; Evarts and Vaughan 1978) we did not find a significant delay in the onset of target dependence (ROC Knee), indicating that sophisticated rapid responses are present at a fixed time after perturbation onset regardless of predictability (Gottlieb and Agarwal 1980; Oriain et al. 1979; Rothwell et al. 1980). Taken together, our present results suggest that R2 and R3 responses are not the result of a simple triggered response where one motor output is preprogrammed and released based on the occurrence of a sensory stimulus. Rather R2 and R3 responses combine both current sensory information and prior perturbation history (in addition to the spatial goal) to form an appropriate response; additional work is needed to establish the rules of how these factors are combined.

How are R2/R3 responses related to the volitional motor system?

The volitional motor system possesses an incredible capacity to control direction, distance, speed, accuracy, load, and many other parameters of movement. Our results demonstrate that R2 and R3 responses of multiple upper-limb muscles share some of the key functional attributes of volitional control. For example, we have recently demonstrated that R2/R3 responses possess an internal model of limb dynamics (Kurtzer et al. 2008) and here we show that these responses are appropriately tuned to the metrics of a spatial task. We suspect that such similarities are not accidental and can be readily understood if one appreciates that R2/R3 responses and volitional control share similar neural circuitry, including somatosensory cortex, motor cortex, cerebellum, and other subcortical structures (Cheney and Fetz 1984; Evarts 1973; Lewis et al. 2004; Matthews 1991; Strick 1983). Accordingly, the sophistication of R2/R3 responses would reflect the earliest volley of activity through the same neural circuit that is later engaged by voluntary control (Scott 2004). This concept of an evolving sensorimotor approximation through the same neural structures fits well within recent theories of volitional motor control that emphasize the importance of intelligently using feedback (Scott 2004; Todorov 2004; Todorov and Jordan 2002) and is related to previous work that attributed the task dependence of R2/R3 responses to a hastened voluntary response (Crago et al. 1976; Hasan 2005; Rothwell et al. 1980). It may also explain why a precise definition of reflex has proven difficult to establish.

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DISCLOSURE

S. H. Scott is associated with BKin Technologies, which commercializes the KINARM robotic system.

REFERENCES


