Temporal development of anticipatory reflex modulation to dynamical interactions during arm movement

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Temporal setting of anticipatory reflex amplitude

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**Abstract**

It is known that somatosensory reflex during voluntary arm movement is modulated anticipatorily according to given tasks or environments. However, when and how reflex amplitude is set remains controversial: Is the reflex modulation completed preparatorily before movement execution or does it vary with the movement? Is the reflex amplitude coded in a temporal manner or in a spatial (or state-dependent) manner? Here we investigated these issues while subjects performed planar reaching movements with upcoming opposite (rightward/leftward) directions of force fields. Somatosensory reflex responses of shoulder muscles induced by a small force perturbation were evaluated at several points before the arm encountered predictable force fields after movement start. We found that the shoulder flexor reflex responses were generally higher for the rightward than for the leftward upcoming force fields, while the extensor reflex responses were higher for the leftward force field. This reflex amplitude modulation depending on the upcoming force field direction became prominent as the reflex was evoked closer to the force fields, indicating continuous changes in reflex modulation during movement. An additional experiment further showed that the reflex modulation developed as a function of the temporal distance to the force fields rather than the spatial distance. Taken together, the results suggest that, in the force field interaction task, somatosensory reflex amplitude during the course of movement is set anticipatorily on the basis of an estimate of the time-to-contact, rather than the state-to-contact, to upcoming dynamical interaction during voluntary movement.

**Keywords**

Somatosensory reflex, Anticipation, Timing, Force field, Voluntary movement
Introduction

The dynamical properties of our musculoskeletal system, such as the torque and stiffness of limbs, should be appropriately regulated for skillful interaction with variable external environments. Previous studies have suggested that musculoskeletal dynamics during voluntary movements are regulated not only by top-down motor commands (Burdet et al. 2001; Franklin et al. 2003) but also by automatic or “reflex” sensory-motor transformation (Lacquaniti and Maioli 1989; Hore et al. 1990; Goodin and Aminoff 1992; Bennett et al. 1994; Wang et al. 2001; Gomi et al. 2002). These reflex studies indicate that the somatosensory reflex, the so-called stretch reflex, contributes to effectual regulation of the musculoskeletal dynamics in a given movement situation, such as an enhancement of hand stiffness during ball catching (Lacquaniti and Maioli 1989) and under unstable environments (Gomi et al. 2002). Indeed, many studies have reported that somatosensory reflex amplitude is flexibly modulated according to ongoing tasks (Johnson et al. 1993; Dietz et al. 1994), instruction (Bonnet 1983; Sullivan and Hayes 1987; Yamamoto and Ohtsuki 1989; Goodin and Aminoff 1992; Pruszynski et al. 2008), dynamical environments (Kimura et al. 2006; Perreault et al. 2008) or own limb geometry (Kurtzer et al. 2008). It is unclear, however, when and how reflex amplitude is set during voluntary movements.

A key feature of somatosensory reflex modulation is the *anticipatorily* change (or setup). Several studies have demonstrated, for instance, that the response increases when subjects are instructed to resist an imposed disturbance invoking a stretch reflex compared to an assist instruction condition, with succeeding volitional muscle activation (Evarts and Tanji 1974, 1976; Colebatch et al. 1979; Marsden et al. 1983; Yamamoto and Ohtsuki 1989). Such instruction-dependent changes in reflex amplitude have been often explained by the concept of a *preparatory motor set*.
(reviewed by Bonnard et al. 2004), where the reflex amplitude is preset on
the basis of a prior motor intent, implying reflex amplitude setting prior to
movement execution. Indeed, it has been shown that reflex responses
induced by a mechanical perturbation begin to change a few hundred
milliseconds before resist and assist reactions to predictable disturbances,
depending on the reaction directions (Bonnet and Requin 1982; Bonnet
1983; Sullivan and Hayes 1987). However, it would be difficult to
conclude that such reflex behavior indicates a build-up of reflex amplitude
before movement execution, since in these situations the instructed
movement (resist/assist reaction) is very close to the dynamical event
(mechanical disturbance) causing reflex modulation because of the short
delay between them (around 100 ms). In other words, it is hard to strictly
identify when (before the movement or before the event) reflex
modulation occurs. It remains debatable, therefore, whether reflex
amplitude modulation is completed before movement initiation.

Another important issue regarding reflex modulation is what
triggers anticipatory reflex amplitude build-up. There is a long-standing
debate about temporal and spatial coding of neural processing in
voluntary movement control (Hore and Watts 2005; Medina et al. 2005;
Diedrichsen et al. 2007). Temporal control is supposed to be based on an
internal representation of time (e.g., movement speed), while spatial
control is based on an internal representation of state (e.g., limb position).
Several reflex studies have adverted to spatiotemporal aspects of reflex
behavior during voluntary actions (Lacquaniti et al. 1991; Sinkjaer et al.
1996; Xia et al. 2005). It has been reported, for example, that the wrist
and elbow reflexes evoked by torque perturbation change at different
times during catching (Lacquaniti et al. 1991). On the other hand,
Sinkjaer et al. (1996) has shown that stretch reflexes in the calf muscles are
modulated depending on the phases of walking. These studies implied
that temporal or spatial information is involved in the reflex tuning, but did not exactly differentiate their involvement. After all, whether temporal or spatial information is dominant in driving reflex amplitude coding is still unclear.

In the present study, we conducted three experiments to investigate the above issues. In the first and second experiments, we examined reflex modulation behavior to expected dynamical events (opposite directions of force fields) during arm reaching movement, but not before the movement initiation, by assessing reflex responses at several points before the force fields. We hypothesized that if reflex amplitude modulation is not completed before movement start and if it occurs to a dynamical event during movement in a dynamic fashion, the reflex amplitude should change. Then, we examined the spatiotemporal properties for reflex amplitude setting in the third experiment, in which both temporal and spatial distances from reflex responses to the force fields were controlled, and compared these effects on reflex amplitude modulation.

Materials and Methods

Setup and task

Sixteen right-handed healthy male subjects (24 - 32 years of age), who had no known history of neurological disorders and gave informed consent, participated in this study. Not all subjects participated in all three experiments. The study was approved by the local ethical committee.

The experimental setup was almost the same as in our previous study (Kimura et al. 2006). Subjects were comfortably seated in a dental
chair in front of a Parallel Link Drive Air-Magnet Floating Manipulandum (PFM, Gomi and Kawato 1997) with the trunk strapped to the chair so that the right shoulder joint was fixed in the origin ([x, y] = [0, 0]) of the task-coordinate, where x and y indicate the rightward and forward direction away from the body, respectively. The right forearm was tightly attached to the handle of the PFM by a custom-molded thermoplastic cuff and supported against gravity by a horizontal beam. Consequently, arm motion was limited in the horizontal plane without wrist movement. The PFM was controlled by a digital servo at 2000 Hz.

Subjects were instructed to perform start-to-goal right arm movements with as straight a path as possible (Fig. 1A). The proximal start and distal goal positions were projected on a horizontal screen (120 × 100 cm) placed approximately 10 cm above the arm, which occluded the subject’s arm from his view. The current hand position was displayed on the screen by a laser attached to the handle top before movement onset, extinguished at the time of the movement start, and re-displayed at the end of the movement. Therefore, subjects had no on-line visual feedback of their hand position during movement. The movement was executed in time with beeping sounds indicating the desired duration and with a guide marker moved by the desired minimum jerk trajectory on the screen.

One of three force fields was imposed during part of the movement: a null force field (N-FF), where no additional force was applied, a leftward (L-FF), or a rightward (R-FF) trapezoidal-shaped force field (peak of 7 N) in which a transition phase was applied so that force changed gradually over the first and last 2 cm of the force field (total range of 11 cm). Before the movement start, a visual cue for each force field condition and location was presented on the screen as a symbol (L-FF/R-FF, arrow; N-FF, rectangle) and a rectangular frame, respectively, which allowed subjects to
predict the force field condition for each trial before the movement execution. The order of force fields was randomized for each trial. Note here that the null condition was utilized in control trials and the data acquired were not used for quantitative analyses, such as comparing reflexes, as in our recent study (Kimura et al. 2006).

To evoke arm reflex, we used a half-sine wave force perturbation (peak amplitude of 20 N, duration of 50 ms) in the leftward (L-PTB) or rightward (R-PTB) direction. The perturbation was designed to be small enough to not severely disrupt ongoing movement and was applied before the arm encountered the force field. The L-PTB and R-PTB primarily stretched the shoulder extensor and flexor muscles, respectively, and accordingly elicited somatosensory reflex, so-called stretch reflex, responses in these muscles. By means of such perturbation setting, we could obtain somatosensory reflex responses of the shoulder muscles anticipatory to upcoming force fields.

Figure 1

Experiments

We controlled the perturbation points, force field locations, start and goal positions and movement durations in every experimental condition to examine the spatiotemporal properties of anticipatory reflex modulation. In the first experiment (n=9), the start and goal positions were set at [0, 30] and [0, 55] cm in the task-coordinate, respectively. The force fields began at a fixed point 12 cm from the start position (42 to 53 cm in y-direction). The perturbations were given at one of three points before the force field
initiation (see Fig. 2A). The first perturbation (PTB1) occurred after the hand had passed through 2 cm forward from the start position. The second (PTB2) and third (PTB3) perturbations were applied 100 and 200 ms after the first one, respectively. We determined these perturbation points so as to avoid the phases just after the movement initiation and just before encountering the force fields in which muscle activity would change drastically. For the same reason, we requested subjects to perform relatively slow (1.5 s duration) movement with the help of the given guide marker. This experiment was designed as factorial combinations: three force fields (L-FF, R-FF, N-FF) × seven perturbation conditions (two perturbations (L-PTB, R-PTB) × three perturbation locations (PTB1, PTB2, PTB3) + no perturbation) for a total of twenty-one combinations. Subjects randomly performed fifteen trials in each combination, giving a total of 315 trials. We assessed continuous reflex behavior anticipatory to upcoming force fields during movement in this experiment.

The second experiment (n=8) was conducted to control arm posture when a perturbation was applied. We designed workspaces, including all start and goal, force field and perturbation, at three locations along the movement direction (L1/L2/L3) so that arm posture at perturbation application corresponded to that at each perturbation point in the first experiment (PTB1/PTB2/PTB3). The start position was set at 30, 32 or 34 cm on the y-axis. The goal position and initiation point of the force field were fixed at 25 and 12 cm from the start position, respectively. A single perturbation point was also fixed at 2 cm from the start (i.e., L1: 32, L2: 34 or L3: 36 cm on the y-axis). That is, the relative spatial relation for the movement, force field, and perturbation was kept constant across the workspace locations. In this experiment, we used rightward perturbation (R-PTB) only. Accordingly, we targeted the shoulder flexor reflexes.
Each workspace condition was performed in a randomized separate block. Each block consisted of six patterns for force fields and perturbations: three force fields (L-FF, R-FF, N-FF) \times two perturbation conditions (R-PTB, no perturbation). Subjects performed fifteen trials in each pattern of each block, giving a total of 270 trials in this experiment.

We conducted the third experiment (n=9) to control the temporal distance (TD) and spatial distance (SD) between the perturbations and the force fields independently so as to assess the effects of these parameters on reflex behavior. In this experiment, the force field locations and movement duration were varied, while the perturbation point was fixed at 3 cm from the start position (see Fig. 6A). Three force field locations were used here: the same location as in the first experiment (MidDst, 42 to 53 cm in y-direction) and 2 cm farther from (FarDst) and closer to (NearDst) the MidDst. Three movement durations were also used to vary movement speed: the same duration as in the first experiment (base, 1.5 s) and a short (1.2 s) and long (1.8 s) duration. These short and long durations mean fast (FastSpd) and slow (SlowSpd) movement speeds compared to the base one (IntSpd), respectively. Five combinations of the force field location and movement duration were designed: MidDst-IntSpd, MidDst-FastSpd, MidDst-SlowSpd, FarDst-FastSpd, NearDst-SlowSpd. Each combination was done in a randomized separate block. Each block consisted of nine patterns for force fields and perturbations: three force fields (L-FF, R-FF, N-FF) \times three perturbation conditions (L-PTB, R-PTB, no perturbation). Subjects performed fifteen trials in each pattern of each block, giving a total of 675 trials in this experiment. From the data obtained in the no perturbation trials, we estimated the position in the y-direction and the time for the perturbation and force field that would be given in the perturbation trials. Then, we calculated the time interval and the distance between the perturbation and
force field to obtain TD and SD, respectively.

Prior to the experiments, subjects practiced straight arm movements for each force field with the requested movement duration. A few dozen trials, whose number was depended on subject performance, were repeated for each block condition with on-line visual feedback of their hand position on a projector screen and with guidance of their movement duration and performance from the experimenter.

**Measurements and processing**

Surface electromyography (EMG) was recorded from two mono-articular muscles around the shoulder joint, the shoulder flexor (pectoralis major) and extensor (deltoid posterior), using pairs of Ag-AgCl electrodes (diameter 10 mm) with an interelectrode distance of 20 mm and standard skin preparation. The EMG signals were amplified with a bioelectric amplifier (MME-3132, NIHON KOHDEN) and digitized at a sampling rate of 2000 Hz. The digitized EMG signals were full-wave rectified after subtracting the DC component, band-pass-filtered at 10-500 Hz, and then moving-averaged at 10 ms. In our experimental settings, the reflex responses in the flexor and extensor muscles were induced at onset latencies of 43.9 ± 3.9 ms (mean ± s.d. across all subjects) and 50.3 ± 4.1 ms, respectively, and continued for more than 50 ms (see Fig. 2B). We therefore quantified reflex amplitude as the mean EMG signals in each trial over the fixed reflex period (50-100 ms after the perturbation onset). Background EMG activity (BGA) was calculated as the mean EMG signals over the same time period in trials where no perturbation was applied. The calculated reflex response and BGA in each trial were normalized by a maximum reflex value in all trials for every muscle in each subject.

The PFM's handle position and the external force exerted at the
handle were measured with a position encoder and force sensor, respectively, at a sampling rate of 500 Hz. We estimated kinematic parameters, which are described in detail elsewhere (Gomi and Kawato 1997). Joint angle was obtained from the handle position using the kinematic relationship. Joint velocity and acceleration were calculated by first- and second-order time-differentiations of each joint angle, respectively. To characterize both kinematic state when a perturbation was applied and kinematic response induced by a perturbation, we evaluated the position and velocity of the hand, shoulder, and elbow joints. The positional response to the perturbation was quantified as the maximum displacement over a fixed time period (80 ms duration after the perturbation onset) based on the differential profile between each perturbation trial (R-PTB/L-PTB) and the mean waveform of no-perturbation trials. The velocity response was quantified as the peak value after the perturbation. The kinematic state for each parameter was quantified as the mean value over the same period in trials where no perturbation was applied.

Statistical analysis

Our previous study, in which we used experimental conditions and a task similar to those in this study, showed a significant decrease of BGA in the no force field condition compared to force field conditions, while there was no difference between force field directions (Kimura et al. 2006). Since reflex amplitude strongly depends on background activity (Matthews 1986), it is inappropriate to directly compare reflex responses whose BGA differs. Thus, we excluded the data in the null trials from quantitative analyses of reflex modulation, as mentioned above, so as to focus on comparing reflexes between force field directions (R-FF and L-FF).
Accordingly, in the first experiment, we used a two-factor repeated-measures ANOVA with factors of force field directions (L-FF/R-FF) and perturbation points (PTB1/PTB2/PTB3) for each muscle to test for significant differences in reflex responses, BGA, and kinematic parameters between force field directions and across perturbation points. We used a similar ANOVA with factors of force field directions (L-FF/R-FF) and workspace settings (L1/L2/L3) in the second experiment or with factors of force field directions and task settings (five combinations of force field locations and movement speeds: MidDst-IntSpd, MidDst-FastSpd, MidDst-SlowSpd, FarDst-FastSpd, NearDist-SlowSpd) in the third experiment to test for the differences between force field directions and across settings. The significance level was set at p < 0.05. Tukey post-hoc comparisons were used to further verify significant main effects. For these analyses, the means of each subject’s values in each condition were dependent variables. Subjects were treated as a random factor.

Our main concern in the present study was whether anticipatory reflex modulation associated with force field directions changed during movement. We therefore calculated the difference in mean reflex amplitude between force field directions in each perturbation condition, i.e., the mean R-FF amplitude minus the mean L-FF one, which we defined as the reflex modulation level (RML). We tested for significant differences in the RML across experimental conditions using a one-factor repeated-measures ANOVA.

Figure 2
RESULTS

Figure 1B shows an example of the mean hand trajectories in the N-FF (thin black), R-FF (thick black), and L-FF (thick grey) trials without the perturbations for one subject in the first experiment. The bar-graph on the right of Fig. 1B shows hand curvature in each condition, which was defined as the absolute value of positional deviation in the x-direction from a straight line connecting between the start and goal positions at the end boundary of the cued force field (y = 53 cm). Compared to the null trajectory, the force fields distorted the hand trajectories in the direction of the imposed field, but the amount of these distortions was comparable between the force field conditions. Post-hoc test following repeated-measures ANOVA showed no significant difference in the hand curvature between the force field conditions (p>0.70), whereas the curvatures in the L-FF and R-FF were greater than that in the Null condition (both p<0.001). Therefore, subjects learned symmetric compensation for each imposed field direction appropriately, though it was imperfect. Figure 1C shows an example of the mean waveforms for the exerted hand force in the x-axis (right and left) direction and the corresponding EMG activities of the shoulder flexor and extensor muscles according to encountering the force fields, without any perturbations. Note that time 0 indicates the corresponding time for the first perturbation (leftmost arrow in the bottom panel) applied in other perturbation trials of the first experiment. We quantified the time when volitional EMG activities began to dissociate depending on the force field direction, calculated from the mean waveform for each force field every subject. The group means of the time for the flexor and extensor muscles were calculated as 19.0 (s.d. ± 52.3) ms and 25.1 (± 40.2) ms, respectively, on the basis of the time for encountering the force field. We applied perturbations, whose timings are indicated by the three arrows in Fig. 1C,
to evoke reflex responses before such force field-dependent volitional
compensatory activities had begun. The changes of EMG activities around
the perturbations were relatively small because of the instructed slow
movements.

Changes in reflex modulation according to expected force
field directions during movement

We applied a perturbation at any of three points during the movement
before the arm encountered the force fields (Fig. 2A). Figure 2B shows an
example of the mean waveforms of reflex responses (thick lines) of
shoulder flexor (left panels) and extensor (right panels) muscles at each
perturbation point (PTB1/PTB2/PTB3) during the movement. Thin lines
illustrate the mean waveforms without the perturbation. Each arrow
indicates each time of the perturbation points. Note that the arrows and
the thin lines (no perturbation trials) in Fig. 2B correspond to the arrows
and the EMG profiles (thick lines) in Fig. 1C, respectively, with the same
labeled time (time 0 represents the timing of PTB1). The temporal profile
of shoulder velocity caused by the perturbations is depicted above the
EMG waveform in each condition. For both muscles, reflex responses
were almost elicited over a period of 50 to 100 ms after the perturbation
onset. Their onset latency and duration were somewhat longer than the
stretch reflex responses reported by others (Lewis et al. 2006; Pruszynski
et al. 2008). This difference may be due to experimental settings, such as
actively moving the movement when the perturbation was applied or the
application of small force perturbation at the hand (Kimura et al. 2006;
Perreault et al. 2008), and/or due to involvement with slower afferent or
other sensory circuits (Bonasera and Nichols 1996). It is likely, however,
that the observed response includes the long-latency, possibly transcortical,
stretch reflex component, at least over our evaluated period (50 to 100 ms). Notably, it was observed that the induced reflex amplitudes were different between force field directions. Figure 3A shows the group means of reflex responses for each perturbation point. In general, the flexor reflex responses were greater in the R-FF than in the L-FF condition and the extensor reflex was conversely greater in the L-FF condition. A two-factor repeated-measures ANOVA with factors of force field directions (L-FF/R-FF) and perturbation points (PTB1/PTB2/PTB3) showed a significant main effect of force field directions in both muscles [flexor: F(1,8)=15.74, p<0.01; extensor: F=20.68, p<0.01]. That is, the reflex response was enhanced when the homonymous muscle could activate its voluntary activity afterward to counteract upcoming force field, indicating anticipatory reflex modulation according to the expected force field direction, as already reported in our previous study (Kimura et al. 2006).

More interestingly, however, the differences in reflex amplitudes between force field directions were not constant through perturbation points; they became clearer at the later points (Fig. 3A). The ANOVA showed a significant main effect of perturbation points [F(2,16)=14.91, p<0.001] and significant interaction between the factors [F(2,16)=8.87, p<0.01] for the extensor reflexes. Figure 3B shows the differences between force fields (R-FF minus L-FF) in the mean reflex amplitudes, represented as a reflex modulation level (RML). Note here that the code is opposite between the muscles: a positive RML value means greater reflex amplitude in the R-FF. A one-factor repeated-measures ANOVA revealed significant differences in the RML across perturbation points (PTB1/PTB2/PTB3) in both muscles (flexor F(2,16)=14.60, p<0.001, extensor F=7.13, p<0.01). That is, the RML were greater in the later perturbation points.
These modulations of reflex amplitude occurred regardless of the comparable effect of the perturbation on hand and joint motion. Table 1 (upper table) of the Appendix shows the group means of position displacement and peak velocity of the hand (x-direction), shoulder, and elbow joints immediate after each perturbation. A two-factor repeated-measures ANOVA showed no significant difference in the positions and velocities of the hand and elbow between the force fields and across the perturbation points, the details of which are shown in the Appendix (Table 1, lower table), though the shoulder long-latency reflex response could be affected by other segment motion (Kurtzer et al. 2008). The shoulder motion was slightly smaller at the later perturbation points (Table 1). It is unlikely, however, that such shoulder motion has much effect on the observed reflex changes, because the reflex amplitude (Fig. 3A), or the extent of the modulation (Fig. 3B), was rather greater at the later perturbation points.

We should also pay attention to the background states when the perturbation was applied. From the trials where no perturbation was applied, we evaluated the muscle activities and the positions and velocities of the hand and two joints just after the perturbation timing in other perturbation trials, which are depicted in Fig. 4. Though background muscle activity basically affects the amplitude of reflex responses (Matthews 1986), we observed no significant difference in either muscles across the perturbation points and the force fields (Fig. 4A), which was revealed by a two-factor repeated-measures ANOVA [main effect of perturbation points: flexor F(2,16)=1.07, p>0.36, extensor F=3.37,
p>0.06; main effect of force fields: flexor F(1,8)=4.89, p>0.05, extensor F=0.95, p>0.36]. This may be, as noted in the Materials and Methods section, because we used relatively slow movement and avoided the phases just after the movement initiation and just before encountering the force fields when the perturbation was applied so as to minimize variation of muscle activity. In association with this, as shown in Fig. 4B, there was no significant difference in kinematic states, the position and velocity of the hand (x- and y-direction), shoulder, and elbow joints, between the force fields [main effect: x-hand position F(1,8)=0.02, p>0.89; x-hand velocity F=0.58, p>0.46; y-hand position F=0.01, p>0.90; y-hand velocity F=0.04, p>0.84; shoulder position F=0.43, p>0.52; shoulder velocity F=1.08, p>0.32; elbow position F=0.01, p>0.94; elbow velocity F=0.02, p>0.89]. However, these kinematic parameters were certainly different across the perturbation positions, depending on the movement phase [y-hand position F(2,16)=335.9; y-hand velocity F=126.8; shoulder position F=212.1; shoulder velocity F=57.7; elbow position F=170.6; elbow velocity F=86.0, all p<0.001], except for the hand position and velocity in the x-direction [x-hand position F=0.62, p>0.55; x-hand velocity F=3.36, p>0.05].

Our results suggest not only that the reflex amplitude was modulated according to the force field direction (Fig. 3A), but also that the extent of reflex modulation (i.e. RML) increased as the reflex was evoked closer to the force fields (Fig. 3B). There remains, however, a nonnegligible possibility that such changes in reflex modulation according to the perturbation points are due to the differences in background kinematic states, especially arm posture and movement speed as demonstrated above. We did the second experiment to examine the effect of arm posture on the reflex modulation behavior.
Postural effect on reflex modulation during movement

We conducted the second experiment to move workspaces, including start and goal, force field and perturbation, at three locations (L1/L2/L3) along the movement direction so that arm posture when applying a perturbation corresponded to that at each perturbation point in the first experiment (PTB1/PTB2/PTB3). In this setting, the relative spatial relation for the movement, force field, and perturbation was kept constant across the workspace locations.

Figure 5A demonstrates the group means for background kinematic states, the position and velocity of the hand (x- and y-direction), shoulder, and elbow joints, in the three workspace locations (L1/L2/L3). The position of the hand (y-direction), shoulder, and elbow joints naturally changed with the difference in workspace locations (Fig. 5A, left panels) [main effect of two-factor repeated-measures ANOVA: all p<0.001], but the changes in these position parameters were almost comparable to that in the first experiment (Fig. 4B, left panels). The range of the positional changes in the present (L1~L3) and first (PTB1~PTB3) experiments were, on average, as follows: y-hand 32.0~36.0 (L1~L3) versus 32.0~37.1 (PTB1~PTB3) cm, shoulder 0.52~0.61 versus 0.49~0.61 rad, elbow 2.04~1.88 versus 2.04~1.82 rad. On the other hand, the velocity of these arm regions did not change across the workspace locations (Fig. 5A, right panels) [main effect: y-hand F(2,14)=2.46, p>0.12; shoulder F=1.62, p>0.23; elbow F=1.47 p>0.26], while that in the first experiment clearly changed across perturbation points (Fig. 4B, right panels). There is less variation
across the locations for the hand position [F=0.06, p>0.93] and velocity
[F=0.28, p>0.75] in the x-direction. We observed comparable kinematic
states between the force fields for all the parameters. There is also no
significant difference in the perturbation effects, the position and velocity
for each hand and joint, between the force fields and across the workspace
locations (Appendix, Table 2). Therefore, we could assess the effect of
different states of arm posture without changing in the movement phase.

We found that the flexor reflex responses changed depending on the
force field directions: the responses were greater in the R-FF (Fig. 5C),
while the background muscle activities did not change (Fig. 5B), as
demonstrated in the first experiment. A two-factor repeated-measures
ANOVA showed a significant main effect of force fields in the reflex
response [F(1,7)=9.54, p<0.05] and no significant main effect in the muscle
activity [F=4.46, p>0.06]. A notable point here is the comparison of the
force field-dependent reflex change across the workspace locations, rather
than that of the reflex difference between the fields itself. Figure 5D
shows that the group mean RML for each workspace location. The RMLs
were almost the same across the locations, which were revealed by a
one-factor repeated-measures ANOVA [main effect: F(2,14)=0.25, p>0.78].
This tendency is distinct from the first experiment (Fig. 3B), despite
identical variation in arm posture in both experiments, indicating less
effect of these arm postures on the reflex modulation level. It is unlikely,
therefore, that the continuous changes in reflex modulation observed in
the first experiment are due to changes in arm posture, at least in the
range of arm postures in our study.

Figure 5
Temporal and spatial relation between force fields and anticipatory reflex modulation

How do the changes in reflex modulation during the course of movement happen? One possibility is that the reflex changes might be dependent either on predicting the time interval (temporal distance: TD) to upcoming force fields or on predicting the spatial distance (SD) to the fields. To test this possibility, we controlled experimentally the TD and SD to the force fields. These factors could not be separated in the first experiment because they were coupled to each other in controlling the perturbation point only. Thus, in the third experiment, we controlled two parameters, the movement duration and the force field location, to disrupt the fixed relationship between TD and SD. Note here that controlling the movement duration corresponds to changing the movement speed.

Experimental combinations for the force field locations and the movement speeds (MidDst-IntSpd, MidDst-FastSpd, MidDst-SlowSpd, FarDst-FastSpd, NearDst-SlowSpd) are illustrated in Fig. 6A. These combinations were categorized as two conditional sets. One is a “temporal” set for the MidDst-IntSpd, MidDst-FastSpd and MidDst-SlowSpd combinations, in which the movement speeds were varied while the force fields were fixed at one location. The left panel of Fig. 6B shows a typical example of the temporal profiles of mean hand velocity (y-direction) in control (no perturbation and force field) trials for each combination of this set. Vertical solid and dashed lines indicate the estimated time of the perturbations (time 0) and the estimated time of force field appearance for each combination, respectively. In this set, the time intervals between perturbations and force fields (i.e., TDs) were different with the movement speeds. The estimated TDs (Fig. 6B, vertical dashed lines in left panel) were 318.2 ± 11.6 ms (mean ± s.e.), 243.7 ± 10.5 ms and 428.9 ± 16.0 ms for MidDst-IntSpd (abbreviated as M-I),
MidDst-FastSpd (M-F) and MidDst-SlowSpd (M-S), respectively, while the SD was a fixed value of 9 cm (MidDst). These TD values covered the TD range of the first experiment [PTB1: 405.5 ± 18.3 ms, PTB2: 305.5 ms (-100ms from PTB1), PTB3: 205.5 ms (-200ms)]. The other category is a “spatial” set for the MidDst-IntSpd, FarDst-FastSpd and NearDst-SlowSpd combinations, in which both the force field locations (middle, far, and near) and the movement speeds (intermediate, fast, and slow) were systematically varied (Fig. 6A). Consequently, the SDs were different across combinations, while the TDs were nearly constant (Fig. 6B, vertical dashed lines in right panel). The SDs for the FarDist-FastSpd (abbreviated as F-F) and NearDist-SlowSpd (N-S) conditions were set at 11 cm (+2 cm from the MidDist-IntSpd) and 7 cm (-2 cm), respectively, which were also comparable to those in the first experiment (PTB1: 10 cm, PTB2: 8.3 cm, PTB3: 6.5 cm). The TDs were almost identical across combinations (322.9 ± 9.6 ms for FarDist-FastSpd, 317.1 ± 8.9 ms for NearDist-SlowSpd, and 318.2 ± 11.6 ms for MidDst-IntSpd as mentioned above). These manipulations also allowed us to examine the effect of background movement speed on reflex amplitudes, which had remained as another possible factor affecting the changes in reflex amplitudes during movement found in the first experiment. If movement speed affects reflex amplitude, we should observe the reflex changes in both experimental sets because movement speeds were varied in both sets in a similar fashion. The perturbation was always applied at a fixed arm location (3 cm from the start).

Figure 6
Figure 7 depicts the group mean of reflex responses (A) and background muscle activities (B) for each muscle and background velocities (C) for the hand and each joint in each experimental combination for the force field locations and the movement speeds (MidDst-IntSpd: M-I, MidDst-FastSpd: M-F, MidDst-SlowSpd: M-S, FarDst-FastSpd: F-F, NearDist-SlowSpd: N-S). Presentation for the background position is omitted because of identical arm postures due to a single fixed perturbation point in all combinations. We observed some differences in the reflex responses between the force fields but little difference in the background muscle activities and velocity states. A two-factor repeated-measures ANOVA showed a significant main effect of the force fields in the reflex responses [flexor F(1,8)=7.38, p<0.05, extensor F=12.53, p<0.01] but no main effect of those in the background muscle activities [flexor F=4.61, p>0.06, extensor F=0.55, p<0.47] and the background velocity [x-hand F=0.60, p>0.46, y-hand F=0.32, p>0.58, y-hand F=0.32, p>0.58, shoulder F=1.37, p>0.27, elbow F=0.38, p>0.55]. We also found, as denoted in Table 3 of the Appendix, no significant difference between the force fields in the kinematic effects immediately after the perturbation.

Figure 7

To examine change in reflex modulation to the temporal and spatial distances to upcoming force fields, we further assessed the RML in each set of combinations. Figure 8A shows the group mean RML value for each combination (MidDst-IntSpd, MidDst-FastSpd, MidDst-SlowSpd) of the temporal set plotted against measured TD (left-side panel) or SD.
(right-side panel) in each muscle. Note again that the code is opposite
between muscles. A one-factor repeated-measures ANOVA, as in the
first and second experiments, showed significant differences in the RML
across combinations in the temporal set in both muscles [main effect:
flexor F(2,16)=18.37, p<0.001; extensor F=6.12, p<0.05]. The figure shows
linear relations against TD variation (left-side panels in 8A). On the other
hand, Fig. 8B shows the RML values for the spatial set (MidDst-IntSpd,
FarDst-FastSpd, NearDst-SlowSpd) plotted against TD (left-side panel) or
SD (right-side panel). We observed no difference in the RML across
combinations in either muscle [flexor F=2.78, p>0.09, extensor F=0.82,
p>0.45], which means there was no clear relation against SD variation
(right-side panels in 8B). These results indicate that preparatory
modulation of reflex amplitude to an upcoming force field develops as a
function of the TD to the force fields rather than as a function of the SD.

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**Figure 8**

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We should here take notice of the effect of movement speed on the
changes in reflex amplitude across the experimental combinations,
because changing movement speed can produce different background
muscle activity. Indeed, we found greater muscle activity in faster
movement conditions. Figure 9 shows the group mean BGA (white bars),
quantified as the mean BGA for both force field conditions, of each
combination of each experimental set (MidDst-IntSpd abbreviated as M-I,
MidDst-FastSpd as M-F, MidDst-SlowSpd as M-S for the temporal set; M-I,
FarDst-FastSpd as F-F, NearDst-SlowSpd as N-S for the spatial set) as well
as the RML (grey bars) depicted in Fig. 8. The BGAs tended to be greater
in the FastSpd compared to other conditions, but the RMLs did not
necessarily. A one-factor repeated-measures ANOVA showed a significant main effect of combinations in the extensor BGA for the spatial set \([F(2,16)=6.20, p<0.05]\). However, no clear difference in the RML was seen across those movement conditions for the spatial set, as mentioned above. Instead, we observed evident reflex modulations in the flexor for the temporal set regardless of a few differences in the BGA \([\text{flexor } F=0.46, p>0.64 \text{ for the temporal set}]\). We also confirmed that there was no significant difference in the kinematic effects of the perturbation across the combinations, which was tested by the above-used two-factor ANOVA (Appendix, Table 3).

Thus the spatiotemporal relation to dynamical events, rather than both muscle activity level and kinematic motion by the perturbation, had a more critical effect on reflex modulation, at least under these experimental conditions. Accordingly, we conclude that somatosensory reflex amplitude for predictable dynamical interaction during movement is set dominantly on the basis of temporal prediction of the interaction.

\[\text{-------------------}\]

**Figure 9**

\[\text{-------------------}\]

**DISCUSSION**

The present study assessed somatosensory reflex responses during arm movements with imposed force fields. Reflex amplitudes in the shoulder flexor and extensor muscles were anticipatorily modulated depending on expected force field direction (Fig. 3A), which is agreement with our recent study (Kimura et al. 2006). Interestingly, the reflex amplitude
modulation was strengthened as the arm approached the force fields (Fig. 3B). An additional result showed that such change in reflex modulation was strongly dependent on the time interval to the force fields (Fig. 8), rather than on the spatial distance. These findings indicate that (i) reflex amplitude itself is not necessarily completed before movement execution, but is instead dynamically modulated even after its initiation, and (ii) the reflex amplitude setting is based on the estimate of time to the expected dynamical event rather than on the estimate of the spatial relation. This temporal setting of reflex amplitude may play a critical role in continuous regulation of our dynamical properties such as stiffness.

Anticipatory modulation of reflex amplitude during movement

Anticipatory modulation of reflex amplitude has been studied for decades in monkey (Evarts and Tanji 1974, 1976) and human (Colebatch et al. 1979; Bonnet and Requin 1982; Bonnet 1983; Marsden et al. 1983; Sullivan and Hayes 1987; Yamamoto and Ohtsuki 1989; Bonnet et al. 1991; Schieppati and Nardone 1995; Kimura et al. 2006; Nakazawa et al. 2008). However, those studies have mainly aimed at demonstrating the existence of anticipatory modulation. A few have examined the time course of the modulation, but they limited only the foreperiod of task movement (Bonnet and Requin 1982; Bonnet 1983; Sullivan and Hayes 1987; Bonnet et al. 1991). The present study aimed to assess change in reflex modulation during movement so as to clarify whether reflex amplitude is determined to a dynamical event during movement execution. In the first experiment, where we used multiple perturbation points before the reaching hand encountered the force fields, the reflex amplitude changed with impending force field direction (Fig. 3A) and was enhanced as reflex
induction became close to the force fields (Fig. 3B). It is unlikely that this is caused by the effect of background muscle activity variation, since we found no significant difference in the muscle activity between the force fields and across the perturbation points, as mentioned in the RESULTS section. It is also unlikely to merely arise from different arm postures (or hand position) due to different perturbation points during reaching, because no change in the reflex modulation level was observed in the second experiment with changes in arm postures (Fig. 5D) and, further, the modulation occurred in the third experiment with a fixed perturbation position (Fig. 8). We therefore believe that the observed reflex amplitude modification is based not on these peripheral effects but on other higher effects, as demonstrated in the third experiment and discussed later.

Our finding raises two new assumptions about anticipatory reflex control. First, reflex amplitude build-up is not completed before movement initiation, but instead occurs even during movement. This interpretation would not deny but rather extend the traditional concept of the preparatory motor set (Bonnard et al. 2004), which often accounts for preparatory change in reflex amplitude before motor execution (Bonnet 1983; Bonnet and Requin 1983; Sullivan and Hayes 1987). Such preparatory reflex change has often been observed in a reaction task paradigm, in which a subject is asked to react to a mechanical disturbance inducing reflex response, creating a situation where the reaction onset is adjacent to the disturbance. Given our finding, we speculate that if a disturbance is close to the movement onset, reflex amplitude appears to change prior to the movement start, whereas if a disturbance exists during movement enough apart from its start, the change occurs after the movement start. We propose that the previously reported preparatory reflex modulation reflects part of the prospective feature for the reflex amplitude coding observed in this study. Secondly, in association with
the first assumption, reflex amplitude setting happens in a dynamical event (or disturbance) -locked manner. From the functional viewpoint, such behavior of reflex amplitude seems quite reasonable, since it means that the reflex amplitude changes toward a predictable event during movement but that it is not constant throughout the movement. Some studies have indicated that if a subject knows when a muscle stretch will occur, reflex amplitude to a do-not-resist instruction is reduced compared with an unknown stretch (Rothwell et al. 1986; Yamamoto and Ohtsuki 1989). Reflex amplitude would probably be kept relatively low when no disturbance is predicted during movement so that reflex-derived correction does not produce large errors and instability, whereas it is modified (increased) adequately toward predictable disturbance. We suggest that the coding of reflex amplitude is preset in a dynamic fashion according to the emergence of a dynamical event requiring the modification.

**Temporal setting of anticipatory reflex amplitude**

The first experiment demonstrated “when” predictive reflex amplitude setting occurs, but it remains debatable as to “how” the predictive system is driven. Our main motivation in this study was to elucidate what information triggers the anticipatory reflex coding process during movement. For this purpose, we focused on temporal and spatial information that can predict an impending dynamical interaction. Heretofore, many studies have argued a role of temporal (or time-dependent) and spatial (or state-dependent) regulation in motor control and learning and have tried to differentiate the contributions of temporal and spatial information to various motor behaviors (Alberts et al. 2002; Karniel et al. 2003; Hore and Watts 2005; Medina et al. 2005;
Diedrichsen et al. 2007). For example, Hore and Watts (2005) have demonstrated that finger opening during overarm throwing, which strongly correlates with the onset of ball release, happens at a hand angular position irrespective of different throw speeds. Medina et al. (2005) showed that, after monkeys had learned smooth eye pursuit to track a target that moved horizontally for a fixed time interval and then jumped vertically for a fixed position, infrequent purely horizontal target motion (probe motion) evoked a vertical eye movement. An additional experiment in which they varied initial fixation positions showed that the peaks of vertical eye velocity in probe trials were better fitted as a function of the time of target change, compared to the position. These studies have nicely suggested a contribution of spatiotemporal information to action control, though the interpretations leave some complications, whereas no study has attempted such an investigation for reflex amplitude setup, at least to our knowledge.

We therefore conducted the third experiment, in which we controlled both the temporal (TD) and spatial (SD) distances to the force fields by changing the movement speeds and the force field locations. Consequently, we found a clear increase in reflex amplitude as the TD was shortened but not as the SD was (Fig. 8), indicating that predicting the time interval to the force field drives the reflex amplitude setting process. This interpretation would be supported by the following three arguments. First, it is unlikely that the result is due to the peripheral effect of background muscle activities, since we did not necessarily find difference in reflex amplitude between fast and slow movements (i.e., FarDst-FastSpd v.s. NearDst-SlowSpd) even when there was a significant difference in BGA between those (Fig. 9), as described in the RESULTS. The peripheral effects of movement speed and corresponding afferent state, such as muscle spindle discharge regulated by the fusimotor system...
(Prochazka 1989), are also unlikely to account for the observed reflex modulation. This is because (i) we observed reflex modulation in the temporal set but not in the spatial set regardless of the identical changes in movement speeds in both sets, and (ii) several studies have shown that as the speed of voluntary contraction increases, muscle spindle discharge rather decreases (Burke et al. 1978; Baumann and Hulliger 1991).

Secondly, the unchanged reflex amplitudes against the SD (left panels in Fig. 8B) is, at least, not due to an insufficient experimental setting for the SD range, though this could produce a deficient change in reflex amplitude. This is because the SD range used in this experiment (7-11 cm) was comparable to that in the first experiment (6.5-10 cm), which showed a clear reflex modification. Third, the observed reflex tuning can not be explained by the time from movement initiation nor by the movement phase, since (i) we did not find tuning between the spatial conditions, MidDst-IntSpd, FarDst-FarSpd and NearDst-SlowSpd (Figs. 8B and 9, right panels), in which the times from movement onset were different, and (ii) we found tuning across different movement speeds with a fixed hand position, i.e., a fixed movement phase (MidDst-IntSpd, MidDst-FastSpd and MidDst-SlowSpd, Figs. 8A and 9, left panels). From the combination of evidence, our finding indicates that reflex amplitude is set on the basis of an estimate of the time interval to upcoming dynamical interaction during movement rather than an estimate of the spatial distance.

The changes in reflex modulation against the temporal distance (Fig. 8A, left panels) were very similar to the changes in modulation in the first experiment (Fig. 3B), indicating that the reflex modulation of the first experiment depends on temporal rather than spatial variations. In that experiment, we found clear reflex differences between the force field directions (Fig. 3A) with identical background activities (Fig. 4A) after
PTB2, which corresponded to the temporal distance of approximately 300 ms. This value is comparable to previous observations of significant preparatory changes of arm reflex at 400 ms (Bonnet and Requin 1982; Bonnet 1983) and leg reflex at 200 ms (Schieppati and Nardone 1995) before reaction movements. Though these and our studies targeted different phases of movement (before versus after movement start), the time course of reflex amplitude build-up is similar. However, several reflex studies have indicated a spatial modification of reflex amplitude, such as phase dependency of the amplitude during walking (Sinkjaer et al. 1996) and rhythmic hand movement (Xia et al. 2005), as demonstrated in voluntary movement (grasping Alberts et al. 2002; overarm throwing Hore and Watts 2005), which contradicts our finding indicating the temporal coding of reflex amplitude rather than its spatial coding. We speculate, however, that such dissociation may be attributable to the task demands and situation. That is, the tasks in our and previous studies indicating temporal tuning of reflex amplitude include some dynamical compensations to a disturbance from the external environment during aimed movement, which seems distinct from tasks, such as walking and throwing, performed under relatively static and fixed environments. In such a task situation, subjects would probably need to adjust reflex amplitudes according to added dynamic interaction during movement. As a possible explanation, we presume that reflex amplitude is set in the time domain to unstable dynamical interactions during movement. It may be that the reflex amplitude setting shifts and fixates in the spatial domain as adaptation and/or learning to a given environment progresses.

Possible neural mechanisms

Our previous study using transcranial magnetic stimulation (TMS)
showed that appropriately timed TMS over the primary motor cortex (M1) disrupts force field-dependent anticipatory reflex modulation in the shoulder muscles, which was evoked in an experimental setting similar to that on this study, but that electrical stimulation of a peripheral nerve does not (Kimura et al. 2006). This would indicate that the evaluated upper limb somatosensory reflexes include a transcortical component and that such transcortical reflex amplitude is represented within the M1, rather than by other peripheral mechanisms such as the fusimotor system. This is in line with several monkey studies showing that the M1 responses to a mechanical stretch of upper limb muscles are anticipatorily modified by task instruction (Evarts and Tanji 1974, 1976). It is therefore suggested that transcortical reflex represented in the M1 is coded in a feedforward manner on the basis of temporal predictions of forthcoming dynamical interactions during actions.

We presume that such reflex amplitude coding in the M1 is commanded from upstream or higher, perhaps multiple, reflex control centers in the brain. One of the possible brain areas is the supplementary motor area (SMA), which is thought to play a role in modifying responses to sensory inputs (Tanji et al. 1980; Hummelsheim et al. 1986, 1988; Dick et al. 1987). Tanji et al. (1980) demonstrated instruction-dependent modulation of neural discharges to a mechanical stretch in the SMA, as observed in the M1 (Evarts and Tanji 1974, 1976). Hummelsheim et al. (1986) showed that intracortical stimulation of the SMA had an inhibitory effect on responses of area 4 neurones to kinematic stimuli. Another possible area is the cerebellum, which has been shown to be involved not only in voluntary action but also in reflex behavior (Strick 1983; Hore and Vilis 1984). For instance, it has been found that the dentate neuron responses of the cerebellum to limb perturbations change by a prior motor set (Strick 1983), while motor set-related reflex responses are abolished by
cerebellar nuclear cooling (Hore and Vilis 1984). Cerebellar dysfunction is also known to produce various motor deficits in timing and coordination aspects (Mauk et al. 2000; Ivry et al. 2002). It is conceivable that these areas act as a kind of “modulator” and “time controller” in the setting process of reflex output represented in the M1.

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Figure captions

Figure 1

Experimental setup and the movement-related profiles without perturbation

A: Using a manipulandum system, subjects performed start-to-goal right arm movements as one of three force fields (null, rightward and leftward fields) was imposed during part of movement. The force field condition was indicated before movement start by a visual cue displayed on a screen placed just above the workspace. B: Typical example of the mean hand trajectories in the null (N-FF, thin black line), rightward (R-FF, thick black line) and leftward (L-FF, thick grey line) force field trials without perturbation application. The gray area shows force field location. The bar graph indicates the group mean and standard error of hand curvature in each condition (L: L-FF, R: R-FF, N: N-FF). The asterisks express a significant difference across conditions (** p<0.001), which is based on the Tukey post-hoc test following a repeated-measures ANOVA. C: Typical example of the mean hand force profiles in the x-direction and shoulder flexor and extensor EMG waveforms without perturbation. Grey areas denote force field period. Downward arrows indicate the perturbation timings in other perturbation trials of the first experiment. The waveforms are aligned by the first perturbation timing (0 ms). Note that muscle activities were almost identical at these timings, before the arm encountered the force fields.

Figure 2

Perturbation scheme of the first experiment and examples of reflex responses

A: Schematic diagram for three perturbations used in the first experiment. One of three perturbations (PTB1, PTB2, PTB3) was randomly applied. B: Example of the mean waveforms of reflex responses in the flexor and extensor muscles for the R-FF (thick black line) and L-FF (thick grey line) conditions at the three perturbation points for a single subject. Thin lines illustrate the EMG waveforms in no perturbation trials. The lines above the EMG waveforms show the mean shoulder angular velocity profiles in the perturbation trials. The waveforms are aligned by the application of PTB1 (0 ms). Arrows denote the time of each perturbation onset. Grey areas denote the period (50-100 ms after each perturbation onset) in which reflex responses were calculated. Note that there were differences in reflex responses between force fields, especially in the perturbation conditions closer to the fields.
**Figure 3**

**Comparison of reflex responses between force field directions and of RMLs across different perturbation points**

A: Each bar represents the group mean and standard error of reflex responses for each muscle in each perturbation point (PTB1/PTB2/PTB3). The asterisks express a significant difference between force field conditions (** $p<0.01$, *** $p<0.001$), which is based on the Tukey post-hoc test following two-factor repeated-measures ANOVA with factors of force fields and perturbation points for each muscle. Note that the reflex amplitudes in the flexor and extensor muscles were generally greater in the R-FF and L-FF conditions, respectively. B: Each bar denotes the group mean and standard error of RML, which was calculated as the difference in the subject means of reflex responses between the force fields (R-FF minus L-FF), for each perturbation point. Asterisks express a significant difference between perturbation points (* $p<0.05$, ** $p<0.01$, *** $p<0.001$), which is based on the post-hoc test following one-factor repeated-measures ANOVA for each muscle. Note that RMLs became larger as the perturbation was applied closer to the fields.

**Figure 4**

**Comparison of background state parameters across different perturbation conditions**

Each bar represents the group mean and standard error of background muscle activities for each muscle (A) and background kinematic states for position and velocity of the hand and each joint (B) in each perturbation point (PTB1/PTB2/PTB3). Note that there were no clear differences in any background parameters between force fields.

**Figure 5**

**Comparison of background states, reflex responses and RMLs for the second experiment**

In the second experiment, we moved workspaces, including start and goal, force field and perturbation, at three locations (L1/L2/L3) in the movement direction. Each bar represents the group mean and standard error of background kinematic states for position and velocity of the hand and each joint (A), the background muscle activities (B), reflex responses (C), and RMLs (D) for the shoulder flexor muscle in each workspace location (L1/L2/L3). The asterisks express a significant difference between force field conditions (** $p<0.01$), which is based on the post-hoc test following two-factor
repeated-measures ANOVA. Note that the reflex amplitudes in the flexor muscles were generally greater in the R-FF (C), but the RMLs were almost identical across workspace locations (D).

Figure 6

Experimental scheme for the third experiment and hand velocity profiles in control trials

A: In the third experiment, we varied force field location (MidDst, FarDst, NearDist) and movement duration (i.e., movement speed, IntSpd, FastSpd, SlowSpd) to control the temporal (TD) and spatial (SD) distances to the force fields. One of five combinations (MidDst-IntSpd, MidDst-FastSpd, MidDst-SlowSpd, FarDst-FastSpd, NearDist-SlowSpd) for the locations and speeds was done in a separate block. B: Typical example of the temporal profiles of mean hand velocity (y-direction) with neither perturbation nor force field in each combination of two separate sets: Temporal (MidDst-IntSpd abbreviated as M-I, MidDst-FastSpd as M-F, and MidDst-SlowSpd as M-S) and Spatial (M-I, FarDst-FastSpd as F-F, and NearDist-SlowSpd as N-S) sets. Vertical solid lines (time 0) show the estimated perturbation time. Vertical dashed lines denote the estimated time of force field occurrence corresponding to each profile (same color and thickness).

Figure 7

Comparison of reflex responses and background states for the third experiment

Each bar represents the group mean and standard error of reflex responses (A) and background muscle activities (B) for each muscle and background kinematic states for each hand and joint velocity (C) in each of five combinations (MidDst-IntSpd abbreviated as M-I, MidDst-FastSpd as M-F, MidDst-SlowSpd as M-S, FarDst-FastSpd as F-F, NearDist-SlowSpd as N-S) for the force field locations and the movement speeds. The asterisks express a significant difference between force field conditions (* p<0.05, ** p<0.01, *** p<0.001), which is based on the post-hoc test following two-factor repeated-measures ANOVA with factors of force fields and combinations.

Figure 8

Comparison of RMLs for the third experiment
Each plot denotes the group mean and standard error of RML for each of five combinations (MidDst-IntSpd, MidDst-FastSpd, MidDst-SlowSpd, FarDst-FastSpd, NearDist-SlowSpd) for the force field locations and the movement speeds. Right and left panels for each muscle (upper, flexor; lower, extensor) in each combinational set (A: Temporal. B: Spatial) show same data plotted against either the temporal distance (TD) from the force fields (left panel) or the spatial distance (SD, right panel). The asterisks express a significant difference between combinations (** p<0.01, *** p<0.001), which is based on the post-hoc test following the one-factor repeated-measures ANOVA for each muscle, as in Figs. 3B and 5D. Note that, in both muscles, RMLs changed with variation of TD (A, left panels), while little with variation of SD (B, right panels).

**Figure 9**

Specific comparisons of mean background activities and RMLs across the different movement speeds conditions

Each bar represents the group mean and standard error of mean BGA (white bars), averaged for BGAs of both force fields, and RML (grey bars) in each combination for the force field locations and the movement speeds for each muscle. Left panels show comparisons across MidDst-IntSpd (abbreviated as M-I), MidDst-FastSpd (M-F) and MidDst-SlowSpd (M-S) for the temporal set. Right panels show comparisons across M-I, FarDst-FastSpd (F-F) and NearDist-SlowSpd (N-S) for the spatial set. Note that there were some dissociations of significant differences between mean BGAs and RMLs for the spatial and temporal conditions.
Figure 1
Figure 3
Figure 4
Figure 5
Figure 6
Figure 7
Figure 8
Figure 9