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<p>During this first year of USAF grant AFOSR 91-0333, It was determined that: 1) The responsiveness of primary somatosensory (SI) cortical neurons that respond to vibratory go-cues for wrist movement with the greatest fidelity have their activity modulated prior to movement onset. This observation fits with the hypothesis that prior to active movement, sensory inputs that are no longer behaviorally relevant are gated so as not to interfere with monitoring movement parameters by the primate CNS. 2) Previous findings that human subjects acquire a predictable positional target by wrist movements more quickly if vibratory go-cues are presented in addition to visual targets was extending to include unpredictable target locations and movement directions. Equations describing the acquisition of and final performance level during wrist movement tasks were developed. These allow for the prediction of final performance and the time necessary to achieve it from a few days of recorded behavioral performance. The neurophysiological experiments suggest that SI neuronal responsiveness is profoundly influenced by behavioral conditions. The human psychophysical experiments suggest that the adding vibratory go-cues to visual targets may have performance benefits even in more complex control systems.</p>							
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## Research Objectives

Two research goals were accomplished during this first year of USAF grant AFOSR 91-0333.

1) It was determined that sensory responsiveness of primary somatosensory (SI) cortical neurons that respond to vibratory go-cues for wrist movement with the greatest fidelity have their activity modulated just prior to movement onset. This observation fits with the hypothesis that prior to active movement, sensory inputs that are no longer behaviorally relevant are gated so as not to interfere with monitoring movement parameters by the primate CNS. 2) A previous finding that human subjects can acquire a predictable positional target by wrist movements more quickly if vibratory go-cues are presented in addition to the illumination of a visual signal lamp has been extending to include targets and movement directions which are unpredictable. In addition, equations describing the acquisition of and final performance level during wrist movement tasks have been developed. These allow for the prediction of final performance and the time necessary to achieve it from a few days of recorded behavioral performance. The neurophysiological experiments suggest that the responsiveness of SI neurons is profoundly influenced by behavioral conditions. The human psychophysical experiments suggest that the addition of vibratory go-cues to visual indicators may have performance benefits even in more complex control systems.

## Status of Current Research - Statement of Work

Each study used a behavioral paradigm that had many features in common. The basic paradigm will be described and then the variations used in the individual studies.

## Experimental Design and Methods - Animals.

### *Behavioral Paradigm*

The experiments were conducted with four adult male Rhesus monkeys (*Macaca mulatta*, 8-11 kg) that were trained to make wrist flexion and extension movements in response to visual and vibratory cues. During the experiments, each monkey was seated in a plexiglas primate chair with his right hand resting in a prone position upon a plate attached at its proximal end to the axle of a brushless DC torque motor. This device permitted only wrist flexion or extension movements. The animal initiated each trial by centering his wrist and maintaining that position until given a cue to make a wrist movement. A load of 0.07 Newton-meters, which assisted extension movements, was applied continuously to the manipulandum, so that the monkey had to actively center its wrist and hold that position in order to initiate a trial.

Each monkey viewed a visual display, placed 35mm in front of him at eye level, that indicated his current wrist position. The display consisted of a centrally placed, red light-emitting diode (LED) that was bounded above and below by a vertical row of smaller, yellow LEDs. The central LED was illuminated when the monkey moved his wrist to mid-position, whereas illumination of each successive LED from the center corresponded to 1° differences in angular wrist deflection from the center. After the animal maintained its wrist in centered position for an interval of 0.5, 1.0, 1.5, or 2.0s (pseudo-randomly selected), either a visual or a vibratory cue was presented. During vibratory cued trials, the signal to move ("go-cue") was a palmar vibratory stimulus achieved by driving the torque motor with a low-amplitude sine wave at either 27, 57, or 127Hz ( $<0.057^\circ$ , or  $<100\mu\text{m}$  peak-to-peak measured 10cm distal to the coupling of the handle to the torque motor). This signal, which was applied to the same hand that the monkey used to perform the wrist movements, remained on until the animal moved the

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manipulandum at least 5° from the centered position. The presence of a load assisting extension movements assured that the manipulandum remained in contact with the animal's hand even during wrist movements made away from the side of stimulation. Two of the monkeys also performed visually cued trials during which the signal to move was a shift in position of the illuminated lamp away from center in a direction opposite that of the desired movement and by an amount that normally would correspond to 5° of wrist movement. Each animal learned to respond to this go-cue by making a movement of at least 5° back toward the center of the display. Like the vibratory cues, the visual cues remained on until the monkey moved his wrist at least 5° in the appropriate direction. Fruit juice reward was given after the successful completion of each trial.

Presentation of the visual and vibratory cues was alternated pseudo-randomly within a block of 160 trials each. Normally, three blocks of trials were performed, one for each of the three vibratory frequencies. Within each block of trials, the required movement direction alternated between flexion and extension in groups of 10 trials each. The appropriate movement direction was signalled by a small red LED that was located at the periphery of the visual display. This LED was illuminated continuously during each group of extension trials and remained unlit during each group of flexion trials. Likewise, the modality of the go-cue (visual vs. vibratory) was indicated by a green LED that was illuminated at the start of each visually cued trial and remained unlit for vibratory cued trials.

#### *Surgical procedures*

To permit chronic single-unit recording, a stainless steel recording chamber was implanted under aseptic conditions over the hemisphere contralateral to the hand used to perform the behavioral task. Each monkey was sedated with Ketamine (10 mg/kg) and then maintained on halothane and nitrous oxide anesthesia. A craniotomy was performed at approximately A+14.5mm. The recording chamber then was fixed to the skull at a lateral angle of 8° from vertical. The chamber and two small aluminum bars that later were used to permit head immobilization were secured to the skull using surgical cement (Howmedica Surgical Simplex P). After the incision was closed, local antibiotics were applied (Furazone and bacitracin-neomycin-polymyxin ointment). The chamber was filled with sterile saline and a bacteriostatic antibiotic (chloramphenicol, 0.8 mg), and was sealed with a removable translucent acrylic plate. The animal was given butorphanol (0.01 mg/kg/12hr) to provide analgesia for two days after the surgery. For the duration of the study, the recording chamber was flushed daily with sterile saline, and chloramphenicol (0.8 mg) was added to the chamber solution after daily recordings were completed. Animal care was provided in accordance with the *NIH Guide for Care and Use of Laboratory Animals*.

#### *Electrophysiological Recording and Data Collection*

Training was resumed one week after the surgery to permit the animals to adapt to performing the behavioral task with their heads restrained. When the animals again performed the task reliably, daily recording sessions were begun. Glass-coated, platinum-iridium microelectrodes (0.7-2.0MΩ at 1Khz) were used to isolate single units from the somatosensory cortex using conventional extracellular recording techniques. The electrodes were lowered transdurally using a hydraulic microdrive with adaptor (Narishige MO-95B). The neuronal activity was amplified and filtered (500Hz-10Khz), and single-unit discharges were detected with a window discriminator. For recording of EMG activity, multi-unit EMG responses were obtained via needle electrodes, and this activity was also amplified and counted using a window discriminator. An on-line program operating on a PDP-11/23+ microcomputer was used to collect and store the neuronal activity in real-time, the time of onset of task related cues, and other significant behavioral events, with a temporal resolution of 0.1ms. Transducer

output indicating current wrist position was digitally sampled every 10ms. The computer also controlled the behavioral task, including the presentation of stimuli, the pseudo-randomization of the hold period duration and trigger stimulus type, and sequencing of the movement direction requests.

This same system was used to control the behavioral paradigms for the human psychophysical experiments (see below) and the record the time from stimulus presentation to movement onset (RT; reaction time) and the time from movement onset until the handle position coincided with the target (MT; movement time).

### **Experimental Design and Methods - Human Subjects.**

Adult volunteers performed the paradigms described below. They were asked to perform the task with their preferred hand. All had normal or corrected-to-normal vision and normal hearing. These subjects received no compensation for participating in this study.

Subjects were seated in a specially designed chair in a quiet, moderately lit (5 foot-candles) room and viewed a display panel placed 50cm directly in front of them at eye level. This display contained 31 light-emitting diodes (LEDs) located behind a smoky-grey acrylic plate. The details of this display are described above. The subject's hand rested on a flat aluminum handle coupled at one end to the axle of a brushless DC torque motor while the forearm was supported by an arm rest.

#### *Behavioral Paradigms - General*

In most respects, the three paradigms used were identical to that described above for the animals. In the first paradigm, the go cue for movement consisted of the presentation of a visual target alone (VC; visual cue) or the visual target *and* a vibratory stimulus (CC; combined cue) delivered to the palm of the hand that is to be moved. Vibratory components consisted of vibrating the handle by driving the torque motor with a low-amplitude sine wave ( $< 100 \mu\text{m}$  peak-to-peak measured 10cm from the coupling of the handle to the motor) at either 27, 57, or 127Hz. Visual targets consisted of illuminating a lamp away from the center of the display (e.g., a target requiring a wrist movement  $5^\circ$  from center was present at  $\pm 1.7^\circ$  of visual angle from display center). Either cue (CC or VC) remained on until the subject moved to align the wrist position cursor with the target on the visual display, holding the handle in the target position for 0.5-1.0 sec. In each paradigm, the subjects heard a click if a trial's movement was appropriate. This click informed the subject that the trial was successful and also served as a signal to recenter the handle to begin the next trial. On the first training day each subject was be instructed to make either targeted wrist flexion and extension movements as quickly as possible without sacrificing movement accuracy. The speed and amplitudes of these targeted movements were not restricted other than by stops in the apparatus at  $\pm 30^\circ$  of angular deflection from center. However, a trial was be considered a failure if the subject "overshot" the target by  $< 1.0^\circ$  in an attempt to acquire that target, if the subject did not acquired the target within 1sec of movement onset or if the new position was not held for 0.5-1.0 sec.

#### *Fixed Target Paradigm*

Twelve subjects ran the Fixed Target Paradigm in which  $5^\circ$  flexion and extension movements were requested in alternating blocks of 10 trials each. Thus, for each block of trials, the required movement direction and the movement amplitude were known. The two types of cues were randomly presented within blocks for a given vibratory stimulus frequency. Three groups (one for each vibratory frequency) of at least 240 trials were collected daily for 14 days for each subject. The total duration of these manipulations was about 20-30 min.

### *Variable Target Paradigm*

Six subjects ran the Variable Target Paradigm in which 4°, 8° or 12° flexion and extension movements were requested in alternating blocks of 10 trials each. Thus, for each block of trials, the required movement direction was known, but the amplitude of the movement, as indicated by the location of the visual targets, was varied pseudo-randomly. As before, the two types of cues were randomly presented within blocks for a given vibratory stimulus frequency. Three groups (one for each vibratory frequency) of at least 240 trials were collected daily for 14 days for each subject. The total duration of these manipulations was about 30-40 min.

### *Random Target Paradigm*

Four subjects ran the Random Target Paradigm in which 4°, 8° or 12° flexion and extension movements were requested pseudo-randomly. Thus, prior to the start of each trial, neither the required movement direction nor the amplitude of the movement nor the type of go-cue was known. At least 480 trials were collected daily for 14 days for each subject. The total duration of these manipulations was about 45 min.

Four subjects participated in each of the three experiments. This afforded the opportunity of determining the effects of increasing task complexity or decreased predictability in the performance of single subjects rather in addition to the subject populations as a whole.

## **Results - Animals**

### *Data Analysis*

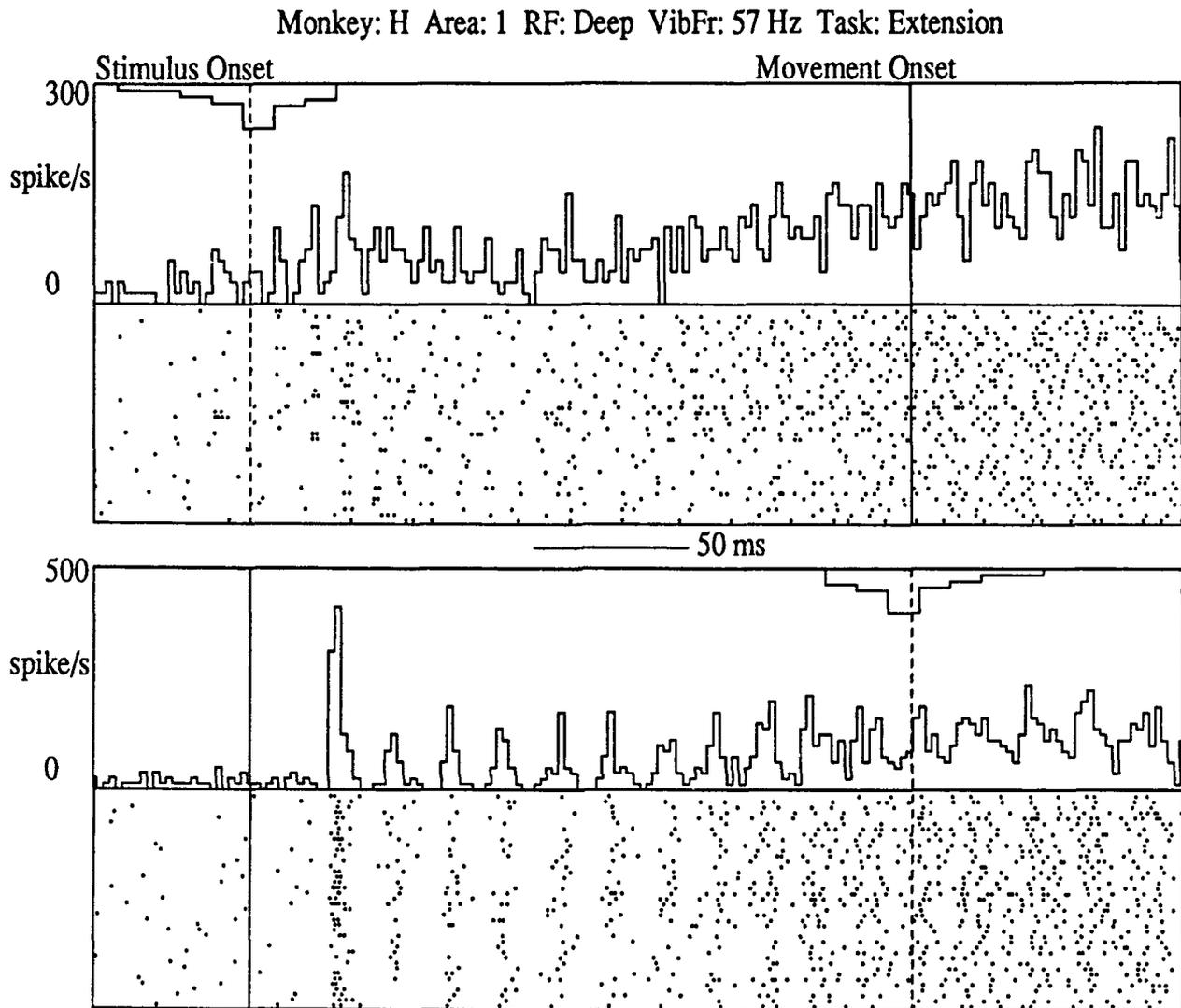
The units that were entrained to the peripheral stimuli were selected for analysis by visual inspection of the discharge raster displays and histograms obtained after primary analysis of the data. An example of such raster displays and histograms for a unit, which was entrained to the stimuli at 57 Hz, is presented in Figure 1. The entrainment of vibratory responses appeared in the form of a periodical pattern in the raster display and the histogram when centered on vibration onset (lower block). In the displays aligned on movement onset (upper panel) the periodical pattern was masked. This unit increased its firing rate at about 80 ms prior to movement onset. It can be seen that during this activation certain changes in the entrainment pattern occurred. Bursts in the stimulus-centered histogram (lower panel) became broader, indicating lowering of response synchronicity.

To describe pre-movement changes in the degree of entrainment quantitatively, special analyses were developed by Michael A. Lebedev, a graduate student in the laboratory. For each spike, the phase relative to the vibratory cycle was calculated (Figure 2, upper plot). Vector representation of phase (i.e., the representation as a complex value) was used (Figure 2, lower left plot). In this representation, phase was calculated as the angle between x-axis and a vector rotating with the frequency of the vibration:

$$\phi(t) = \text{angle}(\exp(i 2\pi f t)), \quad (1)$$

where  $\phi$  is the response phase,  $t$  is the time from vibration onset,  $i$  is an imaginary unit, and  $f$  is the frequency of vibratory stimulus presented to the monkey's hand as a go-cue for wrist movement. All of the following firing rate, phase and synchronicity calculations were applied to the data aligned on stimulus onset as well as on movement onset. In the case where we were interested in pre-movement changes in activity, time  $t'$ , correlated with movement onset was used:

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*Figure 1.* Raster displays and histograms as used for the selection of units entrained to vibratory stimuli. Area 1 unit with deep RF. Vibratory frequency 57 Hz. Extension movements. In raster displays, times of spike occurrence for 40 trials are marked by dots. A separate horizontal line corresponds to each trial. 2 ms binned histograms present mean activity for all trials. Upper panel: trials aligned on movement onset. Lower panel: trials aligned on stimulus onset. Event serving for alignment is marked by a solid vertical line. Other event is marked by a dashed line, and its time histogram is presented. Entrainment to vibratory stimuli is revealed as periodic pattern in raster display and histogram aligned on stimulus onset. In graphs centered on movement onset this periodic pattern is masked.

$$t' = t - t_{mvmt} \quad (2)$$

where  $t_{mvmt}$  is the time of movement onset in a given trial. Phase  $\phi(t)$  was also translated into the new coordinate system:

$$\phi'(t') = \phi(t) \quad (3)$$

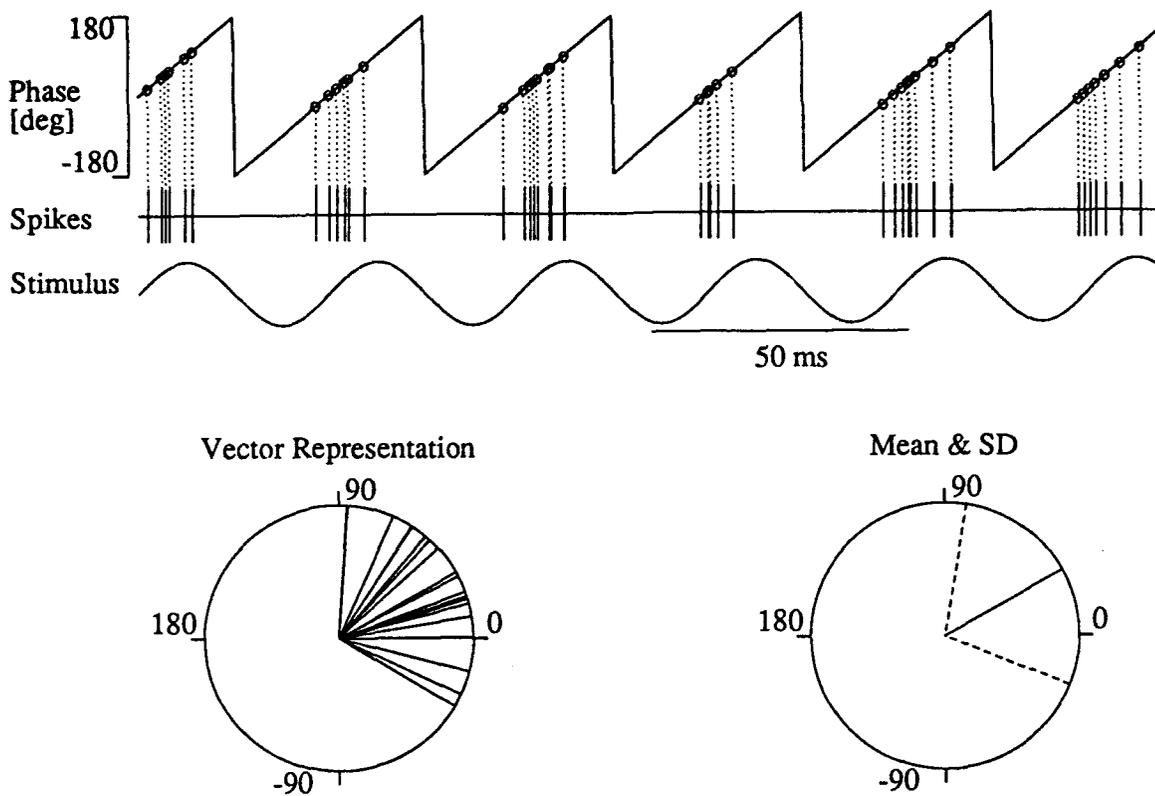


Figure 2. Illustration of calculation of response phase. Upper plot: schematic diagram showing stimulus mechanogram, neuronal spikes and their phase. Lower left: spike phases in vector representation. Lower right: mean and standard deviation of phase calculated using vector representation.

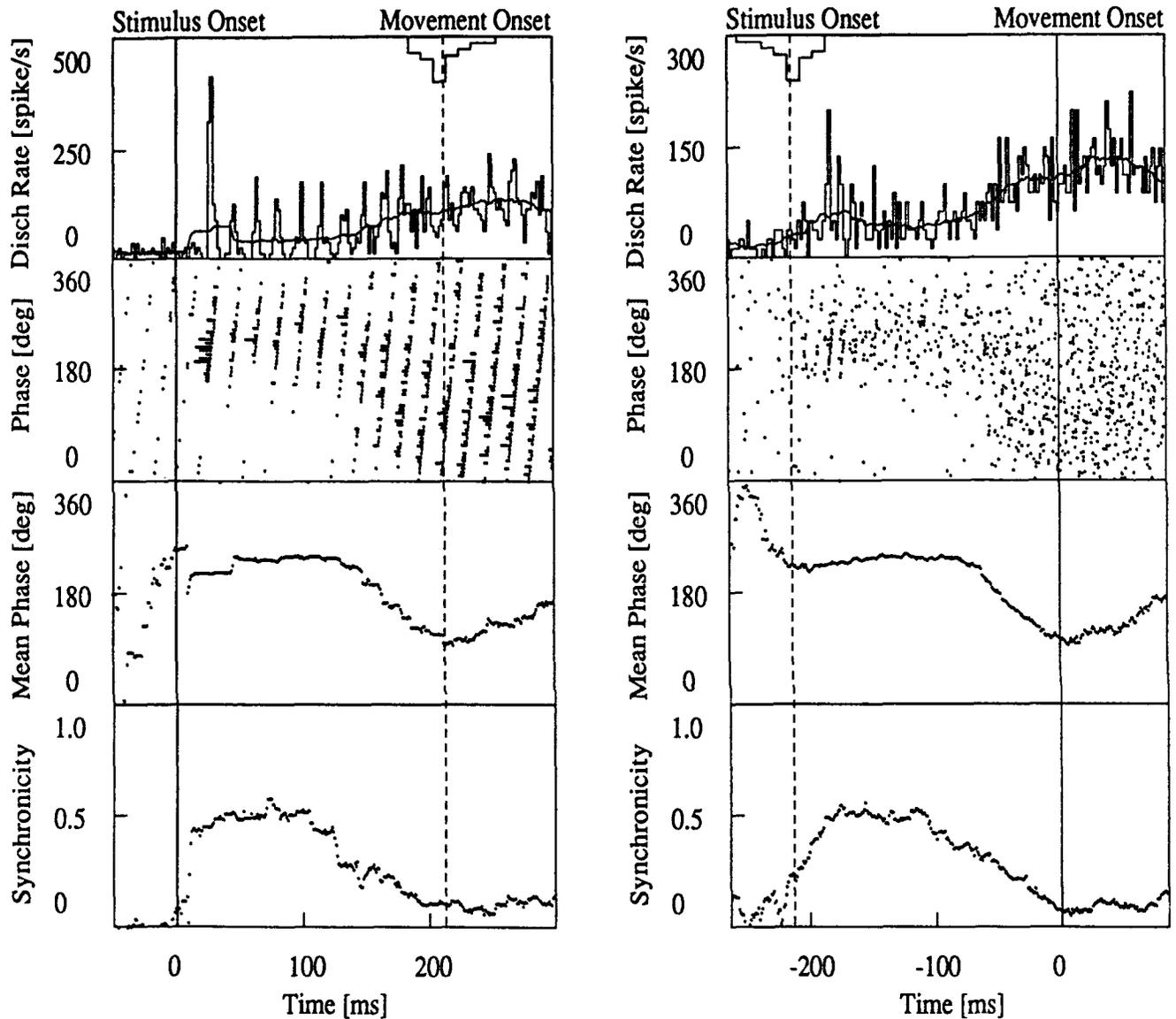
Thus, phase was a statistical value depending on time. We described it using floating mean parameters. These parameters were calculated as average values in a time window with a width equal to one vibratory period at 27 Hz (37.0 ms), two periods at 57 Hz (35.1 ms), and four periods at 127 Hz (31.5 ms). Mean phase  $\vartheta(t)$  was calculated according to the formula:

$$\vartheta(t) = \text{angle} \left( \sum \exp(i \varphi(t_i)) \right), \quad t-T/2 < t_i \leq t+T/2 \quad (4)$$

where  $i$  is an imaginary unit,  $t_i$  is the time of occurrence of  $i$ -th spike within the floating window and  $T$  is time window width.

It was important to calculate the sum of the vectors corresponding to individual response phases (Figure 2, lower plots). Then the mean phase of spike occurrence was calculated as the angle of this mean vector. Estimation of the mean phase as an average of the scalar values of phase could lead to erroneous results. For example, the values of phase  $-180^\circ$  and  $180^\circ$  are indeed very close in a true vector coordinate system. However, an average of the scalar values of phase distributed around  $-180^\circ$  and  $180^\circ$  would tend to give  $0^\circ$ , obviously an incorrect result.

Monkey: H Area: 1 RF: Deep VibFr: 57 Hz Task: Extension



*Figure 3.* The same unit as in Figure 1. Panels from top to bottom: (1) 2 ms binned time histograms of spike occurrence with superimposed traces of mean discharge rate; (2) raster displays of spike phases in 40 trials; (3) trace of mean phase; (4) trace of synchronicity. Left panels: aligned on stimulus onset. Right panels: aligned on movement onset. This unit was additionally activated about 80 ms prior to movement onset. At the same time, response phase shifted towards earlier responses and synchronicity dramatically decreased.

The floating standard deviation of the response phase  $\sigma(t)$  was calculated according to the formula:

$$\sigma(t) = \left\{ \text{mean} \left[ \left( \text{angle} \left( \exp \left( i \left( \vartheta(t) - \varphi'(t_i) \right) \right) \right) \right)^2 \right] \right\}^{1/2}, \quad t - T/2 < t_i \leq t + T/2 \quad (5)$$

where the angle is defined as ranging between  $-180^\circ$  to  $180^\circ$

Standard deviation calculated on a small number of samples tends to be an underestimate. To correct the underestimation resulting from eqs 4-5, we used a numerical model. Based on this model, a correction factor was calculated as a second order polynomial function of the number of samples. Standard deviations calculated according to eq 5, were then multiplied by this correction factor.

We characterized the degree of correlation between the vibratory stimuli and the responses in terms of synchronicity parameters  $s(t)$  and  $s'(t)$ . These parameters were derived from the standard deviations and served to compare a given distribution with a uniform distribution over vibratory cycle. Standard deviation for a uniform distribution  $\sigma_{unif}$  can be easily calculated:

$$\sigma_{unif} = \left( \left( \int_{-180^{\circ}}^{180^{\circ}} \phi^2 d\phi \right) / 360^{\circ} \right)^{1/2} = 103.923^{\circ} \quad (6)$$

The synchronicity parameters  $s(t)$  and  $s'(t)$  were calculated as follows:

$$s(t) = (\sigma_{unif} - \sigma(t)) / \sigma_{unif} \quad (7)$$

As it can be seen from eq 7, synchronicity could change in the range from 0.0 to 1.0. Zero corresponded to the total absence of correlation (uniform distribution), whereas 1.0 corresponded to the ideal case of a constant response phase. Mean discharge rate parameters  $F(t)$  and  $F'(t)$  were also calculated as average values in the same time window with the width  $T$ :

$$F(t) = N(t) / T / n \quad (8)$$

$N(t)$  are the numbers of discharges in the time window,  $n$  is number of trials used for averaging.

Figure 3 illustrates graphically the results of applying these analyses to the same data presented in Figure 1. It is clear that additional information was revealed. One can see that approximately at the same time as the unit was activated prior to movement onset ( $\sim 80$  ms), mean phase shifted, with respect to the earlier response to the ongoing vibratory stimulus. In addition, synchronicity dramatically decreased with respect to the early post stimulus onset level.

To determine the time of occurrence of changes in mean phase, synchronicity or mean discharge rate, a stable part of the appropriate trace first was considered. Mean and standard deviation were calculated for this epoch. Then the computer program searched forward in time to find the point when a change of more than three standard deviations took place. This time was designated as onset of a change in the appropriate trace. It should be stressed that the precision of estimation of this time was limited. The procedure of calculation of floating mean parameters was analogous to low-pass filtering. It tended to broaden sharp edges (compare in Figure 3, left panel, with 2 ms binning of the histogram and mean discharge rate trace). The maximal error in determining time of change occurrence resulting from this broadening was equal to  $T/2$  ( or  $\sim 18$  ms).

To analyze the parameters which influence the characteristics of activity patterns for different primary somatosensory cortical neurons, factorial ANOVA was used (StatView II 1987 Abacus Concepts Inc). Multifactorial ANOVA served to detect with which of the independent variables (i.e., cortical area, receptive field, frequency of vibration, direction of movement etc.) mean firing rate, phase

and synchronicity covaried . Then the data were grouped to isolate combinations of parameters which were statistically significant in their covariance. One factor ANOVA was then applied to test the significance of differences between these groups.

#### *Observations*

After visual inspection of the results of preliminary analyses, 55 primary somatosensory cortical units were selected that were entrained to the frequency of the vibratory stimuli used a go-cues to elicit wrist movements. These consisted of 10 area 3a cells (all with deep receptive fields[RFs]), 13 area 3b cells (4 cutaneous, 3 deep, 6 with unknown RFs), 28 area 1 cells (15 cutaneous, 12 deep, 1 unknown RF), and 4 area 2 cells (1 cutaneous, 1 deep, 2 unknown RFs). It appeared that in some cases, the distribution of responses over vibratory cycle was bimodal. Usually, two phases of maximum responsiveness in these cases were separated by 180°. It is likely that these were responses both to application and withdrawal of the mechanical stimuli. These cases were excluded from the analyses of mean phase and synchronicity.

For different animals, reaction times (the time from vibration onset to movement onset) were in the range 200-400 ms. During this preparatory period, the pattern of activity of neurons from the selected group changed. Typically (Figure 3), the following phases of neuronal activity were observed: (1) background firing preceding the stimulus onset; (2) initial brief response to stimulus onset; (3) stabilized responses to vibration (e.g., 50-100ms from stimulus onset in Figure 3); (4) premovement modulation (in Figure 3 beginning about 80 ms prior to movement onset).

#### *Background Firing and Stabilized Responses to Vibration*

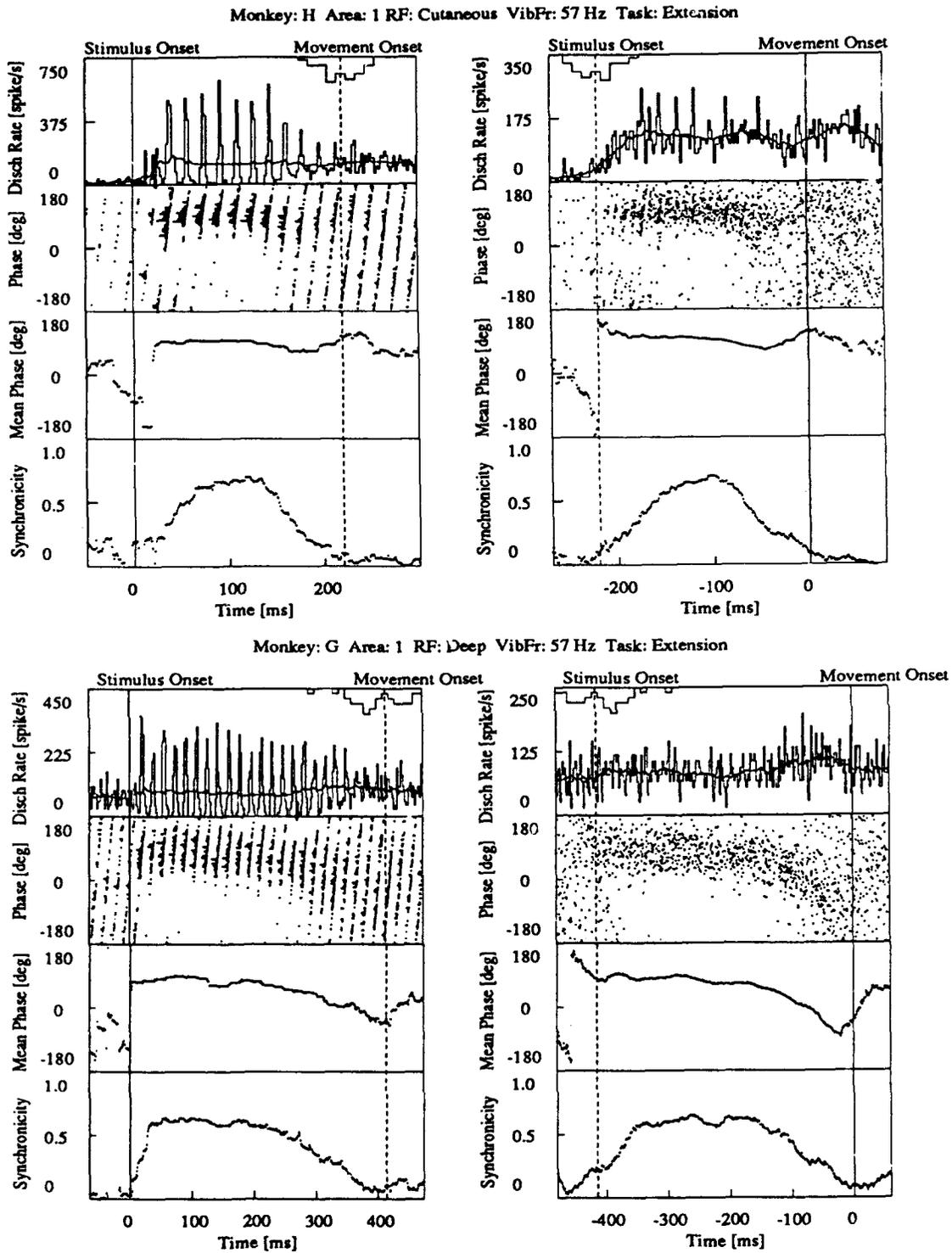
The units within the selected group typically exhibited background activity of about 30 spike/s. During the initial response to vibration, the instantaneous firing rate could reach up to 500 spikes/s (Figure 3). The subsequent stabilized responses were usually less intensive than the first burst. As might be expected, in many cases during the period of stabilized responses the mean discharge rate was higher than background firing rate (Figure 4, upper panels). However, the mean discharge rate could have remained practically unaltered (Figure 4, lower panels). In the latter case, periodic bursts of high instantaneous activity were separated by silent periods. Thus, even though the instantaneous firing rate could be much larger than background firing rate, averaging yielded a post-stimulus mean discharge rate comparative with the background firing rate.

The pattern of stabilized responses could be different depending on vibratory frequency. A unit could respond with well pronounced bursts of spikes at a lower vibratory frequency and not respond or even be suppressed at higher frequency (not shown).

For each case (one particular neuron, direction of movement, vibratory frequency), the mean values of firing rate, response phase and synchronicity were calculated for the background epoch and for the period of stabilized response. Factorial ANOVA was applied to detect factors influencing these parameters. If some factors were not significant, averaging on the set of these factors was performed. We found that there were no significant differences in these parameters as a function of direction of movement. This could be because the sign of the extension-flexion difference varied from unit to unit. To estimate this extension-flexion difference independent of sign, absolute difference was used:

$$D = |X_{\text{ext}} - X_{\text{flx}}| \quad (9)$$

where D is absolute difference,  $X_{\text{ext}}$  is the value of parameter for extension movements,  $X_{\text{flx}}$  is the value of the same parameter for flexion movements.



*Figure 4.* Upper panels: Area 1 unit with cutaneous RF. Vibratory frequency 57 Hz. Extension movements. Unit responded to vibration with increased mean firing rate. About 80 ms before movement, synchronicity decreased. Slight increase in mean firing rate occurred about 100 ms before movement. Slight decrease in mean firing rate about 70 ms prior to movement. The trace of phase followed the trace of mean firing rate. Lower panels: Area 1 unit with deep RF. Vibratory frequency 57 Hz. Extension movements. For this unit mean firing rate during vibration was not substantially different from background firing rate. The change of activity pattern was achieved by rearrangement of responses within vibratory cycles. About 150 ms prior to movement mean firing rate slightly increased. At the same time response phase lowered, and synchronicity decreased. Note the difference in reaction time between the two examples (upper and lower blocks).

Background firing rate was not statistically different depending on cortical area, direction of movement or vibratory stimulus frequency. The differences in background firing rate as a function of the type of receptive field for the neuron appeared to be significant. In average, units with deep RFs exhibited higher background firing rate (30.2 spike/s) than those with cutaneous RFs (21.5 spike/s). The analyses of absolute extension-flexion difference for background firing rate indicated that this parameter was, in average, higher for units with cutaneous RFs (3.2 spike/s) than for units with deep RFs (2.3 spike/s). However, this difference was not significant at 0.05 significance level ( $p=0.072$ ).

For the mean stabilized discharge rate, vibratory frequency and RF type were significant factors. At low vibratory frequencies (27 and 57 Hz) the stabilized mean firing rate was about the same for both units with deep (means, respectively, 44.3 and 48.6 spike/s) and cutaneous (51.8 and 45.7 spike/s) receptive fields. At higher vibratory frequency (127 Hz) stabilized mean firing rate slightly reduced (not statistically significant) for units with deep receptive fields (mean=40.7 spike/s), and it became significantly smaller for units with cutaneous receptive fields (mean=19.4 spike/s).

We also considered the difference between stabilized mean discharge rate and mean background firing rate. This parameter was significantly smaller at vibratory frequency of 27 Hz for cells with deep RFs (mean=11.2 spike/s) than for cells with cutaneous RFs (mean=31.8 spike/s). At 57 Hz, the change in firing rate was also, on average, smaller in units with deep RFs (18.0 spike/s versus 23.8 spike/s for those with cutaneous RFs). This difference, however, was not statistically significant. At 127 Hz, the change in firing rate was dramatically reduced for units with cutaneous RFs (mean=-1.0 spike/s), while it was about the same for units with deep receptive fields (mean=10.1 spike/s). It should be noted that, at 127 Hz, a substantial proportion of units with cutaneous RFs had changes in firing rate that were negative in sign (i.e., reductions in firing rate).

Absolute extension-flexion difference of stabilized mean firing rate was, on average, larger for units with cutaneous RFs than for units with deep RFs at all studied vibratory frequencies (statistically significant only at 57 Hz). At 27 Hz, the mean extension-flexion difference for deep versus cutaneous RF units was 4.5 vs 11.7 spike/s ( $p=0.071$ ); at 57 Hz it was 5.8 vs 10.6 spike/s ( $p=0.036$ ); and at 127 Hz it was 4.3 vs 7.7 spike/s ( $p=0.080$ ).

In terms of response phase, a similar tendency for absolute extension-flexion difference to be larger in units with cutaneous RFs was found. This tendency was not expressed at low vibratory frequency (27 Hz), but at 57 and 127 Hz there was a significant distinction between means of extension-flexion difference of phase for deep versus cutaneous RF units (57 Hz:  $16.3^\circ$  vs  $30.1^\circ$ ,  $p<0.05$ ; 127 Hz:  $30.7^\circ$  vs  $80.9^\circ$ ,  $p<0.05$ ).

The only single significant factor influencing stabilized response synchronicity was vibratory frequency. Moreover, there was no significant difference in synchronicity at 27 Hz (mean=0.38) and 57 Hz (mean=0.38). At 127 Hz response synchronicity became significantly smaller (mean=0.24). Absolute extension-flexion difference for stabilized synchronicity was not dependent on any of factors.

#### *Basic Patterns of Premovement Modulation - Activation Prior to Movement*

An example of premovement activation pattern is presented in Figure 3 (upper part). It can be seen that this area 1 unit with a deep receptive field was well entrained to the stimuli. About 80 ms prior to movement onset it was additionally activated. An increase of the mean firing rate is especially obvious in the histogram aligned on movement onset. There were also considerable changes in mean phase and synchronicity, correlated with the increase of firing rate. Synchronicity diminished significantly, and mean phase shifted in direction, corresponding to an earlier response time.

As a working hypothesis for the causes of these changes, we suggested that, prior to movement, an asynchronous centrally generated signal is added to the signal synchronized to the peripheral stimuli. This would explain the increase in firing rate and the decrease of synchronicity. This would also explain the earlier response phase. Indeed, when two excitatory signals are added, the neuron may be brought to firing threshold earlier in comparison with the condition where it is activated by only one input.

In some cases not all of these effects, that is, an increase of firing rate, desynchronization, and a phase shift, were clear. In the lower part of Figure 3 an example of activity of an area 1 neuron with a cutaneous RF is presented. This unit was not of the pure premovement activation type. There was an obvious qualitative change in the firing pattern of this neuron, preceding movement onset. The responses desynchronized. However, there was no increase in mean firing frequency (clear from the histogram aligned on movement onset). There was also no significant change in response phase. This example of a deviation from the ideal case described by the working hypothesis, indicates that the real process of integration of sensory and central modulatory inputs is much more complex than the simplistic scheme. The analyses of the data did reveal that for the same neuron in a given type of trial requiring either flexion or extension movements, the premovement activation pattern was preserved. If a unit was activated before movement, this activation took place at all frequencies of vibration. The amount of change in synchronicity and phase, however, could be different at different frequencies.

#### *Basic Patterns of Premovement Modulation - Suppression Prior to Movement*

The second basic activity pattern was characterized by premovement suppression of activity. An example of an area 3a unit that exhibited this pattern of firing in flexion trials is given in Figure 5. Its activity was suppressed about 70 ms prior to movement onset both at the frequencies of vibration 27 and 57 Hz. As in the case of premovement activation pattern, the template of premovement suppression was obtained for 3 vibratory frequencies (27, 57 and 127 Hz) by means of ensemble averaging. Only those units for which all three frequencies were available, were selected for the averaging procedure. There were 7 cases, including 2 for extension task (area 1: 1, area 3b:1) and 5 for flexion task (area 1: 4, area 3a: 1).

Superimposed traces for different vibratory frequencies were examined. From the results of this averaging it was observed that, as for the group of premovement activated units, the response to vibration onset consisted of an initial burst, followed by a short period of stabilization. The initial response in terms of mean firing rate was the strongest at 57 Hz and the lowest at 127 Hz. After the stabilization period, an increase of mean firing rate was observed. Then the activity was suppressed, on average, to a level slightly lower than the background level observed before initiation of the task. The activation began about 110 ms before movement, and the suppression preceded movement onset by 70 ms. The activation was more pronounced at 127 Hz, and less at 27 and 57 Hz. The amount of premovement suppression of the mean firing rate was similar at all frequencies of vibration. The response synchronicity was high at 27 and 57 Hz (about 0.5) and much lower at 127 Hz. Interestingly, the changes of response synchronicity and phase resembled those observed for premovement activation pattern. There was a pronounced drop of synchronicity preceding the movement onset at 27 and 57 Hz, and there were almost no changes in synchronicity at 127 Hz. At 57 and 127 Hz there was also response phase lowering.

Thus, the second activity pattern, characterized by premovement suppression, included certain features characteristic to premovement activation pattern. These were desynchronization, lowering of response phase and activation that preceded the final suppression. Based on these facts, we suggest that

Monkey: H Area: 3a RF: Deep VibFr: 127 Hz Task: Flexion

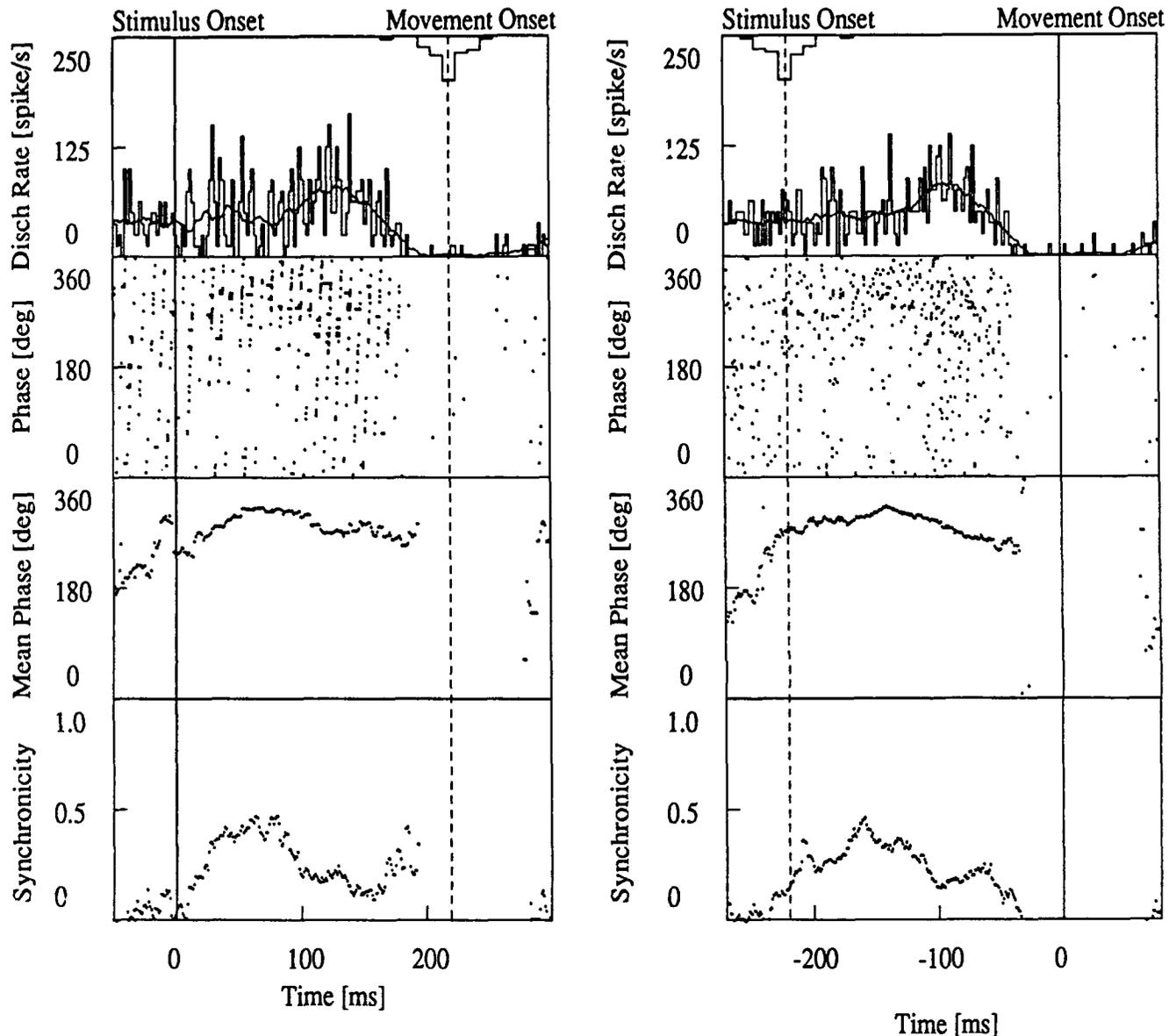


Figure 5. Conventions as in figure 3. Area 3a unit with deep RF. Vibratory frequency 57 Hz. Extension movements. Unit responded to vibration with increased mean firing rate. About 70 ms before movement, firing was suppressed. Mean firing rate drops to essentially zero about 50 ms prior to movement. The trace of phase did not initially follow the trace of mean firing rate, implying that phase was maintained even though firing was reduced.

suppression actually could be interposed upon the pattern of the first type. The premovement activation pattern, that began to develop 110 ms prior to movement, was shut down about 70 ms before movement.

#### Conclusions

These studies suggest that somatosensory cortical neurons that have entrained activity in response to the frequency of peripheral vibratory stimuli do not continually signal the characteristics of these stimuli with great fidelity. Rather these neurons, as we have demonstrated for several other classes of

somatosensory cortical neurons, are subject to premovement modulation of their sensory responsiveness. The analyses of response synchronicity and phase, in addition to conventional methods of firing rate analysis, revealed two basic patterns of premovement modification. The first pattern was characterized by an increase of firing rate, a desynchronization of the firing pattern, and a shift of the response towards an earlier phase relative to vibratory cycle. We suggest that these changes are the result of a summation of synchronous sensory responses and asynchronous centrally generated signals. The synchronicity changed more at lower stimulation frequencies (27 and 57 Hz) than at higher frequency (127 Hz). This effect may reflect the interaction of the frequency components of both the sensory responses and central influences. In the second pattern, neuronal activity was suppressed prior to movement. Moreover, an activation was observed, preceding the suppression, and also a synchronicity decrease and response phase lowering, correlated with this activation. Thus, we suggest that suppression could be interposed upon the pattern of the first type. The same neuron could exhibit the first or the second pattern depending on the direction of movement. These neurons were classified as directional. The majority of nondirectional neurons were activated prior to movement, and a small portion was suppressed.

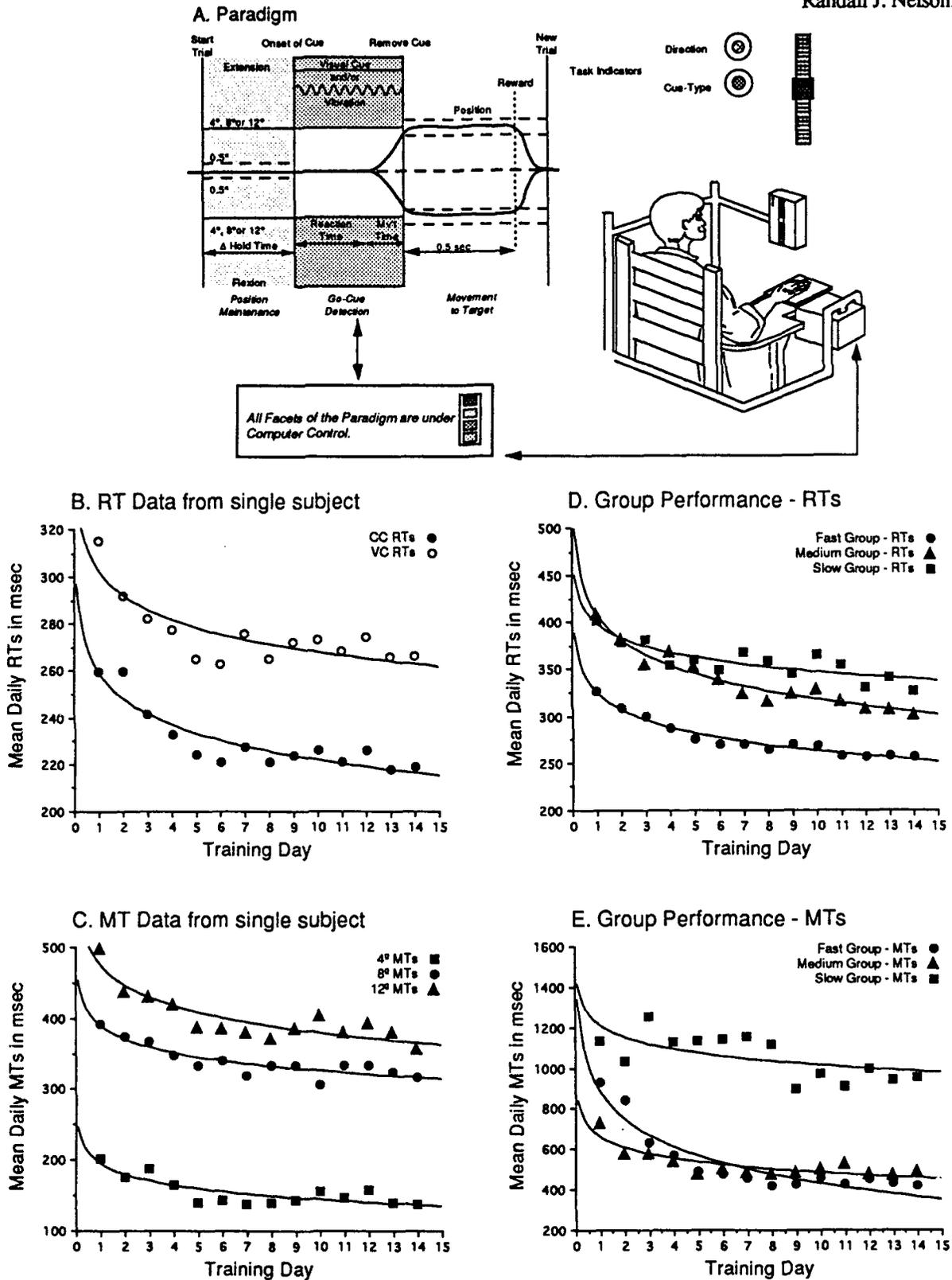
## Results - Human Subjects

### *Data Analysis*

In the fixed task paradigm, the independent variables that could have influenced RTs and MTs were go-cue type (CC or VC), the frequency of the vibratory stimulus component of the CC (27, 57 or 127Hz) and movement direction (flexion or extend). All movements were made to targets 5° from the centered position held at the start of the trials and the movement direction for a block of trials was held constant for the entire block. In the variable and random target paradigms, movement amplitude (4°, 8° or 12°) became an additional independent variable. For the random target paradigm, only 57Hz CCs were used for reasons that will be described below. For each subject, daily mean RTs and MTs were calculated for each unique combination of the independent variables of that task. After all experiments were completed, an Analysis of Variance (ANOVA) was conducted to determine whether varying any of the independent variables resulted in statistically significant changes in the dependent variables, in this cases RTs and MTs. All the results were examined using a K-Means Cluster Analysis to determine whether there were any natural groupings in the results of subjects from the whole population of a given experiment. Once groups were determined, group daily mean RTs and MTs were determined split along those combinations of independent variables that resulted in significant differences in group RTs and MTs. The results were subjected to further analysis using a non-linear regression model to describe the characteristics of group performance. These characteristics included improvement in performance from the first day, time in days until stable performance was reached and final performance ceiling (or shortest RTs and MTs).

### *Observations*

In general, for each task, subjects improved with practice. Figure 6A presents a schematic rendition of the paradigm timing and requirements. Figure 6B&C illustrate examples of the mean daily RTs and MTs for a single subject. For all subjects, RTs and MTs became significantly shorter with practice. Improvement characteristically continued from the first training day until stable performance was reached, usually at about the fifth day for RTs and the seventh day for MTs. For each subject, corresponding RTs and MTs for the last five training days were not significantly different from one another (ANOVA;  $p > 0.05$ ). Therefore, the RTs and MTs for the last five training days were averaged



**Figure 6.** Panel A; Schematic representation of the behavioral paradigm. Panel B; Mean Daily RTs for CC and VC trials plotted as a function of training day. Panel C; Mean Daily MTs for flexion movements made by the same subject as a function of training day. Extension movement Mean Daily MTs were indistinguishable from those illustrated. Panel D; Mean Daily RTs for the fast, medium and slow performance groups for VC trials as a function of training day. Panel E. Mean Daily MTs for large VC trial movements for each performance group plotted as a function of training day. (see text for details)

to yield final mean RTs and MTs for each unique set of independent variables for each subject. All values for the last five training days were subjected to an ANOVA. For RTs, the only significant covariance was with changes in cue-type. MTs varied only with the amplitude of the movement made. Based upon these findings, daily mean RTs and MTs were subjected to a K-Means cluster analysis.

The RTs and MTs of subjects that performed the fixed and variable target paradigms were neatly distributed into three groups. Figure 6D&E show some of the characteristics of the three performance groups. In general, the fast performance group had quick initial RTs and MTs, showed improvement over the first five days, and reach stable behavioral performance which was maintained after this point. The medium performance group initial had slow RTs and intermediate MTs. With practice, their MTs reached the level of the fast group. Their RTs improved, but were still significantly different from those of the fast group (see Table 1). The medium group took somewhat longer to reach stable performance than the fast group (to be discussed below). The slow group had slow initial RTs and MTs, showed meager improvement over a longer time course with respect to the other groups, and ended with final RTs that were not statistically different from the medium group, but MTs that were different for each movement condition. A cluster analysis was also conducted for the results of the random target task. This analysis split the results into two groups, as might be expected due to the limited number of subjects (n=4). The groups had the same general characteristics as the fast and slow groups previously determined for subjects that performed the fixed and variable target paradigms.

Each mean daily RTs and MTs from each task show that subjects began movements more quickly during CC trials than during VC trials. This difference appeared to become less as task complexity increased. Table 1 lists the final mean RTs and MTs by task, performance group, movement direction and, where applicable, movement amplitude. In addition, the mean differences in the values for CC trials as compared with VC trials are listed. For the simplest cue movement combination, occurring during the fixed target paradigm where movement amplitude and direction are known before go-cue onset, mean RTs during CC trials were faster by  $\approx 51$ ms or approximately 20% of the average RTs for the fast group. For the variable target paradigm, where movement direction was known but amplitude was varied pseudo-randomly, RTs differences were  $\approx 41$ ms or about 15% of the mean RTs values for the fast group. RTs differences were approximately 25ms or slightly less than 10% of the fast performance group mean RTs values for subject that ran the random target paradigm. In this task, neither the movement direction nor the movement amplitude were predictable. MTs varied with movement amplitude but not significantly with cue type. Increased task complexity resulted in both longer RTs and longer MTs for movements of the same amplitude. However, at least for the fast performance group, the differences in RTs and comparable MTs for the variable and random target task (the two multiple target tasks) were not significantly different statistically.

Characteristics of group performance were best fit by a non-linear model that can be used to predict some facets of subject performance. We sought to determine if the daily RTs and MTs could be modeled. If this could be done, it was reasoned that given the results of a few days of task performance, accurate prediction could be made about a subject's ultimate performance group, their final RTs and MTs and the time it would take for them to reach a stable performance level. To model the performance of subjects in each performance group, data were analyzed using the following equation:

$$\text{Performance}_{\text{training day}} = \text{Best Performance} + \alpha * \text{EXP}(-(\text{Training Day} - 1)/\beta) \quad (10)$$

Table 1.

<i>Fixed Target Paradigm</i>							
	<u>Combined Cue</u>		<u>Visual Cue</u>		<u>Flex Diff</u>	<u>Ext Diff</u>	
	<u>Flex</u>	<u>Ext</u>	<u>Flex</u>	<u>Ext</u>			
<b>Performance Group -RTs</b>							
Fast (N=8)	219.4 ± 20.7†	217.0 ± 17.9†	273.1 ± 23.6†	271.0 ± 17.0†	53.7*	54.0*	
Med (N=2)	282.8 ± 35.5	264.5 ± 17.5	318.5 ± 21.9	301.5 ± 18.0	35.7*	36.9*	
Slow (N=2)	284.3 ± 20.1	280.3 ± 33.6	341.9 ± 35.6	332.5 ± 39.8	57.5*	52.2*	
Total	240.8 ± 37.3	235.5 ± 32.9	292.1 ± 36.9	286.4 ± 30.6	51.3*	50.8*	
<b>Performance Group - MTs (5°)</b>							
Fast	154.5 ± 34.3	156.0 ± 30.9	157.2 ± 35.9	157.1 ± 32.1	2.7	1.1	
Med	163.4 ± 11.7	169.9 ± 24.8	155.9 ± 17.6	165.5 ± 18.7	-7.5	-4.4	
Slow	265.4 ± 24.0†	258.8 ± 35.0†	268.8 ± 23.3†	262.6 ± 31.3†	3.4	3.8	
Total	174.5 ± 50.8	175.5 ± 48.5	175.6 ± 52.5	176.1 ± 49.2	1.1	0.6	
<i>Variable Target Paradigm</i>							
	<u>Combined Cue</u>		<u>Visual Cue</u>		<u>Flex Diff</u>	<u>Ext Diff</u>	
	<u>Flex</u>	<u>Ext</u>	<u>Flex</u>	<u>Ext</u>			
<b>Performance Group -RTs</b>							
Fast (N=3)	259.6 ± 47.10	263.6 ± 52.40	297.7 ± 41.10	294.8 ± 46.60	38.1*	31.2*	
Med (N=2)	311.9 ± 10.6	312.9 ± 22.4	358.8 ± 25.5	364.4 ± 43.7	46.9*	51.6*	
Slow (N=1)	343.6 ± 21.7	340.3 ± 24.7	395.7 ± 29.6	386.6 ± 36.5	52.1*	46.4*	
Total	291.0 ± 49.6	292.8 ± 51.8	334.4 ± 53.3	333.3 ± 60.2	43.4*	40.5*	
<b>Performance Group - MTs</b>							
<b>Fast</b>							
4°	176.0 ± 45.6	169.2 ± 46.1	176.8 ± 46.6	182.0 ± 45.0	0.8	12.8	
8°	345.5 ± 29.4	322.3 ± 49.7	329.5 ± 48.5	318.7 ± 63.0	16.0	3.6	
12°	436.7 ± 71.2	417.1 ± 72.2	427.6 ± 72.3	402.6 ± 92.1	9.1	14.5	
<b>Med</b>							
4°	217.6 ± 55.8	225.2 ± 26.3	219.9 ± 55.0	225.3 ± 37.4	2.3	0.1	
8°	388.4 ± 55.5	372.0 ± 37.1	373.6 ± 54.9	354.6 ± 52.8	14.7	-17.3	
12°	495.2 ± 66.0	456.4 ± 47.6	471.1 ± 69.0	436.3 ± 57.9	24.0	20.1	
<b>Slow</b>							
4°	457.8 ± 35.90	446.5 ± 42.60	431.9 ± 28.60	421.3 ± 25.90	-26.0	-25.1	
8°	740.8 ± 72.60	706.4 ± 48.70	691.1 ± 40.10	654.9 ± 48.50	-49.6	51.4	
12°	921.3 ± 80.70	947.1 ± 89.50	848.2 ± 63.40	899.4 ± 96.10	-73.2	-47.6	
<b>Total</b>							
4°	236.8 ± 112.4	234.0 ± 108.1	233.7 ± 102.8	236.3 ± 94.8	-3.1	2.3	
8°	425.7 ± 151.6	402.9 ± 147.2	404.5 ± 141.3	386.7 ± 134.9	-21.2	-16.2	
12°	537.0 ± 190.8	518.5 ± 207.2	512.2 ± 169.4	496.7 ± 199.8	-24.8	-21.9	
<i>Random Target Paradigm</i>							
	<u>Combined Cue</u>		<u>Visual Cue</u>		<u>Flex Diff</u>	<u>Ext Diff</u>	
	<u>Flex</u>	<u>Ext</u>	<u>Flex</u>	<u>Ext</u>			
<b>Performance Group -RTs</b>							
Fast (N=3)	295.3 ± 22.9	296.7 ± 18.8	320.6 ± 18.5	322.3 ± 15.5	25.3*	25.6*	
Slow (N=1)	389.6 ± 13.0	389.0 ± 22.3	413.7 ± 12.0	422.3 ± 19.6	24.0*	33.3*	
<b>Performance Group -MTs</b>							
<b>Fast</b>							
4°	268.1 ± 37.4	249.8 ± 34.9	260.3 ± 34.9	240.4 ± 26.4	-7.8	-9.3	
8°	396.6 ± 34.3	399.6 ± 42.3	372.8 ± 27.5	380.6 ± 34.9	-23.8*	-19.0*	
12°	533.3 ± 51.2	525.4 ± 50.7	518.1 ± 42.9	506.3 ± 47.9	-15.1	-19.0*	
<b>Slow</b>							
4°	374.1 ± 66.5	346.8 ± 51.0	343.8 ± 38.8	342.5 ± 33.3	-30.3	-4.3	
8°	495.9 ± 76.5	517.2 ± 53.0	517.8 ± 38.5	510.3 ± 46.1	21.9	-6.9	
12°	674.7 ± 85.9	662.9 ± 73.2	646.2 ± 61.1	638.5 ± 62.9	-28.5	-24.4	

† denotes value different from other groups ( $p < .05$ ); Scheffé F-test  
 ◊ denotes value different from other groups ( $p < .001$ ); Scheffé F-test  
 \* denotes  $p < .005$ ; unpaired t-test

where performance is the value of the variable under consideration, Best Performance is the mean value for the final 5 training days,  $\alpha$  represents the improvement from first training day until stabilized performance and  $\beta$  is the time constant. However,

$$\alpha = \text{Performance}_{\text{day1}} - \text{Best Performance} \quad (11)$$

and  $\beta$  actually represents the time in days at which 63% of the improvement in performance is reached. The time in days for a subject to reach a given performance level can be expressed by the following equations:

$$\text{Training Day} = 1 + \beta * \ln (\alpha / (\text{Performance}_{\text{Training Day}} - \text{Best Performance})) \quad (12)$$

$$\text{Training Day} = 1 + \beta * \ln \left( \frac{\text{Performance}_{\text{day1}} - \text{Best Performance}}{\text{Performance}_{\text{Training Day}} - \text{Best Performance}} \right) \quad (13)$$

If we re-write eq. 13 we have:

$$\text{Training Day} = 1 + \beta * \ln \left( \frac{100\%}{100\% - R} \right) \quad (14)$$

where R is the improvement expressed as a percentage of optimal improvement. For example, shortening of RTs to within 95% of optimal improvement would be reached at:

$$\text{Training Day} = 1 + \beta * \ln (1/0.05) = 1 + \beta * \ln (20) = 1 + \beta * 2.99 \quad (15)$$

We found that, in general, fast and medium performance groups improve their RTs and MTs at similar similar rate and by similar amounts with respect to started values. The exception to this generalization is that very little improvement was observed for the medium performance group during the simplest (fixed target) task. While the slow performance group subjects also improved by about the same absolute value as the other groups, due their their larger starting values, their improvement was actually proportionally less than the other groups. These results are listed in Table 2.

### Conclusions

The results of these experiments indicate that visually guided movements are performed more quickly when a vibratory signal to the hand that is to be moved is presented in conjunction with the visual target. They also indicate that movement times, though somewhat faster without the presence of vibratory stimuli that lasts until the target has been reached, are not significantly different as a function of the type of go cue that a subject receives. These studies suggest that a paradigm of this sort could be used to assess the potential performance of individuals on precision wrist movement tasks. Each performance group has certain characteristics that are evident and expressed in the measures behavior after only a a few days of task performance. Therefore, RTs and MTs collected over only a few days of training may be used to predict the eventual level of performance of which an individual is capable.

**Table 2.**

$$\text{Performance}_{\text{training day}} = \text{Best Performance [Const]} + \alpha * \text{EXP}(-(\text{Training Day} - 1) / \beta) (10)$$

<i>Fixed Target Paradigm</i>						
	<u>Const</u>	<u>Combined Cue</u> $\alpha$	$\beta$	<u>Const</u>	<u>Visual Cue</u> $\alpha$	$\beta$
<b>Performance Group - RTs</b>						
Fast	218.3	59.3	3.5	272.0	84.3	2.9
Med	273.7	24.7	1.0	310.0	15.2	0.1
Slow	282.3	68.6	4.7	337.2	68.4	5.5
<b>Performance Group - MTs (5°)</b>						
Fast	155.3	47.1	4.7	157.2	52.7	4.6
Med	166.7	36.2	4.8	160.7	43.2	4.7
Slow	262.1	51.1	8.4	265.7	54.6	7.4

<i>Variable Target Paradigm</i>						
	<u>Const</u>	<u>Combined Cue</u> $\alpha$	$\beta$	<u>Const</u>	<u>Visual Cue</u> $\alpha$	$\beta$
<b>Performance Group - RTs</b>						
Fast	261.5	76.4	2.6	296.5	95.9	1.9
Med	312.1	83.7	3.2	360.4	95.8	2.7
Slow	341.9	90.6	3.4	391.1	94.7	3.9
<b>Performance Group - MTs</b>						
Fast						
4°	172.5	188.5	2.6	179.9	180.6	2.6
8°	334.3	329.9	2.7	324.2	322.6	2.7
12°	421.8	589.2	2.1	414.9	559.7	2.2
Med						
4°	222.4	141.2	2.1	222.3	118.9	2.6
8°	379.8	192.7	1.3	364.6	203.5	1.8
12°	475.7	219.9	1.6	453.2	235.4	2.0
Slow						
4°	426.9	163.6	4.1	408.2	139.8	4.6
8°	743.2	144.1	5.8	661.1	234.4	5.7
12°	927.6	271.0	6.1	899.1	304.2	6.4

<i>Random Target Paradigm</i>						
	<u>Const</u>	<u>Combined Cue</u> $\alpha$	$\beta$	<u>Const</u>	<u>Visual Cue</u> $\alpha$	$\beta$
<b>Performance Group - RTs</b>						
Fast	296.0	45.5	4.3	321.5	41.6	3.5
Slow°	389.4	46.0	7.7	418.0	52.1	6.7
<b>Performance Group - MTs</b>						
Fast						
4°	228.2	60.1	8.8	227.1	50.6	7.4
8°	376.3	59.6	5.3	359.2	44.3	5.7
12°	495.1	94.1	5.2	479.5	78.2	6.4
Slow						
4°	335.2	43.1	12.2	313.0	46.9	14.2
8°	440.8	130.4	8.5	473.5	74.7	10.0
12°	592.1	181.2	6.5	585.2	110.9	8.9

These predictions may be made using the equations listed above and may be useful in selecting the appropriate individuals for tasks in which the fastest possible RTs and MTs are crucial. These

equations may also be useful in determining the duration of training necessary before optimal performance is reached.

The findings of these psychophysical experiments suggest several further studies. As proposed in this grant, we will investigate whether vibratory signals can be used to abort movements that have already been triggered but that have not yet occurred (see original proposal). In addition, we will determine if the faster MTs for VC vs. CC trials still occur, are enhanced or are diminished if the vibratory stimuli transient, e.g., presented for only a brief period and then turned off prior to movement onset. These studies will better assess the practicality of using vibratory in addition to visual stimuli for the control of precise wrist movement. Regardless, the use of vibratory signals in addition to visual targets which act as go-cues for wrist movements results in faster total performance times.

### **General Statement**

The overall goal of the research conducted by this laboratory continues to be to understand the role that behavioral contingencies play in regulating the responsiveness of neurons that are involved in the control of wrist movement. Advances in this understanding make two contributions; the first to our general understanding of how the primate nervous system functions and the second to practical applications for device control.

We have chosen to study SI neurons because of our expertise with these neurons and because of their pivotal position in sensorimotor integration that ultimately results in controlled, goal-oriented behavior. It was previously thought that the responsiveness of SI neurons to peripheral and central inputs was essentially unaltered by behavioral contingencies. Findings from this laboratory and others have suggested that SI neurons undergo sometimes profound and sometimes subtle changes in responsiveness to both peripheral and central inputs. These findings have implications for the understanding of motor control because SI neurons provide direct or indirect inputs concerning limb position and muscle tension to other cortical regions such as posterior parietal, motor, premotor and supplementary motor cortices, as well as to the basal ganglia. All of these structures have been implicated in the control of movement. The demonstration of changes in the responsiveness in SI neurons then implies that the regions mentioned above may receive "pre-processed" information that differs depending upon the behavioral conditions present at any given time. Clearly, to understand motor control, the factors that influence it must be understood, and thus an understanding of the contributions which SI makes to this control are of great importance.

The practical application of this understanding may lead to more efficient design of control systems which utilize changes in wrist position. The results of human psychophysical experiments suggest that the timing of wrist position controlled target acquisition may be improved without any degradation in movement performance or accuracy. Caution is warranted and further studies are needed, however, because it has been established that vibratory stimuli can adversely effect wrist position control if the signals are of great enough amplitude. By modeling human RT performance, predictions can be made about an individual's capacity for behavioral improvement and the time course of that improvement.

### **Status of Future Research**

We are nearly ready to begin recording from monkeys who are being trained to perform the "Unexpected Failure" Paradigm (see original proposal). We will continue to do so during year 02 of this grant. We currently have two monkeys trained to perform most aspects of this task.

We have an additional set of human psychophysical experiments planned. We will randomly introduce an "abort signal", consisting of a small positional deflection of the control handle, to determine if pre-planned wrist movements can be aborted given the presentation of additional sensory information. This will be done to determine when in the movement initiation and execution cycle the movements are committed and unalterable and whether there is any difference in this timing as a function of the type of go-cue (visual only or visual plus vibration) used.

#### **List of Written Publications**

R. J. Nelson, B. Li, and V. D. Douglas. Sensory response enhancement and suppression of monkey primary somatosensory cortical neurons. Brain Res. Bull. 27:751-757

#### **Presentations of Supported Work**

R. J. Nelson and T. W. Gardiner. A Comparison of Premovement Activity in monkey neostriatum and sensorimotor cortex. Abst. Soc. Neurosci. 17:1218.

#### **Submitted Abstracts**

M. A. Lebedev and R. J. Nelson. The Activity of Vibratory responsive monkey primary somatosensory cortical neurons is modulated prior to hand movement. Abst. Soc. Neurosci. (Submitted).

#### **Associated Personnel**

John M. Denton continues to be employed as a Research Assistant. He has, over the two years, proved to be of crucial importance in the studies conducted under this grant. He now has expertise in data analysis and behavioral training of monkeys.

Michael A. Lebedev joined the laboratory this year as graduate student following his arrival from the then Soviet Union. He brings to the laboratory an extensive background in mathematics and physics. He is largely responsible for the phase analysis of the vibratory responsive neurons described herein and will present this work at this year's Annual Meeting of the Society for Neuroscience. He is truly a remarkable individual and an asset to the laboratory. Beginning July 1, 1992, he is receiving 50% of his support for funds of AFOSR 91-0333. The other 50% of his support comes from an award by the Center of Excellence in Neuroscience at the University of Tennessee, Memphis.

Erica D. Thomas, an undergraduate student from Christian Brothers University, has worked in the laboratory since the summer of 1991. She has been responsible for collecting data from human subjects as they performed the psychophysical experiments outlined above. Part of this work served as her Honors Project for her undergraduate degree. She is currently employed as a Non-UT Student Assistant. She has been diligent in conducting these rather time consuming experiments and has been able to show some very interesting results with regard to what parameters affect reaction and movement times during hand movements toward a target.

#### **Interactions**

1991 Society for Neuroscience Annual Meeting, New Orleans, LA Nov. 10-15 .

1992 Winter Conference on Brain Research, Steamboat Springs, CO Jan. 25-Feb. 1.

#### **New Discoveries**

None.