Time Course and Magnitude of Movement-Related Gating of Tactile Detection in Humans. II. Effects of Stimulus Intensity

STEPHAN R. WILLIAMS1,2 AND C. ELAINE CHAPMAN1–3
1Centre de Recherche en Sciences Neurologiques, 2Département de Physiologie, and 3École de Réadaptation, Faculté de Médecine, Université de Montréal, Montreal, Quebec H3C 3J7, Canada

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Williams, Stephan R. and C. Elaine Chapman. Time course and magnitude of movement-related gating of tactile detection in humans. II. Effects of stimulus intensity. J Neurophysiol 84: 863–875, 2000. This study examined the effect of systematically varying stimulus intensity on the time course and magnitude of movement-related gating of tactile detection and scaling in 17 human subjects trained to perform a rapid abduction of the right index finger (D2) in response to a visual cue. Electrical stimulation was delivered to D2 at five different intensities. At the lowest intensity, approximately 90% of stimuli were detected at rest (1 × P90); four multiples of this intensity were also tested (1.25, 1.5, 1.75, and 2.0 × P90). At all intensities of stimulation, detection of stimuli applied to the moving digit was diminished significantly and in a time-dependent manner, with peak decreases occurring within ±12 ms of the onset of electromyographic activity in the first dorsal interosseous (25–45 ms before movement onset). Reductions in the proportion of stimuli detected were greatest at the lowest stimulus intensity and progressively smaller at higher intensities. No shift in the timing of the decreases in performance was seen with increasing intensity. Once the weakest intensity at which most stimuli were perceived during movement had been established (2 × P90), magnitude estimation experiments were performed using two stimulus intensities, 2 × P90 (5 subjects) and 3 × P90 (3 subjects). Significant movement-related decreases in estimated stimulus magnitude were observed at both intensities, the time course of which was similar to the time course of reductions in detection performance. As stimulus intensity increased, the magnitude of the movement-related decrease in scaling diminished. A model of detection performance that accurately described the effect of stimulus intensity and timing on movement-related reductions in detection was created. This model was then combined with a previous model that described the effects of stimulus localization and timing to predict detection performance at a given stimulation site, intensity, and time during movement. Movement-related gating of tactile perception represents the end result of movement-related effects on the transmission and subsequent processing of the stimulus. The combined model clearly defines many of the requirements that proposed physiological mechanisms of movement-related gating will have to fulfill.

INTRODUCTION

Transmission of somatosensory stimuli is modulated during movement. Studies in rat, cat, monkey, and human, examining somatosensory-evoked potentials (SEPs) (Brooke et al. 1997; Chapman et al. 1988; Coquery et al. 1972; Jiang et al. 1990; Morita et al. 1998; Starr and Cohen 1985) or single-unit responses (Chapin and Woodward 1982; Jiang et al. 1991; Shin et al. 1994), have documented movement-related decreases in somatosensory transmission to the primary somatosensory cortex (SI) during movement. Psychophysical studies in humans have confirmed the existence of concomitant decreases in the detection of near-threshold stimuli during movement (Chapman et al. 1987; Coquery et al. 1971; Pertovaara et al. 1992; Post et al. 1994; Williams et al. 1998). However, wide variations have been reported with regards to the timing of the onset of movement-related gating, ranging from 200 ms before the onset of movement (Chapman et al. 1988; Coulter 1974; Ghez and Lenzi 1971) to 30 ms after movement onset (Kristeva-Feige et al. 1996), and in the magnitude of the effects, with observed reductions ranging from 7.5% (Coulter 1974) to more than 90% (Kristeva-Feige et al. 1996). The reasons for these important variations in the parameters defining movement-related gating remain unclear.

We recently demonstrated that the time course for movement-related decreases in detection of near-threshold tactile stimuli in humans is similar to that observed for decreases in somatosensory transmission to SI in monkeys (Williams et al. 1998). Our results indicated that peak decreases in detection can occur as early as 50 ms before the onset of movement, at about the same time movement-related electromyographic (EMG) activity begins. We also demonstrated the importance of stimulus location in determining the timing and magnitude of the movement-related modulation of perception. Reductions in detection were greatest and occurred earliest when the stimulus was delivered near the moving body part, the index finger (D2), and time-dependent movement-related decreases were restricted to the homolateral upper limb. Time-dependent reductions in detection were smaller and occurred up to 60 ms later as the distance between D2 and the stimulation site was increased. A modest (~10%) non-time-dependent decrease in detection was also observed at all stimulation sites (including distant ones such as the contralateral D2 and ipsilateral leg). We suggested that the latter decrease was most likely explained by the attentional demands placed on the subjects who were asked to divide their attention between two tasks, one motor (D2 abduction) and the other perceptual (detection of weak stimuli).

While our previous results contribute to explaining some of
the wide variations in the time course and magnitude of gating effects, another potentially important variable is the intensity of the test stimulus employed to evaluate sensory responsiveness. Most of the preceding studies used relatively strong test stimuli (several times threshold). In contrast, we used a single, near-threshold intensity (90% detected at rest, \( P_{90} \)) and did not examine the effect of higher stimulus intensities. The present study addressed this issue by determining the influence of systematically increasing the intensity of the test stimulus on the time course and magnitude of movement-related decreases in tactile perception. To facilitate comparisons with our previous results, we used the same motor task, D2 abduction. The effects of movement on stimulus perception were quantified using a detection task for weak stimuli and a stimulus scaling task for suprathreshold stimuli. A model describing the effect of stimulus intensity and timing on detection performance was created and combined with a previous model describing the effect of stimulus location and timing (Williams et al. 1998) to clarify the relative importance of each of these factors in determining detection performance. Preliminary accounts of these results have been published (Williams and Chapman 1996, 1999).

**METHODS**

**Subjects**

A total of 17 naive, paid volunteers (9 males and 8 females, ages 16–28 yr) participated in the study. All subjects but one were right-handed for writing. The institutional ethics committee approved the experimental protocol, and all subjects or their legal guardian gave their informed consent before participating in the study. Nine subjects participated in the stimulus detection tasks. Eight other subjects participated in the stimulus scaling tasks. Data from each subject were gathered in one or two sessions lasting 1–3 h each. At the beginning of each session, subjects received verbal instructions about the motor and perceptual task that they were to perform. This was followed by a series of practice trials, after which data collection began. Many of the experimental methods have already been published (Williams et al. 1998); a brief recapitulation as well as a description of salient differences is included below.

**Motor task**

In trials involving movement, subjects were asked to actively abduct the right index finger (D2) as soon as possible after the illumination of a visual GO cue within a discrete 2-s “trial” period (see following text) (see also Fig. 1C in Williams et al. 1998). Subjects initiated the movement from a relaxed, neutral position and produced an abduction of at least 15° and no more than 45° (Fig. 1A, Williams et al. 1998). In trials not involving movement (rest trials), the digit remained in the neutral position for the duration of the trial.

**Perceptual tasks**

The detection task was identical to the one described in Williams et al. 1998. The stimulus consisted of a single, 2-ms, constant-current pulse applied via surface electrodes to the glabrous skin of the middle and distal phalanges of D2. Subjects were asked to report whether or not they detected the occurrence of a stimulus within a trial period; 90% of trials contained a stimulus, while 10% did not (catch trials). No information regarding the proportion of trials with or without a stimulus was given to the subjects, and no feedback was given with regard to the accuracy of subject’s perceptual judgements. Although the experimental design was not strictly bias independent, we have shown that the same results are obtained using a bias-independent two-alternative forced-choice version of the task (Williams et al. 1998). The shorter and simpler trials reduced the effects of memory and fatigue on the results. Five different electrical stimulus intensities were tested in separate blocks of trials. The lowest stimulus intensity produced detection at rest of approximately 90% of stimuli (\( P_{90} \)) (current range 0.55–1.12 mA); this was estimated as in the previous paper by using the method of Wetherill and Levitt (1965). Four multiples of this current intensity were also examined: \( 1.25 \times P_{90} \), \( 1.5 \times P_{90} \), \( 1.75 \times P_{90} \), and \( 2 \times P_{90} \). All nine subjects that participated in the detection experiments were tested at every intensity. The order of testing for different intensities was counterbalanced between subjects. Data gathered at \( 1 \times P_{90} \) is a subset of a previously published 41-subject data set (Williams et al. 1998). Perceptual performance in the subset was not significantly different from perceptual performance in the complete data set (\( P > 0.05 \), Kolmogorov-Smirnov test).

In the scaling task, subjects were asked to rate the intensity of a single 2-ms constant current electrical stimulus delivered to the glabrous skin of the middle and distal phalanges of D2 on a continuous numeric scale. Two stimulus intensities were tested: \( 2 \times P_{90} \) (5 subjects, current range 1.4–1.76 mA) and \( 3 \times P_{90} \) (3 subjects, current range 1.98–2.22 mA). The \( 2 \times P_{90} \) stimulus intensity was chosen because data from the detection experiments showed that this was the lowest intensity at which the vast majority of stimuli were perceived during performance of the movement task. The higher stimulus intensity was included to examine the effect of increasing intensity on scaling during movement. Each subject was tested using only one stimulus intensity. A stimulus of identical intensity was delivered in every trial. Subjects were told that “in each trial, a stimulus may or may not be delivered and that the intensity of the stimulus may or may not vary from trial to trial”. Subjects were completely free to choose the rating values they desired, including fractions and decimals if they preferred, and were told to use an open scale, i.e., no fixed maximum or minimum. Subjects established their scale in a series of practice trials before data collection began. No scaling performance feedback was given at any time during the practice trials or the experiments.

**Experimental design**

The position of D2, as well as EMG activity from first dorsal interosseous (1st DI), were recorded during each trial. Data were collected in discrete trials lasting 2 s each. Each trial consisted of a 500-ms preperiod, followed by the illumination of the GO cue (Fig. 1C, Williams et al. 1998) and a 1,500-ms observation period. Before each trial, subjects were verbally instructed whether or not to move. At a variable time thereafter, the trial was initiated by the experimenter (inter-trial interval, 1–10 s). The GO cue served two purposes: a signal for subjects to perform the appropriate perceptual task and a signal to initiate a movement in the movement trials. After the GO cue was turned off, subjects were asked in the detection experiments to report verbally whether or not they had detected a stimulus. In the scaling experiments, the subjects were asked to verbally rate the intensity of the stimulus. Responses were stored along with the rest of the trial data. Approximately 75% of trials involved movement. In the remaining 25% the subject remained immobile, providing a running estimate of perceptual performance at rest for both the detection and scaling tasks. All trials were initiated with D2 in the same position (relaxed, neutral position). Three trial types were used in the detection experiments: movement + stimulation trials, rest + stimulation trials, and catch trials (no stimulus, movement or rest). Two trial types were used in the scaling experiments: movement + stimulation trials and rest + stimulation trials. To sample variations in perceptual performance over time for each perceptual task, nine different stimulus presentation delays were used at each stimulus intensity. All trials at a given delay were performed before another delay was tested; the order of testing for the various stimulation delays was randomly determined and varied from inten-
Intensity was varied were evaluated for movement calculated for each stimulus intensity using combined data from all (movement proportion of stimuli perceived for each of the three trial types intensity on performance in the experiments.

For each stimulus intensity, the overall means using combined data from all subjects were also calculated. The existence of significant inter-intensity differences in these parameters, which could be seen in the initial 500 ms of the trial (prior to the GO cue) were eliminated from further analysis. For each subject and stimulus intensity, the mean value for each of these parameters was calculated. For each stimulus intensity, the overall means using combined data from all subjects were also calculated. The existence of significant inter-intensity differences in these parameters, which could affect perceptual performance (Angel and Malenka 1982; Chapman et al. 1996; Williams et al. 1998), were evaluated using two-way ANOVA (level of significance, \( P < 0.05 \)) for the detection experiments and t-tests (level of significance, \( P < 0.05 \)) for the scaling experiments.

To provide an overview of the effect of movement and stimulus intensity on performance in the detection experiments, the overall proportion of stimuli perceived for each of the three trial types (movement + stimulation, rest + stimulation, catch trials) was calculated for each stimulus intensity using combined data from all subjects. Significant changes in detection performance as stimulus intensity was varied were evaluated for movement + stimulation, rest + stimulation trials.

### TABLE 1. Temporal and kinematic parameters describing the performance of the motor task in the detection experiments and the results of ANOVAs comparing values across the 5 stimulation intensities

<table>
<thead>
<tr>
<th>Movement-Related Parameter</th>
<th>Mean Response</th>
<th>ANOVA*</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>( F )</td>
<td>( P )</td>
</tr>
<tr>
<td>Temporal, ms</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RT</td>
<td>239 ± 43</td>
<td>1.32</td>
</tr>
<tr>
<td>1st DI EMG onset</td>
<td>200 ± 45</td>
<td>1.50</td>
</tr>
<tr>
<td>EMG lead time</td>
<td>38 ± 7</td>
<td>0.51</td>
</tr>
<tr>
<td>Movement duration</td>
<td>179 ± 45</td>
<td>0.45</td>
</tr>
<tr>
<td>Kinematic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peak amplitude, °</td>
<td>34 ± 5</td>
<td>4.15</td>
</tr>
<tr>
<td>Peak velocity, °/s</td>
<td>440 ± 100</td>
<td>1.93</td>
</tr>
<tr>
<td>Peak acceleration, °/s²</td>
<td>6900 ± 1400</td>
<td>0.36</td>
</tr>
</tbody>
</table>

Results for 45 experiments and 9 subjects. Values are means ± SD. 1st DI, first dorsal interosseous; ANOVA, analysis of variance; D2, digit two; EMG, electromyogram; RT, reaction time. * \( df = 8, 4, 44 \). † Significant interintensity difference, range 32° (\( P_a \)) to 36° (1.5 \( P_a \)). ANCOVA showed no significant intensity-dependent trend for peak amplitude (\( df = 1, P = 0.79 \)).

To analyze the effect of movement and stimulus intensity on scaling performance, only trials in which a stimulus was perceived were retained (see Results). For each subject, the magnitude estimate in each trial was normalized by dividing the response by the mean magnitude estimate of the rest + stimulation trials. This approach allowed data from different subjects (using different absolute scales) to easily be compared and pooled while preserving the relative changes in reported stimulus magnitude over time and stimulus intensity. Data from all subjects at each stimulus intensity was pooled, and the mean proportion of stimuli detected along with the 95% confidence intervals in movement + stimulation and rest + stimulation trials (trials with no stimulation, with or without movement) were performed at each delay (minimum of 22 trials/intensity). Catch trials were retained for scaling experiments (minimum of 20 trials/intensity).

Thus for each detection experiment, a minimum of 198 trials were recorded, and for each scaling experiment, a minimum of 180 trials were recorded.

Data analysis

As described in Williams et al. (1998), an automatic algorithm calculated movement onset, duration, and amplitude along with peak velocity and peak acceleration for each trial. In addition, an interactive algorithm attempted to minimize total squared error between the model and actual data. The fitting descriptions were evaluated by comparing the total squared error where no time-dependent reductions were observed, while logistic functions were tested as they provided better descriptions of time-dependent reductions in detection. The fitting algorithm attempted to minimize total squared error between the descriptive function and the data points. The goodness of fit of the linear and logistic descriptions was evaluated by comparing the total squared error between the model and actual data to the appropriate \( \chi^2 \) distribution [df = number of points that defined perceptual performance at the site – (number of parameters in the fitting equation + 1)].

The best fitting model (linear or logistic) was retained if it provided an adequate description of the data, i.e., if the probability of obtaining the observed amount of total squared error was more than 0.05. If a linear model was retained, the presence of a slope significantly different.
from zero was evaluated using a t-test. If a logistic descriptor was retained, four parameters were determined: the maximum predicted perceptual performance, the minimum predicted perceptual performance, the peak slope (measure of the peak rate of decrease in perceptual performance), and the timing of the peak slope (the time at which perceptual performance decreased most rapidly). Since movements were of varying duration (defined in this study as the time needed to reach peak amplitude), the shortest movement duration was determined for each stimulus intensity and only data up to the end of the shortest movement were fitted.

For the data gathered in the detection task experiments, the effects of intensity on the logistic parameters described in the preceding text were evaluated using correlation coefficients (adjusted for the number of parameters used to fit the data) and F tests to determine the best fitting between a linear and a logistic model for parameters constrained to the interval [0,1]. Polynomial functions were also considered for variables not limited to this interval.

RESULTS

Performance of the motor task

A total of 45 detection and 8 scaling experiments were performed in 17 subjects. Before examining intensity-related differences in perceptual performance, the possibility that the movements themselves might have varied when stimulus intensity was changed was evaluated. For detection experiments, all movement-related kinematic and timing parameters (Table 1) but one, mean peak amplitude, showed no significant change across the five stimulus intensities. Peak amplitude varied significantly (P = 0.01) but very little in absolute terms (32–36%), and the amplitude did not covary with stimulus intensity (ANCOVA). For the scaling experiments, comparisons between the two stimulus intensities for the movement kinematic and timing parameters were also made. No significant difference was seen except for peak velocity, which was significantly higher at intensity 2 × P90 as compared with intensity 3 × P90 (t-test, P < 0.05).

First DI EMG activity preceded movement onset by 38 ms on average and, as was seen previously (Williams et al. 1998), was highly correlated with movement onset (r = 0.98). The fact that 1st DI EMG preceded and was highly correlated with the onset of movement is consistent with 1st DI being the major agonist of the abduction movement studied here.

Performance of the detection task

Table 2 summarizes the global detection performance of all subjects in the rest + stimulation, movement + stimulation, and catch trials. At intensity 1 × P90 (approximately 90% detected at rest, see METHODS), subjects actually detected 94% of stimuli delivered at rest, a result similar to the detection performance reported previously at this stimulus intensity (Williams et al. 1998). At all other stimulus intensities, detection performance was higher (99–100%). As a result of this difference, a two-way ANOVA found a significant inter-intensity difference in the proportion of stimuli perceived at rest, and an ANCOVA showed a significant correlation between stimulus intensity and the proportion of stimuli perceived at rest (see legend for details).

To determine whether practice or fatigue significantly altered detection performance over the course of the experiments, perceptual performance in the first 10% of rest + stimulation trials was compared with perceptual performance in the last 10% of rest + stimulation trials for each stimulus intensity. No significant differences were observed at any of the stimulus intensities (P > 0.01, Fisher exact probability test).

Of 747 catch trials (all detection experiments combined), only 4 false-positive responses were noted (0.5%), indicating that subjects used a very conservative response strategy throughout the series of experiments. As detailed in the legend for Table 2, no stimulus intensity was associated with significantly more false positives than any other.

Significantly fewer stimuli were detected during movement for all five stimulus intensities, as compared with detection performance at rest (P < 0.001, Fisher exact tests). Subjects perceived 62% of the stimuli presented during movement + stimulation trials. A two-way ANOVA (Table 2) showed that there was significant inter-intensity variability in perceptual performance for movement + stimulation trials, while an ANCOVA demonstrated the existence of a positive correlation between stimulus intensity and detection performance during movement trials.

Table 2. Detection experiments: perceptual performance in the three trial types as a function of the stimulus intensity

<table>
<thead>
<tr>
<th>Stimulation Intensity × P90</th>
<th>Proportion of Positive Responses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest + stimulation*</td>
<td>Movement + stimulation*</td>
</tr>
<tr>
<td>1.0</td>
<td>0.94 (0.88, 0.97)</td>
</tr>
<tr>
<td>1.25</td>
<td>1.00 (0.99, 1.00)</td>
</tr>
<tr>
<td>1.5</td>
<td>0.99 (0.98, 1.00)</td>
</tr>
<tr>
<td>1.75</td>
<td>0.97 (0.97, 1.00)</td>
</tr>
<tr>
<td>2.0</td>
<td>1.00 (0.98, 1.00)</td>
</tr>
<tr>
<td>Overall</td>
<td>0.98 (0.97, 0.99)</td>
</tr>
</tbody>
</table>

Results from 45 experiments, 9 subjects (95% confidence intervals in parentheses). * Two-way ANOVAs showed that there was significant inter-intensity variation in perceptual performance during rest + stimulation trials (df = 8, 4; 4; F = 12.35; P < 0.0001) and movement + stimulation trials (F = 49; P < 0.0001) but not catch trials (F = 0.51; P = 0.73). ANCOVA showed that perceptual performance increased with intensity for both the rest + stimulation trials (F = 13; P = 0.001) and the movement + stimulation trials (F = 152; P < 0.0001). † Performance during movement + stimulation trials was significantly lower than performance during trials at rest for each stimulus intensity (P < 0.001, Fisher exact test for a 2 × 2 contingency table).

Time- and intensity-dependent changes in the detection of stimuli

Detection performance data from individual subjects were first pooled into 40-ms bins relative to EMG or movement onset. ANCOVAs demonstrated that both stimulus timing and intensity explained a significant portion of the variance present in the data (P < 0.001), while inter-subject differences explained <0.5% of the variation accounted for by the ANCOVA (P > 0.01). Since the contribution of inter-subject differences to performance was small, all trials from all subjects for a given stimulus intensity were pooled for further analyses.

Using the pooled data, detection performance was plotted relative to the time of EMG onset and movement onset for all five stimulus intensities. Given the high correlation between EMG onset and movement onset (preceding text), the move-
ment onset curves were almost identical to the EMG onset curves, except for a 40-ms shift in the timing values that corresponded to the lead time between EMG onset and movement onset. Consequently, only curves plotted relative to EMG onset are presented. Figure 1 shows the effects of D2 movement on the ability to detect stimuli applied to the moving digit over time at each of the five intensities tested. Logistic functions were retained to describe detection performance over time at all five stimulus intensities, and are also shown on Fig. 1. At the lowest intensity (1 × P90, Fig. 1A) only, maximum performance in the three earliest bins (−110 to −70 ms) was approximately 10% lower on average than performance at rest, with two of the three bins having detection performance significantly different from that at rest (●). The maximum
detection performance estimated by the logistic function which best described the $1 \times P_{90}$ data was only 0.82. We previously argued that this early decrease reflected a non-time-dependent reduction in detection performance (Williams et al. 1998). When stimulus intensity increased modestly to $1.25 \times P_{90}$ (Fig. 1B), detection performance in the earliest bins ($-110$ to $-70$ ms) was close to that seen at rest (○ in all 3 bins, 0.98 estimated maximum detection performance in movement + stimulation trials), suggesting that the non-time-dependent reduction in detection was no longer present. Similar results were obtained at all other intensities (Fig. 1, C–E). A time-dependent decrease in detection, on the other hand, was observed at all stimulus intensities. At all but the highest stimulus intensity, detection performance was seen to decline precipitously around the time of EMG onset, with the timing of the peak decrease occurring within the bin immediately preceding EMG onset at $1 \times P_{90}$ and the bin immediately following EMG onset at all other intensities tested. At the highest intensity ($2 \times P_{90}$), a modest decrease in detection performance could still be observed at approximately the time of EMG onset (Fig. 1E), with a small but significant reduction in detection being observed in the initial 80 ms after EMG onset (●).

A partial rebound in detection performance appeared to occur for stimuli delivered more than 100 ms after EMG onset, especially at the higher stimulus intensities. When detection performance was compared across the first and second 100 ms after EMG onset (Table 3), significantly more stimuli were perceived in the later interval at the three highest stimulus intensities. Rebounds in detection performance appeared to coincide with the time at which peak movement velocity was attained ($92 \pm 11$ ms).

### Table 3. Detection performance after EMG onset

<table>
<thead>
<tr>
<th>Stimulation Intensity ($\times P_{90}$)</th>
<th>$t = 1$–100 ms</th>
<th>$t = 101$–200 ms</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>0.05 (0.03, 0.08)</td>
<td>0.03 (0.01, 0.05)</td>
</tr>
<tr>
<td>1.25</td>
<td>0.11 (0.07, 0.15)</td>
<td>0.14 (0.10, 0.20)</td>
</tr>
<tr>
<td>1.5</td>
<td>0.26 (0.21, 0.31)</td>
<td>0.40 (0.34, 0.47)*</td>
</tr>
<tr>
<td>1.75</td>
<td>0.44 (0.38, 0.49)</td>
<td>0.55 (0.48, 0.62)*</td>
</tr>
<tr>
<td>2.0</td>
<td>0.90 (0.86, 0.94)</td>
<td>0.96 (0.93, 0.98)*</td>
</tr>
<tr>
<td>Overall</td>
<td>0.34 (0.32, 0.37)</td>
<td>0.42 (0.39, 0.45)*</td>
</tr>
</tbody>
</table>

Results from 45 experiments, 9 subjects (95% confidence intervals in parentheses). * Significantly more stimuli were detected in the second 100-ms interval after EMG onset as compared to the first 100 ms after EMG onset ($P < 0.01$, Fisher exact test for a $2 \times 2$ contingency table).

### Modeling the contribution of stimulus timing and intensity on detection performance during movement

To describe the effects of stimulus intensity on detection performance in a manner similar to that used to describe the effect of stimulus location in the previous paper (Williams et al. 1998), the logistic function parameters detailed in Fig. 1 are plotted as a function of stimulus intensity in Fig. 2. Intensity-dependent trends were described using the best fitting of a variety of models (see METHODS). The timing of peak decreases in detection performance (Fig. 2A) was accurately modeled by a second-order polynomial ($P < 0.01$, not shown), but this function was not monotonic over the range of intensities studied, and peak decreases were all within ±12 ms of EMG onset, i.e., within the 20-ms temporal resolution of the analysis. A logistic function provided the best fit for minimum estimated detection performance over a wide range of detection performance values (Fig. 2B). Variation in the peak slope could not be modeled successfully. $R^2_A$, coefficient of determination adjusted for the number of parameters in the fitted equation.
be modeled successfully (Fig. 2C). In the case of maximum estimated detection performance (Fig. 2D), the fitted logistic function was essentially a straight line with a slight inflection at the lowest stimulus intensity.

Based on the results of the preceding analyses, a model of detection performance during movement stimulation trials that incorporated the importance of stimulus timing and stimulus intensity was created (Fig. 3). The detection data during the movement trials were used to define a surface, presented in Fig. 3A. This representation permitted a visualization of modifications in detection performance for all intensities at any given time. A model surface (Fig. 3B) was then fitted to the surface created by the detection data. The equation for the model surface was constructed using the following reasoning, as in Williams et al. (1998). Since logistic functions provided a good description of the effects of time on the proportion of stimuli detected (Fig. 1) and of intensity on both maximum and minimum detection performance (Fig. 2, B and D), this type of function was again used to model these effects (Eqs. 1–3, following text). Several different models were tested for the timing of peak decreases, including fixing the timing of peak decreases at EMG onset, fitting the timing of peak decreases to a constant value different from EMG onset, and varying the timing of peak decreases linearly with stimulus intensity. Even when allowed to vary, the timing of peak decreases remained within ±1.5 ms of EMG onset at all intensities. The very small changes in the timing of peak decreases led to a very small reduction in total error (less than 5%) which did not justify the added variables necessary to implement them. The model used to generate Fig. 3B is detailed in Eq. 4, where $F_{int}$ represents the time- and intensity-dependent proportion of stimuli perceived, $i$ represents time (ms), and $k$ represents stimulus intensity.

Intensity-dependent change in maximum predicted detection performance

$$Int_{maxLogistic}(k) = \frac{1}{1 + e^{-0.54 (k - 0.74)}}$$

FIG. 3. A–C: surfaces showing time- and intensity-dependence of perceptual performance. A: pooled performance data during movement trials (z axis) plotted as a function of time relative to EMG onset (x axis) and stimulus intensity (y axis). B: best-fit model surface for the data shown in A. The timing of peak decreases in performances was modeled as constant (at $t = 0$) for this surface. The model surface was not significantly different from the actual performance data ($P > 0.05$). C: contour map of the squared error between the surfaces plotted in A and B, showing areas of poorest fit.
Intensity-dependent change in minimum predicted detection performance

\[ \text{IntminLogistic}_{i0} = 1/[1 + e^{-(5.75i+0.085i)}] \]  

Time-dependent component (modifies detection performance over time)

\[ \text{InttimeLogistic}_{i0} = 1/[1 + e^{(0.05i)}] \]

Global equation

\[ \text{Fin}(t_{AB}) = \text{IntmaxLogistic}_{i0}\text{IntminLogistic}_{i0} + \text{InttimeLogistic}_{i0}(1 - \text{IntminLogistic}_{i0}) \]

The model surface was not significantly different from the surface generated by the actual data \((P > 0.05)\). The total squared error between the surface described by the detection data and the surface described by the model was 0.34, and the peak squared error was <0.035 (Fig. 3C). The maximum estimated detection performance over the model surface was 1.0, i.e., 100% detected. The minimum estimated detection performance over the model surface was 0.01, though it increased sharply as intensity increased, reaching 0.8 at the highest intensity over the time period considered by the model, therefore adequately describing the effect of stimulus intensity on minimum detection performance as detailed in Figs. 1 and 2B. The model was a concise and accurate description of the experimental results, which could be combined with a previous model (Williams et al. 1998) describing the effect of stimulus location and timing on detection performance to generate quantitative predictions of detection performance during movement (see DISCUSSION).

Time- and intensity-dependent changes in scaling

Subjects perceived and scaled 94% of stimuli delivered during movement + stimulation trials at intensity \(2 \times P_{90}\) and all of the stimuli delivered at intensity \(3 \times P_{90}\). For both stimulus intensities, the mean magnitude estimates in the first and last 10% of the rest + stimulation trials were not significantly different.

Normalized magnitude estimates during movement + stimulation trials were significantly lower than magnitude estimates during rest + stimulation trials at both stimulus intensities \((t\text{-test}, P < 0.001)\), averaging 0.64 ± 0.01 at \(2 \times P_{90}\) and 0.75 ± 0.01 at \(3 \times P_{90}\). A significantly greater relative decrease in magnitude estimates was seen at intensity \(2 \times P_{90}\) than at intensity \(3 \times P_{90}\) \((t\text{-test}, P < 0.001)\).

Magnitude estimates from the movement + stimulation trials were pooled and plotted relative to EMG onset, and logistic functions were fitted (Fig. 4, A and B). The relative intensity of the stimuli delivered earliest relative to EMG onset was more affected at \(2 \times P_{90}\) (maximum rating estimated by the logistic function of only 0.81) than at \(3 \times P_{90}\) (estimated maximum rating: 0.97). Time-dependent decreases in magnitude scaling were observed at both \(2 \times P_{90}\) and \(3 \times P_{90}\). Stimuli presented after EMG onset were rated lower than those perceived before EMG onset at both intensities \((t\text{-test}, P < 0.001)\). At both intensities, peak decreases in scaling values occurred within 10 ms of EMG onset.

Since intensity was rated on a continuous scale, a second analysis was performed on the unbinned data to determine if the data reduction, into 20-ms bins, contributed to the lack of difference in the timing of the peak decrease across the two intensities. The unbinned data were fitted to a third-order polynomial function. The results were similar to those obtained with the binned data using logistic functions: the peak decrease was slightly later for the data obtained at \(2 \times P_{90}\) (estimated maximum rating: 0.97). This observation suggests that the similarity in the timing of the peak decrease in magnitude estimates across two intensities of stimulation could not be explained by a lack of sensitivity introduced by the data reduction.

DISCUSSION

The results of the present study demonstrated that time-dependent and movement-related decreases in tactile detection occurred during a simple abduction movement for stimuli in an intensity range spanning from 1 to \(2 \times P_{90}\). Increasing the stimulus intensity decreased the magnitude of the movement-related decrease in detection but had relatively little effect on the timing of the decrease, with peak decreases in detection always occurring within ±12 ms of EMG (25–45 ms before
movement onset). The subjective intensity of stimuli perceived during movement was also decreased, and this in a time- and intensity-dependent manner that was similar to that observed for changes in detection.

**Methodological considerations**

As discussed in Williams et al. (1998), the electrical stimuli used in this series of experiments represented a reliable, reproducible, easily calibrated source of peripheral afference, identical in all respects but intensity to those used to gather data in a previous series of experiments (Williams et al. 1998). Using these stimuli, subjects consistently detected almost all stimuli delivered during rest trials, while producing a negligible false-positive rate, thus essentially behaving as “perfect receivers” and making analysis and comparisons of detection performance during the motor task relatively simple. The lack of false-positive responses in this experimental paradigm makes it difficult to distinguish whether changes in detection during movement trials reflect changes in stimulus signal-to-noise (S/N) ratio or changes in subject response criterion (see Mechanisms underlying the time-dependent decrease in perception).

Consistent with previous observations (Williams et al. 1998), the onset of 1st DI EMG always preceded movement onset and was highly correlated with movement onset. First DI EMG represented the earliest easily observable response to the motor command and thus an appropriate reference point for evaluating the timing of decreases in perceptual performance during movement. Practice and fatigue effects did not appear to play a significant role on perceptual performance at rest in stimuli detected, this restriction did not apply to the scaling performance. In the case of the data presented in this study, increases in movement amplitude, peak velocity, and peak acceleration are all associated with decreases in the proportion of stimuli detected (Angel and Malenka 1982; Chapman et al. 1996; Rauch et al. 1985; Williams et al. 1998); this must be considered a potential confounding factor when comparing detection or scaling performance. In the case of the data presented in this study, kinematic parameters varied little over the different intensities tested, and the differences in perception across different stimulus intensities could not be explained by any systematic change in movement kinematics.

**Stimulus intensity and detection performance**

The results of this study confirm our previous observation that stimulus timing relative to EMG or movement onset is a key variable in determining detection performance during movement. They extend these observations by showing that the magnitude of the decrease in detection performance after EMG onset is graded as a function of stimulus intensity. At the lowest intensity (1 × P90), only 5% of stimuli were detected in the initial 100 ms after EMG onset; as intensity was increased, performance gradually improved so that 90% of stimuli were detected at the highest intensity tested (2 × P90). The intensity-dependent increase in stimulus detection after EMG onset is consistent with previous observations that detection threshold is elevated during motor activity (Chapman et al. 1987; Post et al. 1994). The results also showed that the timing of the peak decrease in detection was relatively invariant over the range of intensities tested, always falling within ±20 ms of EMG onset, on average about 40 ms before movement onset. While we cannot rule out the possibility that we may have missed more subtle differences in timing because of the 20-ms bin size, several observations suggest that this was not an important factor. First, analyses applied to the original 42-subject data set reported in Williams et al. (1998) gave identical results when a smaller bin size was used (peak decrease at −7 ms for 10-ms bins vs. −8 ms for 20-ms bins). This led us to employ 20-ms bins in all analyses, allowing us to maintain a reasonable number of trials/bin especially for experiments with smaller data sets (no. of trials/bin >30 for all data reported here). Second, the same bin size was used in our previous study (Williams et al. 1998), and the method was sufficiently sensitive to show a 60-ms change in the timing of the peak decrease as a function of distance between the moving digit and the site of stimulation (D2 to pectoral girdle). The same bandwidth was also employed in evoked potential studies (Chapman et al. 1988), and significant differences in timing were demonstrated (e.g., active vs. passive movement, peripheral vs. central stimulation). Third, while the categorical nature of the response in the detection experiments (yes or no) required some form of binning to generate estimates of the proportion of stimuli detected, this restriction did not apply to the scaling data (continuous scale). In the latter case, similar timing values were obtained with and without binning (see RESULTS). Together, these observations suggest that our finding of timing invariance across the range of intensities tested was most likely a robust observation.

These timing values are in agreement with the apparent timing of peak decreases observed using single stimulus intensities in studies that employed psychophysical (Coquery 1978; Coquery et al. 1971), evoked potential (Chapman et al. 1988; Morita et al. 1998) or single-cell methodologies (Jiang et al. 1991). The relative invariance in the timing of peak decreases across a range of stimulus intensities is an interesting contrast with the results obtained from experiments in which stimuli of identical intensity were delivered to sites at different distances from the moving digit (Williams et al. 1998). In the latter experiments, the timing of the peak decrease shifted by as much as 60 ms as distance increased (D2 to pectoral girdle). This difference may reflect differences in the mechanisms by which movement-related gating influences lessen as intensity or distance increases.

The present results demonstrate that differences in stimulus intensity strongly affect the amplitude of movement-related gating and so resolve some of the differences in the amplitudes of reductions reported in the literature. However, changes in stimulus intensity did not affect the timing of these reductions. Several factors probably explain differences in the values reported in the literature with regards to the timing of the onset of movement-related gating of tactile afference (see Introduction). The first factor is the physical relationship between the body part in motion and the site of stimulation, which affects the timing of movement-related decreases in detection as detailed in Williams et al. (1998). Most studies applied stimuli to the moving body part, and we have shown that gating of perception is strongest and earliest in this case. Although our results were restricted to movements of the digit, we have made similar observations for movements about the elbow, both when stimuli were applied to the forearm and when
stimuli were applied to D2 (S. R. Williams, J. Shenasa, and C. E. Chapman, unpublished observations). The second factor is the variable temporal resolution of previous studies, with some reported time courses based on binwidths as wide as 100 ms (e.g., Cohen and Starr 1987). The third factor is variation in the stimulus intensity used in the different studies, experimental paradigms using near-threshold stimulus intensities being more affected by non-time-dependent effects (see following text) and thus generating much earlier estimates of the onset of movement-related gating. The fourth, and related, factor is methodological. In the present study, we concentrated on timing the more robust peak decreases in detection, rather than the first reduction in detection or response amplitude, as in most previous studies (e.g., Chapman et al. 1988, Cohen and Starr 1987). This approach was based on the assumption that the detection function over the interval being modeled is monotonic. Concentrating on the timing of peak reductions in perceptual performance has the advantage of being insensitive to the non-time-dependent decrease seen at the lowest stimulus intensity and avoided the inherent difficulty of attempting to define the first and therefore smallest significant change in detection. Our timing values were based on the largest, and therefore the easiest to measure/identify, change in perceptual performance. Finally, many previous studies have reported the onset of gating relative to movement onset. The results of companion experiments (unpublished observations) indicate that measuring the onset of gating relative to the onset of EMG activity rather than movement onset minimizes differences in timing when comparing results across different motor tasks.

A partial rebound in detection performance began after peak movement velocity was attained (more than 100 ms after the onset of EMG), but the time course of this recovery was not determined because subject behavior was not specified after reaching the criterion amplitude: some subjects maintained D2 abduction, while others actively returned to the start position and others relaxed and so resumed the neutral position. The relatively rapid rebound in detection performance seen with this experimental paradigm is earlier than that observed in previous studies. Recovery in somatosensory evoked potentials has been reported approximately 400–500 ms after the end of movement-related EMG (Angel et al. 1986; Cohen and Starr 1987). Detection and scaling performance has also been seen to recover in the seconds following the end of a finger movement (Schmidt et al. 1990) and 900 ms after the onset of isometric jaw contractions (Kemppainen et al. 1993). The more rapid rebound in detection performance seen in this study may be a function of stimulus intensity and/or motor-task parameters. It could be hypothesized that this rebound in detection coincides with decreases in peripheral movement-related reafference as the movement slows and/or the end of the motor command, since many motor cortical units show a burst that ends at peak velocity in a similar motor task (e.g., Lamarre et al. 1980).

In summary, the present results show that tactile detection is decreased but not abolished during movement, with the minimum proportion of stimuli perceived during movement-related gating increasing as a function of stimulus intensity. The time course of the movement-related gating of detection is invariant across a range of stimulus intensities.

**Stimulus intensity and scaling**

The perceived magnitude of suprathreshold stimuli was found to be reduced in the movement + stimulation trials. This is in agreement with some previous investigations (Coquery et al. 1971; Milne et al. 1988; Post et al. 1994) using both electrical and vibrotactile stimuli but not with others (Chapman et al. 1987). Post et al. (1994) suggested that the amount of cutaneous feedback generated during the motor task is a key factor for observing movement-related decreases in magnitude estimates. The present findings suggest that the intensity of the test stimulus is also a critical factor. We found that stimuli of higher intensity showed less relative reduction in magnitude than stimuli of lesser intensity. Consistent with this, a previous study (Chapman et al. 1987) that did not observe decreases in perceived magnitude employed intensities at far greater multiples of threshold than the stimuli used here (up to 10× detection threshold). The timing of the peak decrease in subjective intensity was similar to the timing of the reduction in detection performance for stimuli of lower intensity, with the peak decrease occurring within ±1 bin (20 ms) of EMG onset. Similar results were obtained with unbinmed data. These results argue in favor of the reduction in magnitude for suprathreshold stimuli being mediated by similar mechanisms as reductions in detection for stimuli of lower intensity. Contrary to the results with the detection task, no recovery in scaling was observed in the later bins. This may reflect a modest difference in sampling: the time of peak velocity was later in the scaling experiments (110 vs. 92 ms after EMG onset in the detection experiments), and data in the scaling task were not available for as long after EMG onset (160 ms after EMG onset vs. 200 ms for detection tasks). Alternatively, scaling performance may simply return to normal more slowly after the end of movement. A differently designed motor task, as well as later sampling, would need to be distinguished between these two possibilities.

**Mechanisms underlying the time-dependent decrease in perception**

Signal detection theory (Green and Swets 1988) provides a framework for systematic analysis of the mechanisms underlying changes in detection performance. Using this approach, reductions in stimulus detectability may reflect changes in one or several of three factors: noise level, signal strength, and response criteria. Which of these three factors can be implicated in movement-related time-dependent reductions in detection?

The first factor to be considered is noise level. Afferent noise is probably increased during movement; signal detection theory predicts that an increase in noise will produce an increase in the false positive rate and no change in the proportion of stimuli detected. However, our results show no increase in the false-positive rate and reduced stimulus detection during movement trials. This suggests that an increase in noise cannot in and of itself explain our experimental results.

The second factor is signal strength. Detailed studies in monkeys of SI evoked responses to cutaneous stimulation (intensity sufficient to elicit a large response at rest) have shown that response amplitude is decreased to an average 37–46% of control during movement (Chapman et al. 1988;
Jiang et al. (1991). The time course of these decreases is similar to that reported here for decreases in stimulus detection. These electrophysiological observations (see Introduction for other references) suggest that the transmission of peripheral signals to SI cortex is subject to a marked attenuation, or gating, during movement. Given the similarity in the time course of the modulation to that reported in the present study, it is possible that observed movement-related changes in stimulus detection reflect a decrease in the amplitude of the central signal generated by the applied stimuli. Our magnitude estimation results can also be explained by a decrease in central response amplitude. Interestingly, as our magnitude estimation data were based on normalized stimulus intensities, if perceived intensity was proportional to the S/N ratio, then reductions in perceived intensity during movement should have been independent of stimulus intensity [normalized intensity = \( \frac{S}{N_{\text{rest}} + N_{\text{movement}}} \)] / (S/N\text{rest}) = \[ N_{\text{rest}}/(N_{\text{rest}} + N_{\text{movement}}) \], where S = signal strength, \( N_{\text{rest}} = \) noise at rest, and \( N_{\text{movement}} = \) extra noise generated during movement). The fact that they were not demonstrates that perceived magnitude is not equivalent to the S/N ratio.

The third factor to be considered in a signal detection theory analysis is changes in the response criterion. Observed changes could reflect a systematic, movement-related change in response criterion on the part of the subjects. Several observations argue against this interpretation. First, we obtained identical results using a bias-independent two-alternative forced-choice procedure, in which each trial consisted of two observation intervals, one with and one without the stimulus (see Fig. 3, Williams et al. 1998), and the subjects were required to identify which interval contained the stimulus. The time course for the movement-related decrease in detection was identical to that seen using our experimental approach, and this in the same subjects. Second, we also showed that there was no movement-related decrease in detection of stimuli at 1 \( \times P_{90} \) when stimuli were applied to a site distant from the moving digit (contralateral D2, contralateral shoulder, ipsilateral leg) (Williams et al. 1998). This observation suggests that the effects seen at sites closer to the movement could not be attributed to the imposition of two tasks on the subjects. For all sites tested (close and distant), subjects had to divide their attention between two tasks (motor and perceptual). Since the time-dependent changes were restricted to the closer sites, then one would have to hypothesize the existence of site-dependent changes in response criterion. We are unaware of evidence suggesting that higher order cognitive processes show such a spatial organization. Third, the results obtained in the scaling experiments—with essentially the same time course as seen in the detection experiments—are consistent with the hypothesis that the time-dependent decrease was produced by a decrease in signal strength rather than a change in response criterion.

In conclusion, reductions in signal strength provide an attractive explanation for our findings. However, although several indirect lines of reasoning argue against the possibility that a change in response criterion (essentially raising the response threshold) contributed to the results, the lack of false positives in our experimental paradigm makes it impossible to exclude this possibility. To formally address this question, further experiments need to be performed in subjects instructed to generate a higher proportion of false positive responses. This would permit a quantitative analysis of the relative contribution of changes in signal strength (gating) versus changes in response criterion to movement-related changes in detection performance. If changes in the response criterion contribute to the results, then the false-positive rate should diminish during movement. On the other hand, it may be for example that threshold shifts are equal to shifts in the noise distribution, thereby confounding the interpretation of the false-positive rate. If this is the case, direct measures of signal strength such as those provided by monkey electrophysiology will further clarify the results, insofar as signal strength is actually measured in the same part of the CNS as that from which the detection “apparatus” samples the signal.

Intensity and non-time-dependent decreases in perceptual performance

We have previously argued that the earliest reduction seen at the lowest stimulus intensity tested (Fig. 1A, significant decreases as early as 140–120 ms before EMG onset) represents a non-time-dependent decrease in detection performance (Williams et al. 1998). A modest (\(<10\%)\), sustained decrease in detection was the only effect seen when stimuli were applied to distant sites (see Introduction), and we attributed the decrease to divided attention because subjects were required to split their attention between two tasks (motor and perceptual). In this study, no evidence of a similar early decrease in detection was observed with stimuli more than 1 \( \times P_{90} \). At all intensities but the lowest one tested, detection performance in the earliest bins during movement + stimulation trials was not significantly different from performance at rest. However, at the lowest intensity tested in the scaling task (2 \( \times P_{90} \)), the perceived magnitude of suprathreshold stimuli delivered quite early (up to 120 ms before EMG onset) was significantly lower than the perceived intensity of stimuli delivered at rest. This result suggests that the same non time-dependent effect which affected detection at 1 \( \times P_{90} \) may still modulate perceived magnitude at higher stimulus intensities, a hypothesis that could be confirmed by performing scaling experiments at more distant sites where it is expected that only a non-time-dependent reduction would be observed.

Predicting the effect of movement on the detection of stimuli

In a previous paper, data were gathered at several stimulation sites using stimuli of intensity 1 \( \times P_{90} \) in subjects performing a motor task identical to the one used in this study. A model was then created that accurately described the effect of distance, expressed in standardized proportions of total body lengths (Contini 1972; National Aeronautics and Space Administration 1978), between the moving digit and the site of stimulation on detection performance (Williams et al. 1998). In Eq. 5 in the following text, the simple model developed in this study to describe the effects of intensity on detection performance (Fig. 3) is combined with the previous model describing the effects of distance on stimulus detection to predict detection performance at combinations of stimulation sites and stimulus intensities that have not been tested experimentally. In this combined model, \( P(i,j,k) \) represents the proportion of stimuli perceived at time \( i \), distance \( j \) and intensity \( k \), \( Fint(i,k) \) is the time- and intensity-dependent model described in this paper (Eq. 4); \( IntmaxLogistic(k) \) corresponds to Eq. 1;
Fdist(i,j) (time- and distance-dependent model) and Max correspond respectively to Eqs. B5 and B4 in Williams et al. (1998). In essence, the intensity-dependent model defines maximum and minimum detection performance for a stimulation site that corresponds to D2 stimulation (j = 0). As the distance between the site of stimulation and the body part in motion increases (j > 0), the proportion of stimuli that remain undetected decreases as a function of the distance-dependent model. To give an idea of the relationship between proportional distances and actual sites on the body, 0 distance corresponds to D2, 0.125 corresponds to the middle of the forearm, 0.25 distance corresponds to the lower third of the upper arm, and 0.425 corresponds to the ipsilateral sterno-clavicular joint; all distances beyond this point correspond to sites that cannot be considered functionally as part of the upper limb.

\[
P(i,j,k) = Fint(i,k) + \left( IntmaxLogistic(k) - Fint(i,k) \right) \times \frac{Fdist(i,0) - Fdist(i,j)}{Max \times Fdist(i,0)} \tag{5}\]

This model makes it possible to predict detection performance at a given time, stimulus intensity, and distance between the moving digit and the site of stimulation. Figure 5 gives examples of the predictions generated by Eq. 5. In Fig. 5A, detection performance over time when stimuli are of intensity 1.5 \( \times P_{90} \) is predicted at distances from the site of stimulation ranging from 0 to 0.5 body lengths. In Fig. 5B detection performance 50 ms after EMG onset is predicted for intensities ranging from 1 to 2 \( \times P_{90} \) and distances from the site of stimulation ranging from 0 to 0.5 body lengths. Detection functions such as those in Fig. 5A, or “psychophysical functions” similar to those in Fig. 5B, can be generated at any distance, intensity, and timing value, producing two-, three-, or four-dimensional prediction arrays, at least within the tested range.

An interesting situation that arises when the two models are combined is the fact that the effect of time on detection performance is modeled twice, once in the intensity model where peak decreases always occur at \( t = 0 \), and once in the distance model where the timing of peak decreases occurs later as distance increases. If this accurately reflects the reality of the distance and intensity effects, two time-dependent equations are appropriate. However, it is also possible that the timing of intensity-dependent decreases varies with distance. If this is the case and shifts in timing over distance are similar in the distance and intensity functions, it may be possible to model the effect of time on detection performance using one equation rather than two. Data from more distant locations at higher stimulus intensities would resolve this question.

For detection performance after EMG onset, the range of stimulus intensities and locations tested was sufficient to sample detection performance over a wide range of values from those approaching zero to those approaching 1 (Fig. 2B). However, for detection performance before EMG onset, distance had no effect while only one stimulus intensity produced a maximum value significantly less than 1 (1 \( \times P_{90} \), Fig. 2D). Therefore for time values less than 0, the current model’s predictions with regards to detection performance as intensity decreases to values less than 1 \( \times P_{90} \) is based on very little information and may need to be adjusted when data from stimulus intensities lower than those tested in our experiments become available. Nonetheless the basic behavior of the model as intensity decreases to values lower than 1 \( \times P_{90} \) is sound: detection performance remains near 0 at time values >0, and also rapidly approaches 0 at time values <0.

In conclusion, the modifications in the timing and/or magnitude of movement-related gating of tactile detection and suprathreshold magnitude estimation described in this paper and the preceding one (Williams et al. 1998) represent the “end result” of all movement-related effects on the transmission and subsequent processing of the stimulus. The combined model provides an accurate description of the timing and intensity of movement-related decreases in tactile detection, makes it possible to clearly define the perceptual consequences of these effects, and therefore defines the requirements that physiological mechanisms brought forward to explain these decreases will have to fulfill. It should be stressed, however, that the model is restricted to the experimental conditions used here (a rapid RT movement of a single joint). In other experimental paradigms, the controls may be altered. One example comes from studies of active touch in which the sensory input to be perceived is generated by the subject during the course of exploratory movements, instead of being externally generated. Although there is some evidence of facilitation of cortical somatosensory evoked responses during exploratory finger movements (Knecht et al. 1993), mixed results have been obtained from studies of perception. Lederman (1981) found no difference in magnitude estimates for roughness of textured...
surfaces when she compared active touch (movement) with passive touch (no movement). In contrast, Blakemore and colleagues (1998) reported that self-generated tactile stimuli (movement) are perceived as less intense than externally generated stimuli (no movement). In addition, the latter reported that neural responses (functional magnetic resonance imaging) were reduced in a number of regions during self-generated stimulation, consistent with the occurrence of sensory gating during active movement. Clearly, further experiments are required to address the relative importance of the type of motor task, and the mode of delivering/generating sensory stimuli, to the controls over the somatosensory system.

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