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Perception of vibrotactile stimuli during motor activity in human subjects

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Abstract Previous studies have shown that voluntary motor activity decreases the ability to detect near-threshold electrical stimuli applied to the skin, but has no effect on the perception of either suprathreshold electrical stimuli or natural thermal stimuli (warmth, heat pain). The present study was undertaken to determine if the perception of natural tactile stimuli (vibrotactile) is diminished by motor activity (rhythmical isometric flexions and extensions about the elbow). The stimuli were applied at three different sites on the operant arm – ventral forearm, thenar eminence and distal digit – to examine also the influence of the proximity of the stimulated site to the active muscles on perception. The ability to detect near-threshold stimuli at the two more proximal stimulation sites was significantly reduced during the motor task, and these effects were more pronounced and widespread with higher levels of target force (20 N vs 50 N). Discrimination of small differences in the intensity of suprathreshold stimuli, at all three sites, was unchanged during the motor task. Finally, the subjective intensity of suprathreshold vibrotactile stimuli was reduced, in a nonlinear fashion, during the motor task; proximity again influenced the degree of modulation. In contrast a previous study showed no change in magnitude estimates of suprathreshold electrical stimuli during isotonic flexion and extension. Some possible reasons for the discrepancy are discussed. In addition, our previous suggestion that movement produces a simple reduction in the signal-to-noise ratio (i.e. the gating signal modelled as a masking stimulus) cannot explain the present results, so more complex models are required.

Key words Cutaneous · Somatosensory system
Psychophysics · Sensory gating · Human

Introduction

There is now considerable evidence indicating that the transmission of cutaneous signals within the dorsal column-medial lemniscal pathway is profoundly diminished, or “gated”, during the course of rapid limb movements (for examples, see Ghez and Lenzi 1971; Chapman et al. 1988; see Jiang et al. 1991 for a more detailed review). It is also clear that this movement-related gating has distinct perceptual consequences. Thus, the ability to detect the presence of weak, near-threshold stimuli is reduced during movement (Coquery et al. 1971; Dyhre-Poulson 1978) and detection thresholds are correspondingly elevated during both active and passive movement (Chapman et al. 1987). Interestingly, parallel observations have also been made in the visual system, where visual thresholds are elevated during the course of saccadic eye movements (Latour 1962; Zuber and Stark 1966) and also during rapid (“saccadic”) displacement of the visual background during fixation (MacKay 1970; Brooks and Fuchs 1975). Such observations indicate that this phenomenon of movement-related gating is of general interest for understanding how sensory information is processed during different behaviours.

The influence of movement on the ability to perceive suprathreshold cutaneous stimuli is, on the other hand, disputed. Discrimination thresholds (the ability to distinguish between two suprathreshold, but similar, stimuli) have uniformly been reported to be unaffected by movement (Lamb 1983; Chapman et al. 1987). Similarly, there is no change in the ability to discriminate between tactile patterns (embossed letters) when these are scanned actively, i.e. subjects moved their digit over a stationary surface, or passively, i.e. the surface moved across the stationary digit (Vega-Bermudez et al. 1991). In contrast, the subjective intensity of suprathreshold cutaneous stimuli (magnitude estimation) has been vari-

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ously reported as diminished (Coquery et al. 1971; Milne et al. 1988) or unaffected by movement (Lederman 1981; Chapman et al. 1987).

Recently, Feine et al. (1990) have reported that the modality of the sensory input is an important factor in determining the perceptual consequences of motor activity. Thus, dynamic isometric contractions increased the threshold for detecting weak low-threshold cutaneous inputs (electrical stimulation) but had no effect on either the threshold for heat pain or the subjective intensity of noxious and innocuous heat stimuli. These results indicate that the results of psychophysical experiments employing electrical stimulation cannot be generalized to apply to the specific tactile sensations mediated by low-threshold cutaneous afferents (e.g. Chapman et al. 1987; Milne et al. 1988). The sensation produced by electrical stimulation bears little resemblance to sensations produced by natural stimuli. Furthermore, it does not necessarily follow that all aspects of discriminative touch subserved by A-beta fibres are similarly affected by movement.

The present study was designed to assess the effects of motor activity on the ability to detect, discriminate and estimate the intensity of vibrotactile stimuli applied to the active limb. Stimuli were generated by an Optacon, a matrix of 144 vibrating pegs. Optacon pulses have been shown to activate both rapidly adapting and Pacinian corpuscle mechanoreceptive afferents innervating the glabrous skin of the hand (Gardner and Palmer 1989). In order to ensure constant contact between the stimulator and the cutaneous testing site, we employed the isometric elbow flexion/extension task previously described by Feine et al. (1990), rather than using our original isotonic task (Chapman et al. 1987). These experiments also examined the influence of the proximity of the stimulated site to the active muscles on the perception of vibrotactile stimuli. Preliminary accounts of the findings have been published (Post and Chapman 1990; Zompa et al. 1991).

Materials and methods

The methodology employed in these experiments was adapted from that used in a previous study (Chapman et al. 1987). Sixteen healthy subjects (8 women and 8 men; 22–32 years of age and all right-handed for writing) were trained to perform two tasks – a detection task and a discrimination task (using the method of constant stimuli; Woodworth and Schlosberg 1954) – under two experimental conditions, rest and motor activity. A further 12 subjects (6 women and 6 men, aged 22–39 years, and all but one right-handed for writing) were trained to perform a third task of scaling, or magnitude estimation, under the same experimental conditions. For the three perceptual tasks, nine different vibrotactile patterns (nine pairs of patterns in the case of the discrimination task) were presented in a quasi-random fashion, under computer control, with the aid of an Optacon (model RIC, Telesensory Systems, Palo Alto, Calif.) applied to the skin of the operant right arm. Testing was carried out with the subjects wearing earphones through which white noise was delivered in order to mask any auditory cues provided by the instrumentation. All subjects gave their informed consent prior to participating in these experiments.

Experimental design

Three series of experiments were performed. In the first series, we evaluated the influence of isometric motor activity (described below), using a low level of force (20 N), on the ability of subjects to detect, discriminate and scale vibrotactile stimuli applied to the active limb. Each perceptual task was evaluated in a separate experimental session (duration 1.5 to 2.5 h). Vibrotactile stimuli were applied to three different sites for the detection and discrimination tasks: (1) the glabrous skin of the distal phalanx of the index finger, (2) the glabrous skin of the thenar eminence and (3) the hairy skin of the mid-ventral forearm. For the scaling task, only the first and third sites were retained (stimulation applied to the tip of the third, instead of the second, digit because thickened skin on the dominant index finger had obliged us to reject some volunteers for the detection and discrimination testing). For all three tasks, there were six alternating blocks of nine trials at rest and nine trials during the isometric contractions. The order of testing (sites and tasks) was counterbalanced within and between subjects.

In the second series of experiments, eight men (including four who participated in the detection and discrimination task testing at 20 N) were tested in those same tasks with a higher target force level for the isometric motor task (50 N). Testing was carried out in two experimental sessions (three sites \times one task per session).

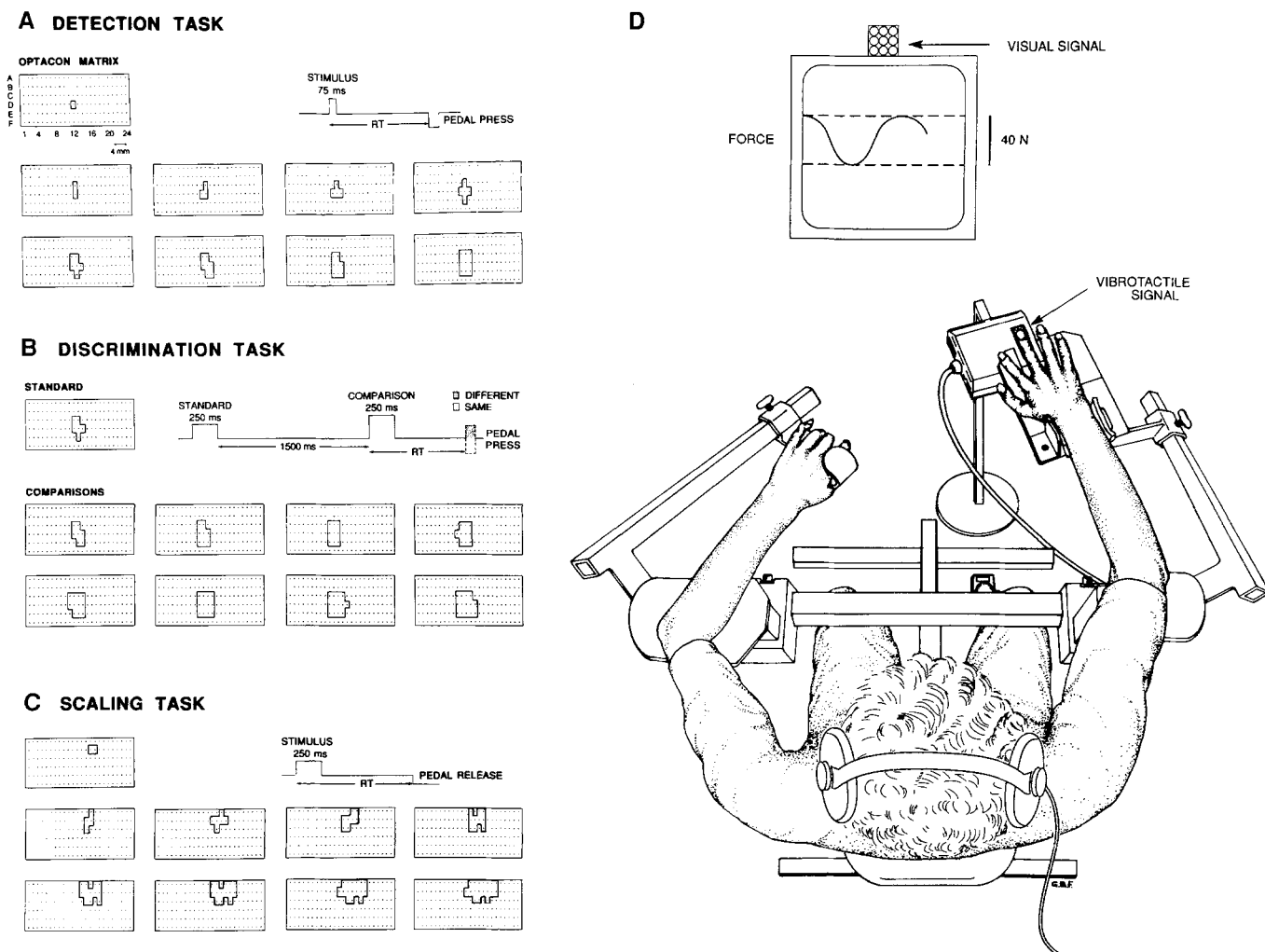
In the third series, four of the subjects who participated in the scaling task (two women, two men) subsequently participated in a second experimental session in which they rated the intensity of vibrotactile or electrical stimuli applied to the forearm, both at rest and during the performance of either an isometric or an isotonic motor task.

Vibrotactile stimulation

The Optacon consists of an array of small pegs arranged in a 6×24 matrix (dimensions: 11×26 mm with peg diameter of approximately 0.25 mm). As shown in Fig. 1D, the subjects were seated with both forearms and hands comfortably supported on two independent manipulanda. The Optacon was mounted on an independent support, not in direct contact with the chair on which the subject was seated, thereby avoiding any accidental transmission of vibration to sites other than that under investigation. It could be positioned to stimulate any of the three sites investigated on the right arm. The tactile array of the Optacon was modified by removing the U-shaped finger support and shearing off the distal ends of the pegs so that they were flush with the planar surface of the overlying perforated plate. This modification permitted us to stimulate all three test sites. The number and location of active pegs, their nominal frequency (40 Hz) and the duration of their activation were controlled by a laboratory mini-computer (PDP 11-73). Bliss et al. (1970) have reported that when the pegs are activated (total period of activation 4.3 ms giving a frequency of 230 Hz), the maximum amplitude of skin indentation is about 65 μ m. The voltage applied to the tactile array (maximum output 45 V), and hence the amplitude of vibration, was individually controlled for each experimental session (see below).

Detection task

Just prior to testing a given site, and with the subject in the test position, the threshold voltage at which a particular array (see below) could be detected 50% of the time was estimated at rest using the method of ascending and descending limits. As described previously (Post and Chapman 1991), a series of vibrotactile arrays, varying in the number of activated adjacent pegs, was presented (see Fig. 1A for an example of the patterns presented to the finger: nominal frequency 40 Hz, duration 75 ms giving four repetitions of the array). The voltage applied to the vibrotactile array was adjusted (to the nearest 1.1 V) so that the middle array was detected in 50% of the trials. For the digit (Fig. 1A), the



patterns were centred about a middle array of 5 pegs (range 1–9 activated pegs, mean voltage 11.4); for the forearm, the patterns were centred about a middle array of 9 pegs (range 1–17 activated pegs, mean voltage 11.5); for the thenar testing site, the middle array was set at 5 pegs for sensitive subjects ($n=10$, mean voltage 10.6) and at 9 pegs for less sensitive subjects ($n=6$, mean voltage 10.2) Note that there were equal numbers of men and women in the more and less sensitive groups, both for the detection and the discrimination task. For the experiment, with the voltage adjusted to the threshold value, nine arrays were presented to the subject (the same as those used for threshold estimation and the same parameters of stimulation). The nine arrays were presented to the subject at unpredictable intervals and in a quasi-random fashion while the subject was at rest and then while performing the motor task (see below). The subjects were asked to indicate when a stimulus was detected by pressing, as rapidly as possible, a foot pedal (right foot).

Discrimination task

Pairs of stimuli, consisting of a standard stimulus (6 activated pegs, 40 Hz nominal frequency, 250 ms duration giving 11 repetitions of the array) followed by a comparison stimulus (delay 1.5 s, stimulus parameters identical and usually differing from the standard in the number of activated pegs in the array as shown in Fig. 1B) were delivered in quasi-random fashion, at times not predictable by the subjects. They were asked to indicate, as quickly as possible, whether the intensity of the comparison was the same or different from the standard by pressing one of two foot pedals (one

located by each foot: right, same; left, different). Just prior to testing a given site, the threshold voltage for the 5- or 9-peg array was estimated as above (Detection task). The voltage was then set at about 1.3 to 1.4 times threshold (range 1.29 to $1.58 \times T$) for the duration of the experiment (mean increment 5.5 V, range 4.8–7.7 V). This provided stimuli that were clearly detectable across the range of patterns employed (6 to 22 activated pegs). Thereafter, the discrimination threshold (50% called different) was estimated with the subject at rest using the method of ascending and descending limits. For the comparison stimuli, the number of activated pegs was increased by either 1 or 2 between patterns. The mean estimated discrimination threshold varied across the site tested, being lowest for the digit site (2.9 pegs), intermediate for the thenar eminence (4.3 pegs), and highest for the forearm (5.8 pegs). In the experiment, the smallest comparison stimulus was identical to the standard to control for possible false alarms. Two series of comparison arrays were used depending upon the sensitivity of the site tested: digit, 6 to 14 pegs (illustrated in Fig. 1B); thenar eminence, $n=10$, 6 to 14 pegs and $n=6$, 6 to 22 pegs; and forearm, 6 to 22 pegs.

Fig. 1 A–C Schematic representations of the nine Optacon arrays presented to the digit for the three perceptual tasks. The locations of the activated pegs are shown within the thick lines. For each task, the time-course of events in a sample trial is also shown. D Subject position for the three perceptual tasks (Optacon shown here in the position used to stimulate the tip of the digit)

Scaling task

Using the procedure described above (Detection task), and prior to testing a given site, the voltage applied to the Optacon was initially adjusted so that the middle array (5 and 9 peps for, respectively, the digit and forearm test sites) could be detected 50% of the time (mean 12 V and 16.5 V). To ensure that the vibrotactile stimuli delivered during the experiment were all suprathreshold, the potentiometer setting was then increased about 1.2 times threshold (range 1.1–1.3 X T, mean increment 3.4 V and range 1.5–6 V). The stimulus duration was 250 ms and the nominal frequency was 40 Hz for this task. Figure 1C illustrates the patterns used for the digit site (number of activated peps, 2 to 18; adjacent arrays increased by 2 peps). A larger range was employed for the forearm testing (6–30 activated peps, with increments of 3 activated peps between adjacent arrays). Prior to the start of the task (subject at rest), three vibrotactile patterns were presented to the subject – a small, large and medium pattern (10 or 18 peps, depending upon the site of stimulation). The subjects were instructed to assign any whole number that seemed appropriate to the last stimulus (medium pattern). They were then instructed to rate the intensity of subsequent stimuli by assigning numbers to them, proportional to their subjective impression of their intensity. The rating, given after the end of each trial, was entered into the computer by the investigator and stored along with the digitized data from the trial. During the performance of the task, subjects were also asked to indicate the time at which they felt the stimulus by releasing a foot pedal. In neither the discrimination nor the scaling task was there any restriction on the cues that the subjects might use to evaluate “intensity”. It is most likely, however, that the number of active peps was the determining factor, since Cholewiak (1979) has found that magnitude estimates of vibration increase linearly as a function of the number of active vibrators in a matrix (slope close to 1.0 for log-log plots), and the slope is independent of the spatial density of the vibrators and the overall amplitude of vibration.

For the third series of experiments, electrical stimuli were applied to the mid-ventral forearm through surface electrodes, using the same parameters of stimulation as used by Chapman et al. (1987): 2 ms duration, constant current, square wave pulses (cathode proximal; electrodes placed so that there was no referred sensation or muscle activation). The time of their delivery was controlled by a laboratory minicomputer. Prior to testing, detection threshold was determined (mean 0.14 mA; range 0.13 to 0.18 mA) and also the highest non-painful intensity. For the task, nine different intensities distributed linearly (equal steps varying from 0.12 to 0.14 mA) about a value lying midway between the two extremes, and covering 75% of the range (0.16–5.13 mA), were chosen. Prior to each trial, the amplitude of the stimulus was manually adjusted according to a predetermined schedule.

Motor tasks

In the first series of experiments, the three perceptual tasks were each performed with the subject at rest and during isometric contractions about the right elbow. The latter task was similar to that described previously by Feine et al. (1990). Briefly, subjects were seated in a chair with their arms placed comfortably on two independent manipulanda (Fig. 1D), facing an oscilloscope. Movement of the manipulandum on the right side was blocked at an angle of approximately 45° of elbow flexion. Subjects were instructed to perform a series of smooth, continuous and rhythmical isometric flexions and extensions about the elbow. The subject exerted force against stops fitted snugly on either side of the wrist. The contractions were performed at a cued frequency of 0.5 Hz, signalled by an array of light-emitting diodes located directly above the oscilloscope (visual signal in Fig. 1D). Two target lines were traced on the oscilloscope, representing 20 N in each direction. The amplitude of the force generated was measured with a pair of strain gauges located just proximal to the wrist support. The force signal was amplified and displayed on the oscilloscope

so that the subjects could monitor their force output (see Fig 1D). In the second series of experiments, subjects performed two of the perceptual tasks (detection and discrimination) at rest and during isometric contractions with the target force level increased to 50 N. In the final series of experiments, subjects performed the scaling task (vibrotactile and electrical stimulation) at rest and while performing either isometric contractions (target force level 20 N) or isotonic contractions (task identical to that used previously by Chapman et al. 1987). For this third experiment only, the Optacon was mounted directly on the manipulandum so that its relationship with the moving limb remained constant throughout the testing. For the isotonic task, the manipulandum was unblocked and free to move. Displacement was measured with a potentiometer, the output of which was displayed on the oscilloscope. Subjects were instructed to make rhythmical, continuous flexions and extensions about the elbow (0.5 Hz; 60° total excursion, target lines indicated 30° in either direction from a neutral position of 45° elbow flexion). Stimuli were given without regard to the phase of movement or contraction in all experiments.

Data analysis and acquisition

The task and data acquisition were under computer control. Trials were initiated by the experimenter at times unpredictable by the subject (intertrial interval about 4 to 10 s). Subjects were given a break of 5–10 min between testing at different sites.

For all tasks, reaction time (RT) was calculated and stored with each trial. This was defined as the time interval between the onset of the stimulus (onset of the comparison stimulus in the case of the discrimination task, see Fig. 1A–C) and the pedal response. Trials were rejected, and later repeated, if RT was less than 100 ms or if the subjects inadvertently changed their position during the trial.

Force (isometric task) or displacement (isotonic task) was also recorded (200 Hz digitization rate). Two measures were made on-line: the force (or displacement) at the time the stimulus was given (both the standard and the comparison in the case of the discrimination task) and at the time that the subject responded with the foot pedal. These values were stored with each trial along with the times at which the stimuli were applied.

Performance in the perceptual tasks was evaluated by calculating, for each subject and in each condition (rest and motor activity), the mean percent of stimuli detected (detection task), the mean percent of stimuli called different (discrimination task) and the mean normalized magnitude estimate (scaling task, individual subjective scales normalized by setting the maximum individual score for each testing site at 100%). In addition, median RTs were also calculated (see Results for details).

Differences in performance or RT were analysed using repeated measures analyses of variance (ANOVA), post hoc contrast analyses and post hoc pairwise comparisons (Scheffé procedure and Tukey's HSD test) (SYSTAT Version 5.1). Factors in the ANOVAs included the motor condition (rest and movement), the size of the array (nine patterns) and subject gender (first two factors repeated). The level of significance was fixed at $P < 0.01$ for most analyses. An exception was made for the results of the third series of experiments in which only four subjects participated (level of significance $P < 0.05$). In interpreting the results of the ANOVAs, the Bonferroni correction was applied to the results of the F -tests (level of significance/number of tests). For most analyses (three way ANOVA involving seven tests), the corrected level of significance was $P < 0.0014$ (low n experiments $P < 0.007$). Additional analyses are detailed in the Results.

Results

Perception of vibrotactile stimuli during isometric motor activity (20 N target force)

Figure 2 and Table 1 show the results obtained from 16 subjects in the *detection task*, at rest and during isometric contractions about the elbow. Averaged stimulus-response functions are shown in Fig. 2A for each of the three sites stimulated – the digit, the thenar eminence and the ventral forearm. Both at rest and during motor activity, subjects detected a significantly greater number of stimuli as the size of the array was gradually increased, and this for all three sites tested ($P < 0.0005$; df 8,14). There was, however, a differential sensibility to the vibrotactile stimulation across the three sites. Thus, the mean detection threshold – defined as the number of pegs at which 50% of the stimuli were detected – was lowest on the digit and highest on the forearm (see also Table 1). During the isometric motor task, there was a rightward shift in the stimulus-response curves at all three sites, and a corresponding increase in detection threshold. ANOVAs indicated that performance of the detection task was significantly affected by the motor task at each site tested ($P < 0.0005$; df 1,14). Subject gender was also a significant factor at the digit and thenar eminence test sites ($P = 0.001$ and $P < 0.0005$; df 1,14). This is explained by the observation that women had lower detection thresholds at rest at these two distal sites than did men (significant only at the digit site, $P < 0.01$, independent t -test, df 14) and so detected more stimuli overall at these sites than the men. At the digit and thenar sites, there was a significant interaction between the motor task and intensity ($P < 0.0005$) whereby the task-related effects were more pronounced at higher intensities of stimuli. Contrast analyses indicated that the effects attributed to the motor task were nevertheless significant at each site (respectively, $P = 0.001$ and $P < 0.0005$; df 2,14).

In order to compare the effects across the three sites, two further analyses were performed. First, the mean percent reduction in performance was calculated at each site. This showed that the largest overall decrease occurred at the thenar eminence (38% fewer stimuli detected), with smaller reductions occurring at the forearm (28%) and digit (24%) test sites. Second, in order to compare thresholds directly across the three sites while taking into account the fact that different arrays were used at each site, threshold in the two conditions was interpolated directly from each subject's individual stimulus-response curves (Table 1). A three-way repeated-measures ANOVA of the latter data (factors: site, motor condition and subject gender) indicated that detection threshold was significantly affected by both the site of stimulation ($P < 0.0005$, df 2,28; lower threshold at more distal sites) and the motor task ($P < 0.0005$, df 1,14), but not subject gender (see, however, above). Post hoc, pairwise comparisons indicated that detection threshold was significantly increased during the motor

Table 1 Mean threshold interpolated from the curves of individual subjects ($n = 16$ subjects; 20 N target force). The values represent the absolute number of activated pegs for detection thresholds, and the difference in the number of activated pegs for discrimination thresholds

	Detection threshold		Discrimination threshold	
	Rest	Contract	Rest	Contract
Digit	3.5	4.8	3.4	4.4
Thenar eminence	5.0	8.1**	5.1	5.6
Forearm	7.2	10.1**	6.9	7.5

** $P < 0.001$ (results of pairwise comparison, Scheffé procedure, rest versus contract, df 15). All other differences were not significant

task at the two more proximal sites, but not at the distal site (see Table 1).

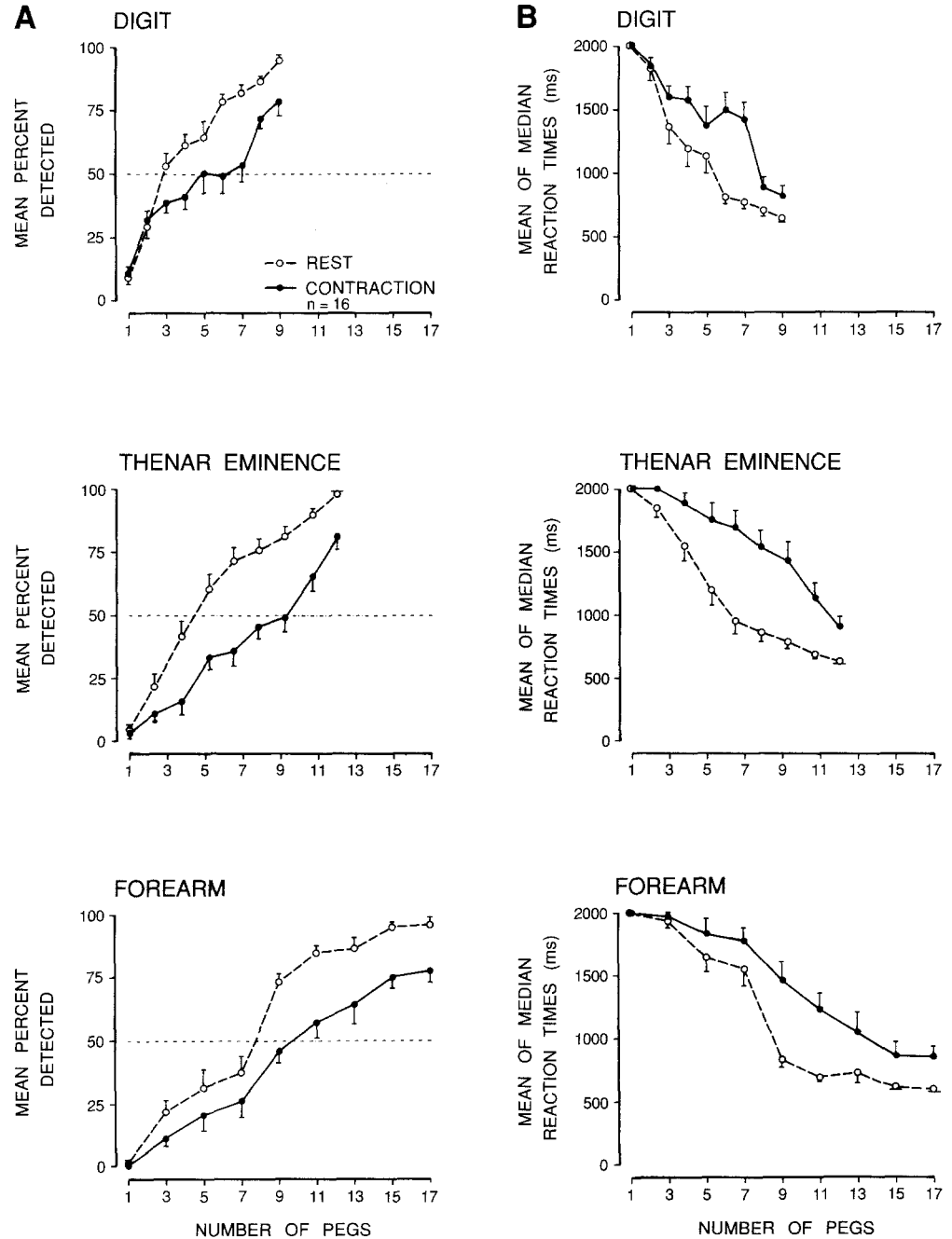
The proportion of false alarms (response in the absence of a stimulus) during the detection task was extremely low: 13 false alarms in 7 subjects as compared with a total of 5,184 stimuli applied in 16 subjects. While a slight majority of these occurred during the motor task (9/13), the overall low rate of false alarms suggested that the subjects' response criteria remained constant throughout the testing. False alarms were, however, most often noted during testing of the digit site (62% vs 23% and 15% for the thenar and forearm sites).

The pooled RT data (Fig. 2b) showed changes that paralleled the changes in performance of the detection task. For each site, it is evident that median RT decreased with an increase in the size of the vibrotactile array ($P < 0.0005$; df 8,14). It was consistent with the suggestion that the motor task hindered the ability of subjects to detect vibrotactile stimuli that RTs were significantly longer during the motor task than at rest ($P < 0.0005$; df 1,14). Reaction times did not vary across the three sites, nor were they influenced by either subject gender or the force exerted at the time of stimulus delivery (trials given during the motor task analysed with linear regressions).

Figure 3 and Table 1 summarize the effects of the motor task on performance of the *discrimination task* in 16 subjects. Both at rest and during the motor task (Fig. 3A), stimuli at all three sites were called different more readily as the size of the comparison array was increased relative to the standard array ($P < 0.0005$; df 8,14). Discrimination threshold – defined as the increment in the number of pegs (comparison over the standard) at which 50% of the comparison stimuli were called different – was lowest on the digit and highest on the forearm (dotted line in Fig. 3A; see also Table 1). The motor task significantly reduced performance at the digit and thenar eminence ($P = 0.001$; df 1,14) but not at the forearm testing sites. Subject gender was not a significant factor. The magnitude of the effect of the motor task was, however, small: 13 and 11% fewer stimuli called different at the thenar eminence and digit testing sites (6% reduction for the forearm). Moreover, there

Fig. 2A,B Effects of isometric elbow flexion/extension (20 N target force) on performance in the detection task ($n=16$ subjects). **A** Percent of trials in which subjects detected the stimulus at rest (*open symbols*) and during isometric contraction (*filled symbols*) as a function of the number of activated pegs in the array. The *dotted line* indicates detection threshold. Note that the data from the thenar eminence are plotted as a function of the number of activated pegs per array, as the same arrays were not employed for all subjects (see Materials and methods). **B** Mean of median RT is plotted as a function of the number of activated pegs. Trials with no response (stimulus not detected) were arbitrarily assigned a maximum RT of 2 s. In this and all subsequent figures, the mean is plotted with its corresponding standard error of the mean (1 SEM)

DETECTION TASK



was a significant interaction between intensity and the motor condition at the digit test site ($P=0.001$), and contrast analyses subsequently indicated that the motor task was *not* a significant factor at this site. A three-way ANOVA applied to the results from the individual threshold measures (Table 1) indicated that only the site of stimulation ($P<0.0005$; $df\ 2,28$), and not the motor task or gender, significantly affected discrimination threshold. Post hoc, pairwise comparisons confirmed the lack of effect at all three test sites. The proportion of false alarms (comparison called different when the stan-

dard and comparison were identical: increment 0 in Fig. 3A) was higher than for the detection task, 11% overall (66/576 trials). Only a slight majority of these occurred during the motor task (61%), suggesting that the modest decrease in performance during the task could not be attributed to any change in the subjects' response criteria. Interestingly, however, half of the false alarms occurred during testing at the digit site (50%, as compared with 24 and 26% for the thenar and forearm sites).

DISCRIMINATION TASK

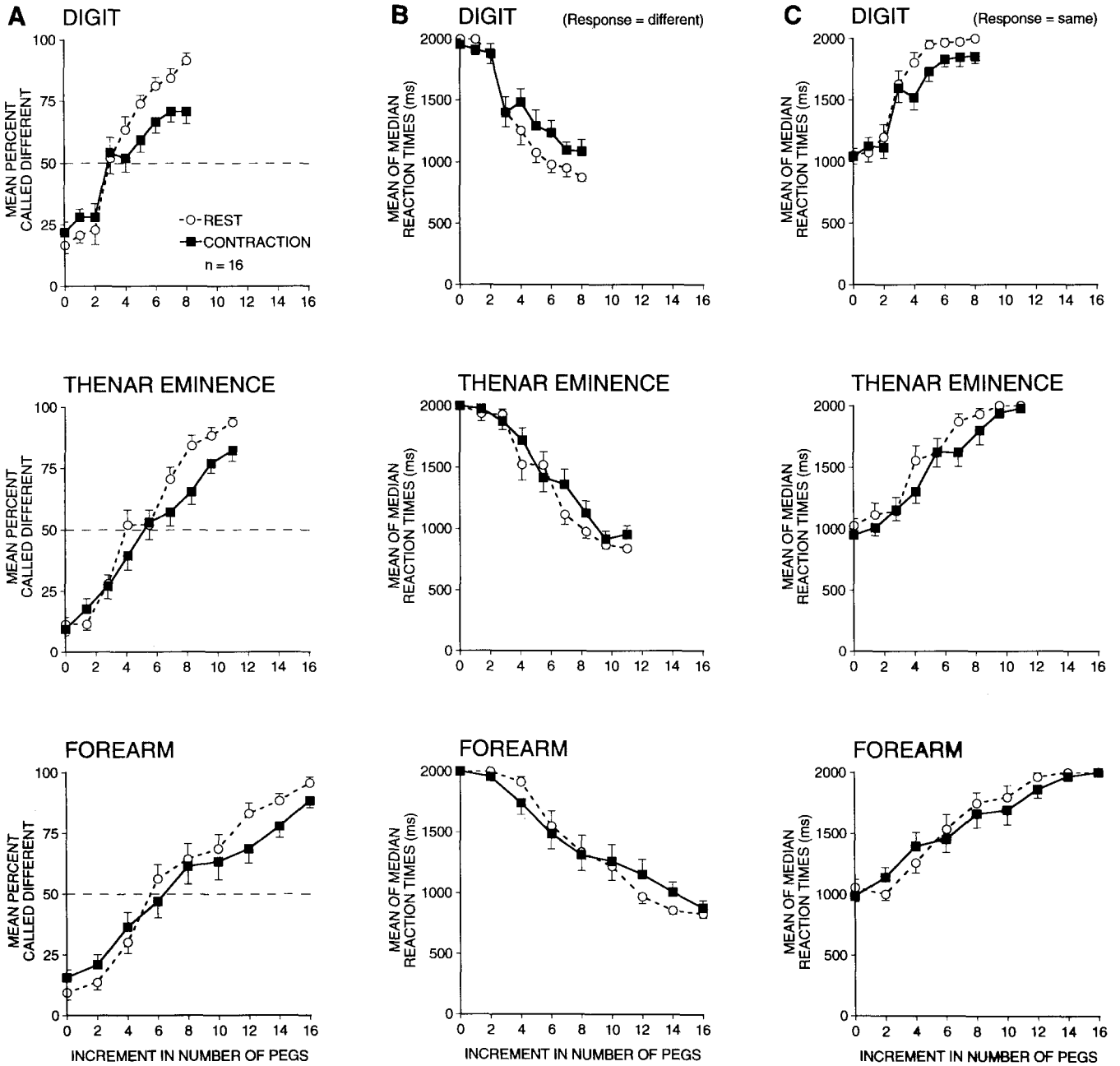
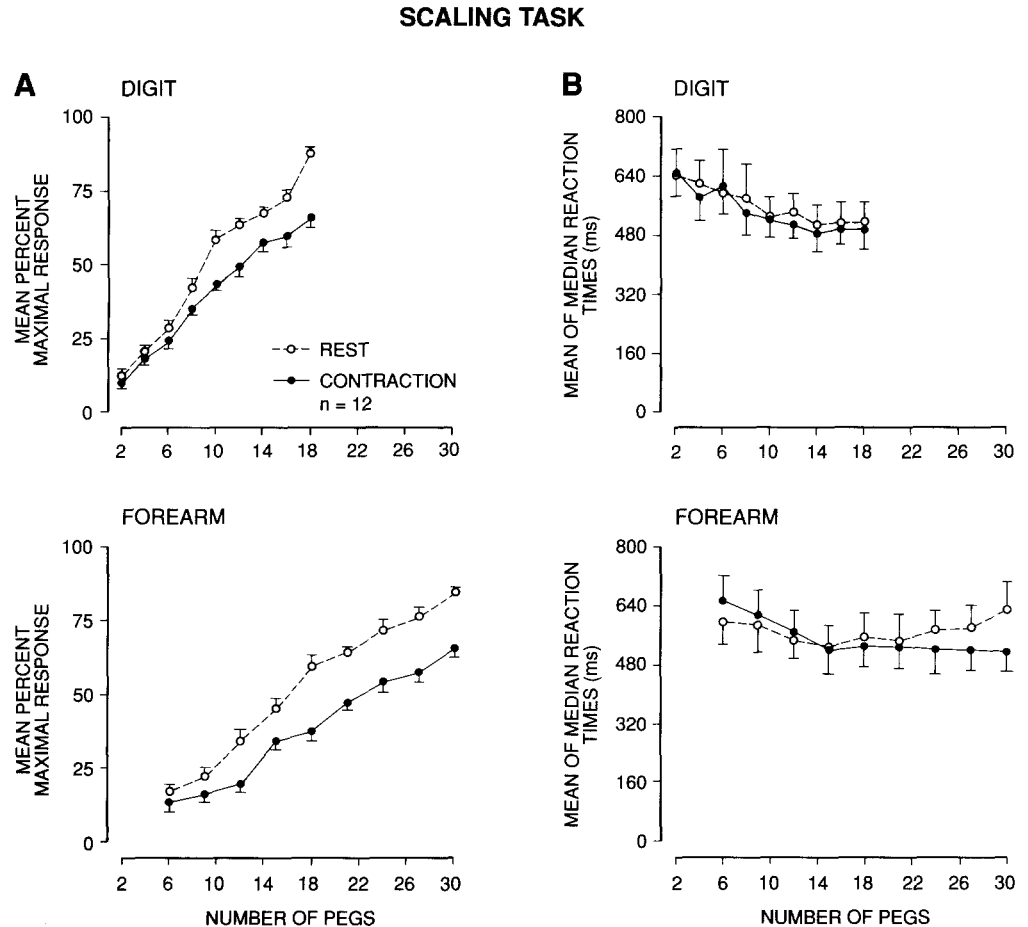


Fig. 3A–C Effects of isometric elbow flexion/extension (20 N target force) on performance in the discrimination task ($n=16$ subjects). **A** Percent of trials in which subjects reported that the comparison stimulus was different from the preceding standard stimulus as a function of the number of activated pegs by which the comparison differed from the standard. **B** Mean of median RTs for calling the comparison “different” plotted as a function of the increment in the comparison array. **C** Mean of median RTs for calling the comparison “same” as a function of the increment in the comparison array. **B,C** A maximum RT of 2 s was assigned to the pedal that was not activated

Figure 3B and C plot, respectively, the median RT data for stimuli called different and those called same. For stimuli called *different*, RT decreased as the size of the comparison array increased ($P < 0.0005$; df 8,14). The opposite pattern was seen for stimuli called *same* ($P < 0.005$). No other factor, including the motor task, the site of stimulation, gender, and force at the time of stimulus delivery, significantly affected the RT values.

Figure 4 summarizes the results obtained from 12 subjects in the *scaling task* at rest and during the motor task. For both stimulation sites (digit and forearm), magnitude estimates increased significantly as a func-

Fig. 4A,B Effects of isometric elbow flexion/extension (20 N target force) on performance in the scaling task ($n=12$ subjects) at two sites. **A** Mean percent maximal response plotted as a function of the number of activated pegs in the Optacon array. **B** Mean of median RTs plotted as a function of the number of activated pegs



tion of the number of pegs activated (Fig. 4A, $P < 0.0005$; df 8,10). In agreement with Cholewiak (1979), the stimulus-response function was, in each case, best fit by a power function although the exponents were slightly different for the two sites (digit 0.90; forearm 1.06; $r = 0.99$ in each case). Linear functions were obtained with log-log plots (not shown). At both testing sites, the stimulus-response curves were shifted to the right during the motor task, an effect that was significant ($P < 0.0005$; df 1,10). This was accompanied by a significant interaction between intensity and motor task, whereby the effects of the motor task were more pronounced at higher intensities ($P < 0.0005$). Contrast analyses indicated that the main effect (motor task) was, nevertheless, significant in each case ($P < 0.0005$; df 2,10), with the effects being localized to the larger patterns (digit, 10–18 pegs; forearm: 12–30 pegs; Tukey's HSD test, $P < 0.01$). In addition, the interaction disappeared after a log-log transformation of the data: for each test site, the slope of the function during the motor task was unchanged from that at rest, but the y -intercept decreased, so shifting the entire curve to the right. Overall, there was a slightly greater reduction in the subjective ratings of stimuli applied to the forearm (15% mean overall decrease in ratings) than to the digit testing site (10%) during the motor task. Subject gender had no influence on the results at either site. Finally,

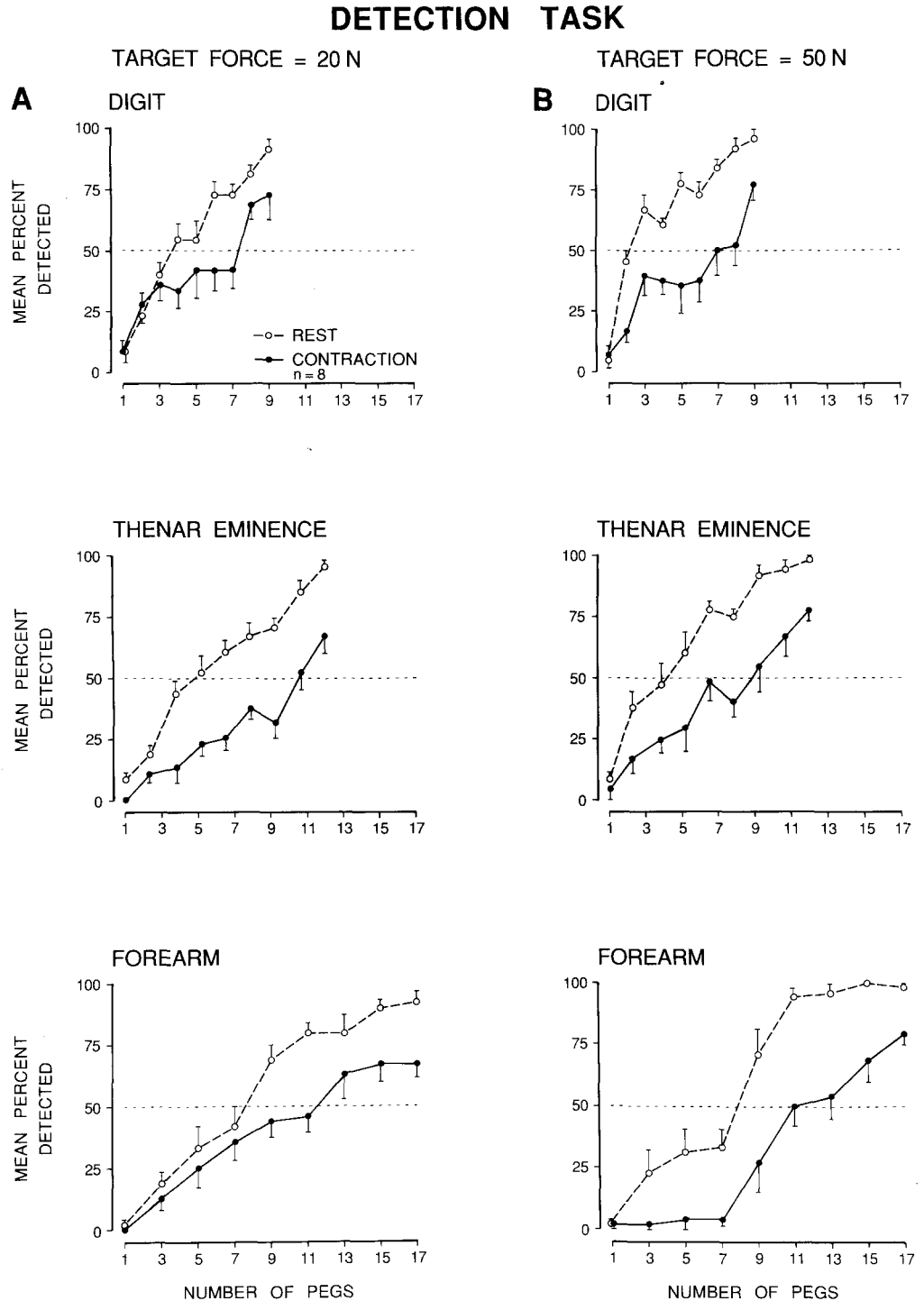
although median RT (Fig. 4B) decreased significantly as array size increased ($P < 0.0005$; df 8,10), the motor task had no significant effect on RT.

In order to determine if the phase of the muscle contraction in which the stimulus was applied had any effect on the subject's response, the performance of six subjects was analysed: two in the detection and discrimination tasks (648 trials), and four in the scaling task (432 trials). For this, we divided the cycle into four equal phases – flexion, flexion turning point, extension and extension turning point. For each phase of contraction, overall performance in each task was calculated. The results indicated that the stimuli were presented in equal proportions across the four phases of isometric muscle contraction and that performance was not significantly affected by the phase of contraction (X^2 tests).

Perception of vibrotactile stimuli during isometric motor activity (50 N target force)

Performance on the detection task was sensitive to the level of the target force utilized in the motor task (Fig. 5 and Table 2). With a target force level of 50 N, performance of the detection task was significantly reduced at all sites during the motor task (digit $P < 0.005$; thenar eminence $P = 0.001$; forearm $P = 0.0002$; df 1,6). In contrast, performance was only significantly reduced at the

Fig. 5 Comparison of the effect of the target force level (A, 20 N; B, 50 N) exerted during the isometric elbow flexion/extension task on the ability to detect weak vibrotactile stimuli applied to three different sites ($n=8$, all men). Data plotted as in Fig. 2A



two more proximal sites with the lower target force level of 20 N (thenar eminence $P < 0.0005$; forearm $P = 0.001$; df 1,6; analysis restricted to the eight men whose data were included in Fig. 2). Three-way ANOVAs applied to the individual threshold measures (see Table 2) showed that detection threshold was significantly increased during both series of experiments ($P < 0.0005$; df 1,6) and that the site of stimulation was a significant factor in each series ($P < 0.0005$; df 2,12). Post hoc pairwise comparisons revealed that detection threshold was

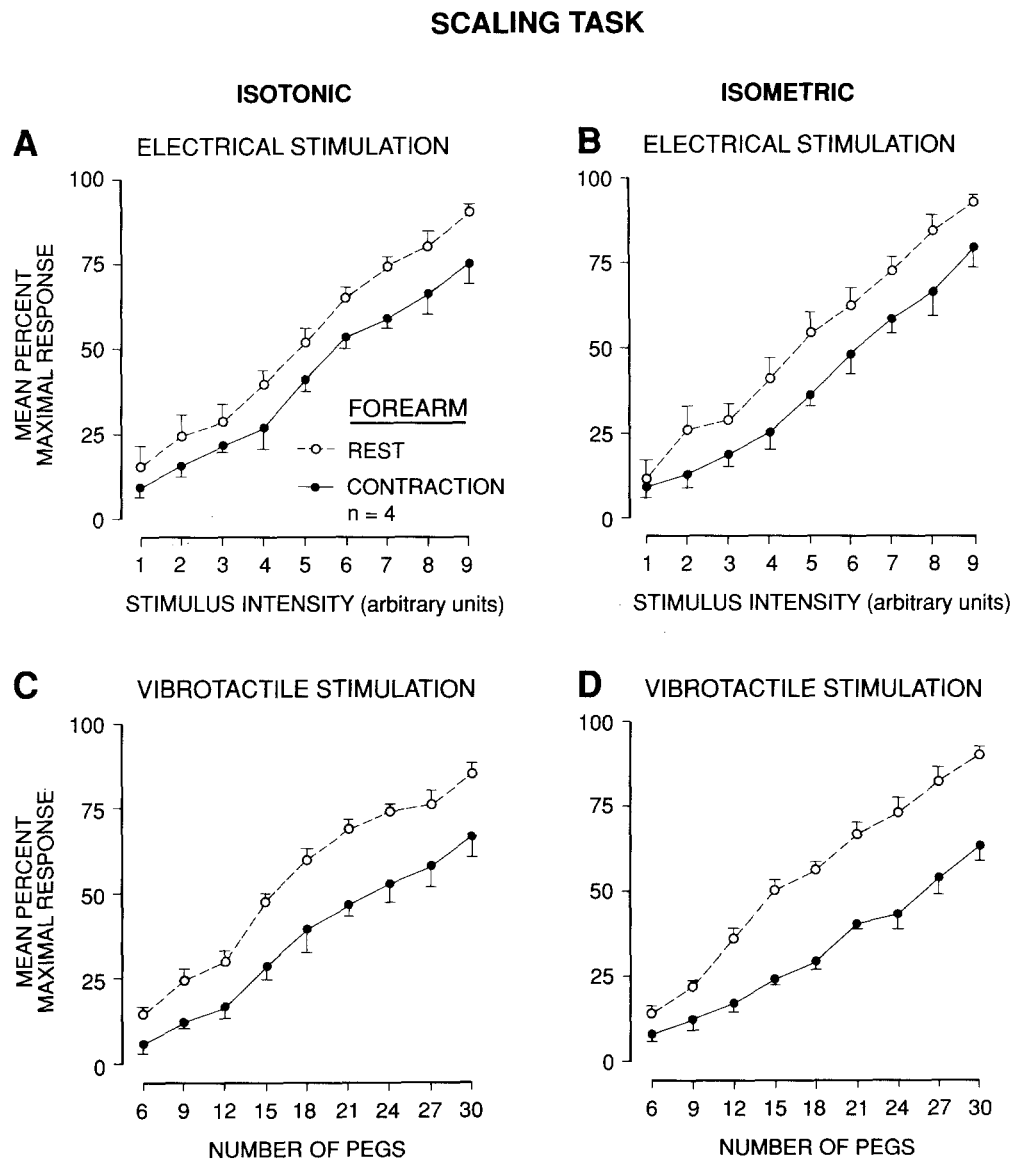
significantly increased at more sites with the higher target force level (forearm and thenar eminence) than at the lower force level (forearm only). Finally, the absolute mean increase in detection threshold at all three sites was greater with the higher target force level. In contrast, no change in performance on the discrimination task was seen with either target force level (not shown), and analyses applied to the individual threshold measures listed in Table 2 confirmed the lack of any effect attributable to the motor task.

Table 2 Mean threshold interpolated from the curves of individual subjects ($n=8$ male subjects for 20 N and 50 N target force). The values represent the absolute number of activated pegs for detection thresholds, and the difference in the number of activated pegs for discrimination thresholds

	Detection threshold				Discrimination threshold			
	20 N		50 N		20 N		50 N	
	Rest	Contract	Rest	Contract	Rest	Contract	Rest	Contract
Digit	4.2	5.2	2.9	6.0	3.4	4.6	3.3	4.0
Thenar eminence	5.8	8.5	4.0	7.9*	5.0	5.0	4.2	5.5
Forearm	7.3	11.0*	6.8	11.8**	7.1	7.1	5.0	6.1

* $P < 0.05$; ** $P < 0.01$ (results of pairwise comparison, Scheffé procedure, rest versus contract, $df 7$). All other differences were not significant

Fig. 6 Comparison of the influence of the nature of the motor task (isotonic, **A,C**; isometric, **B,D**) and the modality of the stimulus (electrical, **A,B**; vibrotactile, **C,D**) on the ability of four subjects to estimate the subjective intensity of cutaneous stimuli applied to the mid-ventral forearm. Data plotted as in Fig. 4A



Comparison of the effects of isometric and isotonic motor tasks on the ability of subjects to scale vibrotactile and electrical stimuli

A decrease in the subjective intensity of vibrotactile stimuli during the motor task had not been expected on

the basis of our previous work (Chapman et al. 1987), where it was reported that the subjective intensity of innocuous electrical stimuli is not modulated during movement. Additional experiments were therefore performed on four of the subjects who took part in the scaling task in order to determine the contribution of

two potentially important factors to the results – the modality of the stimulus (natural vibrotactile vs electrical stimulation) and the nature of the motor task (isometric vs isotonic contractions about the elbow). In order to restrict testing to a single session, only one site of stimulation was tested, the ventral forearm. The averaged results are shown in Fig. 6. Subjective ratings increased significantly as a function of stimulus intensity for both modalities ($P < 0.0005$; df 8,2). Motor activity, either with (A,C) or without (B,D) movement, produced a general reduction in the subjective magnitude of the stimuli, but this was significant for only one of the combinations tested (B, isometric task/electrical stimulation, $P = 0.002$; df 1,2). The overall magnitude of the effect varied slightly across the four conditions, with a greater reduction being observed for natural (C, 16% mean decrease in ratings; D, 18%) than for electrical stimuli (A, 12%; B, 14%). Greater reductions were associated with isometric (B,D) than with isotonic (A,C) contractions.

Discussion

These experiments have shown that the perception of suprathreshold stimuli is, in part, diminished during motor activity. Thus, magnitude estimates of the intensity of suprathreshold vibrotactile stimuli were significantly reduced during isometric contractions about the elbow, an observation that is not consistent with our previous report that magnitude estimates of suprathreshold innocuous electrical stimuli are uninfluenced by isotonic contractions about the elbow (Chapman et al. 1987). On the other hand, the results do confirm our previous observation that motor activity has no effect on the ability to discriminate between the intensity of suprathreshold innocuous stimuli and extend this to include natural cutaneous stimuli. Finally, we have shown that voluntary motor activity elevates detection threshold for vibrotactile stimuli, and that these effects are spatially distributed and sensitive to the level of the target force.

Perception of near-threshold stimuli

In the present study, we observed a very robust decrease in performance of the detection task, and a corresponding increase in detection threshold at the two more proximal test sites (forearm and thenar eminence) during moderate dynamic isometric contractions (20 N target force). While performance of the detection task at the digit test site was significantly reduced during the motor task, analyses of the interpolated threshold data did not show any significant change, and so we conclude, conservatively, that other factors probably contributed to the modest, and insignificant, elevation of interpolated detection threshold seen at the fingertip. It is of interest, in this regard, to note that more than one-half of the false alarms were observed during testing of

the digit site, both in the detection and the discrimination tasks. It could be that feedback from the glabrous skin of the hand, resting upon a support throughout the test session, might have contributed both to these false alarms, and possibly also to the modest reduction in performance at this test site during the motor task.

Reaction time also increased during the performance of the motor task. Part of this increase was probably due to the fact that subjects were asked to perform two different motor tasks at the same time. It is consistent with this suggestion that RT was significantly increased at all three test sites, even though individual threshold measures were not. In many psychophysical studies, however, RT is also taken as an indication of response certainty: subjects take longer to respond when they are less certain of their response (Posner et al. 1980; Bushnell et al. 1985). Looked at in this light, the increased RT probably reflects reduced response certainty, a suggestion which is entirely consistent with the reduced performance in the detection task.

In agreement with a previous study (Feine et al. 1990), we report that proximity between the site of stimulation and the elbow influenced the results obtained, and extend this to show that the sensations elicited by natural, as opposed to electrical, stimuli are influenced in a similar manner by proximity. The observation of greater modulation for sites closer to the "movement" is consistent with the report of Coquery et al. (1971) that the perceived intensity of cutaneous stimuli shows a greater reduction when the stimulation is applied closer to the moving part. Similar observations have also been made more recently by Schmidt et al. (1990) using threshold level intraneural microstimulation to elicit a referred sensation in the digit.

The present study has also demonstrated that the target force level is an important factor with respect to the degree and the spatial extent of the task-related modulation. These observations are consistent with a recent report from Pertovaara et al. (1992) to the effect that detection thresholds on the hand increase, in a load-dependent fashion, in relation to isometric finger flexion. The present results give no indication, however, as to the potential source(s) of the additional gating signal at higher force levels, as both afferent feedback and the central motor command, two of the potential sources for the gating signal (discussed in Chapman et al. 1987, 1988; and Jiang et al. 1990a,b), would have increased in parallel with the increased force level.

Perception of suprathreshold stimuli

The present results indicated that the ability to discriminate between the intensity of suprathreshold vibrotactile stimuli is unaffected by the performance of a motor task. This observation was confirmed by the lack of any motor activity-related change in RT in the discrimination task. The observation that the motor task had no significant effect on the ability to discriminate vibrotac-

tile stimuli is particularly important, as it provides evidence that movement between the skin and the Optacon was not responsible for the reduced perception of vibrotactile stimuli during the isometric motor task. If this had been an important factor, then performance of all three perceptual tasks would have been affected. The functional significance of the lack of effect on discrimination is discussed below.

These experiments were undertaken in an effort to determine if all modalities of cutaneous sensation are equally modulated by motor activity. As described in the Introduction, we had previously demonstrated that scaling of discrete thermal stimuli (innocuous and noxious heat) is unaffected by such motor activity (Feine et al. 1990). With the same motor task, the present results clearly indicate that magnitude estimates of natural vibrotactile stimuli are substantially diminished during motor activity. When, however, we subsequently attempted to replicate the results of our previous study (Chapman et al. 1987) with a broader view towards determining the relative contribution of the type of contraction and modality to the effects obtained (Fig. 6), we obtained a reduction in magnitude estimates for both modalities. While this appears to contradict our previous report of no effect of movement on ratings of innocuous electrical stimuli applied to the surface of the skin (Chapman et al. 1987), it should be pointed out that there was one major difference in the experimental protocol that probably explains the results. In the present experiments, the elbow rested on a support (Fig. 1D), while in our previous experiments the proximal support was provided by a sling under the upper arm, thus minimizing cutaneous feedback from the elbow region caused by movement of the skin. The present approach was dictated by the necessity to ensure constant contact between the Optacon and the skin; pilot experiments indicated that it was impossible to maintain contact between the Optacon and the forearm in the two motor tasks if a sling support was used. Further to this, previous unpublished results (Chapman, Bushnell, Duncan and Lund) showed a slight, but significant, reduction in magnitude estimates of innocuous electrical stimuli when the isotonic motor task was performed with a support at the elbow. Thus, it would appear that the added peripheral feedback from the elbow was the source of the gating effects seen during the scaling task in the present study.

The gating signal

The inhibitory influences, or what could be termed gating signals, that are responsible for the movement-related decreases in detection and magnitude estimates reported here can be characterized as showing a spatial gradient and being sensitive to the associated movement kinematics, including force (reviewed above) and velocity, in the case of isotonic movements (Angel and Malenka 1982). These characteristics are consistent with

the notion that both peripheral feedback from the moving limb and the central motor command (Chapman et al. 1987, 1988; Jiang et al. 1990a) are important sources of these inhibitory influences (see also below). Thus, the spatial gradient probably reflects the pattern of connectivity between these sources of the gating signal and the central structures involved in relaying and processing cutaneous inputs. The sensitivity to movement kinematics can be explained by the fact that both the motor command and movement-related peripheral feedback covary with factors such as the speed of movement.

The influence of these gating signals on the perception of tactile stimuli is such, however, the relative differences between suprathreshold inputs are preserved even though their absolute magnitude is diminished. While we had originally proposed that the gating signals act as a form of masking stimulus (Chapman et al. 1987), interfering with the transmission of weak, but not strong, stimuli, this notion needs to be revised in the light of the present observation of a clear reduction in the sensory magnitude of suprathreshold tactile stimuli. Although one might argue that the "intensities" employed may have been on the lower, masked, part of the stimulus-response curve (see for instance Stevens 1975), two observations lead us to reject this suggestion. First, the stimulus-response functions for the magnitude estimates of vibrotactile stimuli during the motor task showed no sign of an increased positive slope, as would have been expected if masking had occurred: log-log plots of the stimulus-response functions in the presence of gating were instead parallel to those obtained at rest. Second, the magnitude estimates of electrical stimuli, using the same parameters and range of intensities as in our previous study (Chapman et al. 1987), were also diminished under the present experimental conditions, i.e. with an elbow support (Fig. 6). While it may be premature to speculate upon the exact form that the gating signal takes, it seems clear that a simple reduction in the signal-to-noise ratio produced by an increase in background noise *cannot* explain the present observations. Thus, more complex models of the underlying inhibitory processes need to be developed in order to describe how the gating signals interact with the transmission of signals within the central nervous system, and so modify perception as a consequence.

Functional significance

The present results are in accord with the results of experiments examining the influence of motor activity on the transmission of cutaneous input to primary somatosensory cortex (Chapman et al. 1988; Jiang et al. 1990b, 1991). The latter experiments have demonstrated that the transmission of externally applied suprathreshold cutaneous input, natural or electrical, to primary somatosensory cortex is diminished during isotonic and isometric contractions. The conclusion is thus inescapable that externally applied inputs, even when

behaviourally important to a subject within the context of psychophysical testing, are subject to gating controls. This was already evident from the results of experiments studying detection threshold (present results and Chapman et al. 1987; Feine et al. 1990), but these could have been explained with our original masking hypothesis – a very modest reduction in the signal-to-noise ratio. The present results reinforce the importance and magnitude of these gating effects.

On the other hand, one should keep in mind that the types of inputs employed here were somewhat unnatural in the sense that they were externally imposed. Further to this, it appears that another class of tactile input, that which is self-generated during the course of exploratory movements, is spared from movement-related gating influences within certain behavioural contexts (Chapin and Woodward 1982; Chapman and Ageranioti-Bélanger 1991a; Ageranioti-Bélanger and Chapman 1992). These results need to be interpreted cautiously, however, since our recent results indicate that the sparing is only partial and that some apparently meaningful tactile inputs appear to be strongly gated during movement (Chapman and Ageranioti-Bélanger 1991b). It remains to be determined how, and when, specific inputs are selected for relatively faithful transmission to higher centres.

Finally, although the present experiments shed little new light upon the origin of the gating signals, the results do reinforce our previous suggestion that peripheral feedback is an important source of the gating signal (Chapman et al. 1987). Central sources probably also contribute since stimulus detectability has been reported to be decreased prior to the onset of EMG activity (Coquery et al. 1971; Dyhre-Poulsen 1978), and so before any peripheral feedback could be expected. In agreement with this, it has been shown that transmission within the dorsal column-medial lemniscal pathway is significantly decreased at, or before, the onset of EMG activity, and that activation of motor cortex with intracortical microstimulation produces gating effects that are similar to those seen with voluntary movement (Chapman et al. 1988; Jiang et al. 1990a). Motor cortex (and the efference copy) is not likely to be the sole source of central gating influences, and primary somatosensory cortex may in particular play an important role. Other more diffuse control systems may also be involved in this phenomenon. In this respect, attentional influences may be particularly important since these experiments essentially required the subjects to split their attention between two tasks, motor and perceptual. This suggestion is supported by the recent demonstration that the detection of vibrotactile stimuli is modified by the amount of attention directed toward the stimulus (Post and Chapman 1991).

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