Praxce-Related Improvements in Somatosensory Interval Discrimination Are Temporally Specific But Generalize across Skin Location, Hemisphere, and Modality

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This paper concerns the characterization of performance and perceptual learning of somatosensory interval discrimination. The purposes of this study were to define (1) the performance characteristics for interval discrimination in the somatosensory system by naive adult humans, (2) the normal capacities for improvement in somatosensory interval discrimination, and (3) the extent of generalization of interval discrimination learning. In a two-alternative forced choice procedure, subjects were presented with two pairs of vibratory pulses. One pair was separated in time by a fixed base interval; a second pair was separated by a target interval that was always longer than the base interval. Subjects indicated which pair was separated by the target interval. The length of the target interval was varied adaptively to determine discrimination thresholds. After initial determination of naive abilities, subjects were trained for 900 trials per day at base intervals of either 75 or 125 msec for 10–15 d. Significant improvements in thresholds resulted from training. Learning at the trained base interval generalized completely across untrained skin locations on the trained hand and to the corresponding untrained skin location in the contralateral hand. The learning partially generalized to untrained base intervals similar to the trained one, but not to more distant base intervals. Learning with somatosensory stimuli generalized to auditory stimuli presented at comparable base intervals. These results demonstrate temporal specificity in somatosensory interval discrimination learning that generalizes across skin location, hemisphere, and modality.

Key words: somatosensory; vibrotactile; temporal processing; perceptual learning; psychophysics; tactile; touch; human; auditory; hearing; interval; time

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induced changes in interval discrimination thresholds with somatosensory stimuli, and (3) establish whether improvements in somatosensory interval discrimination generalize to untrained skin locations, untrained intervals, or an untrained modality (audition). The results show that naive subjects have similar interval discrimination thresholds for somatosensory and auditory stimuli and that the patterns of learning and generalization of somatosensory interval discrimination are parallel to those previously seen for auditory interval discrimination.

MATERIALS AND METHODS

**Subjects.** Twenty-two volunteers between the ages of 19 and 51 years served as subjects. Two subjects (S10 and S14) were the first and second authors; the rest were paid for their participation. All of the subjects except the authors had no previous experience with somatosensory psychophysics or interval discrimination tasks.

**Stimuli.** Stimuli were presented either to the thenar eminence (the region of the palm that lies in a line between the thumb and the wrist) or to the distal tips of the third digit (middle finger) or fourth digit (ring finger). Sinusoidal vibrotactile stimuli were presented with a flat tip aluminum contact with a diameter of 2.5 mm. The contact was centered in a rigidly secured surround made of acrylic, which had a diameter of 7 mm. The contact and the surround were mounted on a lever arm that was counterbalanced to deliver a constant force of 100 gms. Displacements of the contacts were generated by custom-built displacement feedback tactile stimulators controlled by LabView software on a Macintosh computer. To ensure that each somatosensory stimulus was clearly detectable, we set peak displacement at 100 μm above a static indentation of ~1 mm after skin contact. Skin contact was determined by using an impedance measurement between the body and the metal probe. Although easily audible sounds were not produced by any of the stimuli used in these experiments, masking noise was presented through circumaural headphones to eliminate possible auditory cues. The masking noise was a low-pass-filtered pink noise set at a comfortable level by the subject.

Two pairs of somatosensory pulses were presented to the subject on each trial. Each brief pulse comprised one sinusoidal cycle and had a maximum displacement of 100 μm, a frequency of 40 Hz, and a total duration of 25 msec, including 5 msec rise/fall ramps. The interval marked by the pulses in a pair was measured from the onset of the first pulse to the onset of the second pulse.

**Procedure.** One pair of somatosensory pulses was presented in each observation period of a two-alternative forced choice trial (2AFC). In one observation period, the two pulses of the pair were separated by a fixed interval referred to as the “base interval.” In the other observation period the two pulses of the pair were separated by a target interval that was always longer than the base interval. The target interval was presented randomly either in the first or the second observation period. Subjects signaled which of the two observation periods contained the target interval by pressing a button on an external interface board. A light-emitting diode provided response feedback at the end of each trial. The target interval was the adaptive parameter that was decreased when the subject responded correctly on three consecutive trials and was increased whenever the subject responded incorrectly. The value of the target interval on trials in which the direction of the adaptive parameter changed from increasing to decreasing or vice versa was referred to as a reversal. This “three-down/one-up” rule estimates the 75% correct point on the psychometric function (Levitt, 1971). The step size was 10% of the base interval until the third reversal and was 1% of the base interval thereafter. At the start of each block of trials the target and base intervals were equal, forcing the subject to guess on the first few trials. The first three reversals of each 60 trial block were discarded, and thresholds were estimated by taking the average of the remaining even number of reversals. A threshold estimate was retained from a given block only if there were more than seven total reversals in a block. Thresholds are expressed by Weber fractions, defined as:

\[
\text{Weber fraction} = \frac{\text{Target interval at threshold} - \text{Base interval}}{\text{Base interval}}.
\]

At the first experimental session, to familiarize themselves with the experimental apparatus and the 2AFC experimental paradigm, subjects performed a vibrotactile detection task on the skin location in which they were to be trained. This procedure was used to establish normalcy in somesthetic sensation. The main experiment was initiated at the second session and consisted of pretest, training, and post-test phases. Pretest measurements determined the psychophysical thresholds for interval discrimination for naive subjects. For different subjects the pretest, training, and post-test measurements were determined for stimuli delivered to different skin locations, base intervals, and hands. Of the 22 subjects, 16 participated in all three phases, and six participated in the pre- and post-tests with no training. The various conditions tested during the pre- and post-test phases for all of the subjects are listed in Table 1. The pre- and post-test phases for the condition at which the subject was to be trained were always collected first; thresholds at a corresponding skin location in the opposite hand were collected last (with the exception of subject S8, in which thresholds at the left thenar eminence at a base interval of 125 msec were measured last). The rest of the conditions were presented in a pseudo-random order. Thresholds in the pre- and post-test phases were estimated from five or six blocks per condition.

The training phase occurred between the pre- and post-test phases. It consisted of 1 hr of practice per day for 10–16 d at discriminating longer intervals from a particular base interval. Fifteen to sixteen threshold estimates (900–960 trials) were collected within each training session. The position of the applied stimuli was marked on the hand of each subject who participated in the training phase. Care was taken to ensure that the position was constant across training sessions. A group of control subjects participated only in the pre- and post-test phases and did not undergo any training in the 2–3 weeks between the pre- and post-tests.

In addition to the somatosensory conditions, pre- and post-tests were conducted on auditory interval discrimination tests on one group. These tests were performed by procedures described by Wright et al. (1997a). In these tests the task was the same as in the somatosensory system, but stimulus markers were acoustic pulses (1 kHz tone pips, 15 msec long, including 5 msec rise/fall ramps, at an 86 dB sound pressure level) presented monaurally to the left ear through Sennheiser HD265 headphones. The tone pips were generated digitally with a Tucker-Davis Technologies (TDT) board and sampled at 25 kHz. Stimuli were matched to those used in the training experiments of Wright et al. (1997a), with base intervals of 50, 100, and 200 msec. Before and after training on

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Skin location</th>
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<tr>
<td>Group trained at 125 msec on left digit 4</td>
<td>Base interval</td>
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<tr>
<td>S1–S7</td>
<td>Left digit 4</td>
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<td>75</td>
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<td>S8</td>
<td>Left digit 4</td>
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<td>Group trained at 75 msec on left digit 4</td>
<td>Base interval</td>
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<tr>
<td>S13–S16</td>
<td>Left digit 4</td>
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<tr>
<td>75</td>
<td>125</td>
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<tr>
<td>Control group (no training)</td>
<td>Base interval</td>
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<tr>
<td>S17–S22</td>
<td>Left digit 4</td>
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<tr>
<td>75</td>
<td>125</td>
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*Base intervals tested at each skin location are shown. Only subjects who participated in the post-test phase are listed.*

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interval discrimination in somesthesia, five or six blocks of 60 trials were collected for each of the three auditory base intervals. The auditory pre- and post-test measurements followed the somatosensory testing. The presentation order of the conditions was pseudo-randomized across subjects.

Changes in thresholds from the pre- to the post-test measurements determined the magnitude of learning in the trained condition and the magnitude of generalization attributable to learning in untrained conditions. To compare changes in thresholds across subjects with a wide range of thresholds, it was necessary to normalize these changes to each subject’s initial thresholds. Therefore, the characteristics of learning and generalization were evaluated from the fractional change in thresholds between the pre- and post-test phases in each condition. Fractional change was defined as:

\[
\text{Fractional change} = \frac{\text{Pretest Weber fraction} - \text{Post-test Weber fraction}}{\text{Pretest Weber fraction}}.
\]

Generalization to an untrained condition was considered complete if the mean fractional change in an untrained condition was greater than zero and not significantly different from the mean fractional change in the trained condition. Generalization was considered partial if fractional improvements in trained and untrained conditions were significantly different from zero and each other.

RESULTS

Somatosensory temporal interval discrimination in naive subjects

The first objective of this study was to determine the performance characteristics for somatosensory interval discrimination in naive subjects. This section describes three aspects of that performance.

Skin location

Thresholds for interval discrimination in somesthesia were similar across different skin locations in naive subjects. Figure 1A shows pretest thresholds for interval discrimination, expressed as Weber fractions, for a base interval of 125 msec. Stimuli were delivered to five skin locations, as shown in the abscissa. The numbers in parentheses represent the number of subjects tested at each skin location. B, Interval discrimination thresholds for stimuli delivered to digit 4 of the left hand are plotted against thresholds for stimuli delivered to digit 3 of left hand. The linear regression fit is shown in the dashed line \( r = 0.65; p < 0.05 \). C, Interval discrimination thresholds for stimuli delivered to digit 4 of the left hand are plotted against thresholds for stimuli delivered to digit 4 of the right hand. The linear regression fit is shown in the dashed line \( r = 0.41; \text{ns}, \text{not statistically significant} \).

Figure 1. Effects of skin location. A, Distribution of interval discrimination thresholds expressed as Weber fractions for a base interval of 125 msec. Stimuli were delivered to five skin locations, as shown in the abscissa. The numbers in parentheses represent the number of subjects tested at each skin location. B, Interval discrimination thresholds for stimuli delivered to digit 4 of the left hand are plotted against thresholds for stimuli delivered to digit 3 of left hand. The linear regression fit is shown in the dashed line \( r = 0.65; p < 0.05 \). C, Interval discrimination thresholds for stimuli delivered to digit 4 of the left hand are plotted against thresholds for stimuli delivered to digit 4 of the right hand. The linear regression fit is shown in the dashed line \( r = 0.41; \text{ns}, \text{not statistically significant} \).
ingly, thresholds across individual subjects were linearly and rank orderly correlated between neighboring digits on the left hand [see Fig. 1B; linear correlation = 0.65 (p < 0.05); Spearman’s rank order correlation = 0.753 (p < 0.05)]. By contrast, individual subject thresholds were not correlated significantly between the left and right hands [see Fig. 1C; linear correlation = 0.41 (p > 0.05); Spearman’s rank correlation = 0.36 (p > 0.05)], and the side with the lowest thresholds did not relate systematically to handedness.

Base interval

Thresholds for somatosensory interval discrimination, expressed as Weber fractions, approached a constant value for longer base intervals and were significantly different from thresholds at other base intervals, following a pattern similar to that for auditory duration discrimination (Getty, 1975). Figure 2A shows Weber fraction thresholds for interval discrimination at base intervals of 75, 125, 225, and 525 msec. Because there were no significant differences in thresholds for different skin locations, the data for this analysis were pooled across skin location. A one-way factorial ANOVA with base interval as the factor indicated significant differences in mean thresholds, expressed as Weber fractions, for different base intervals (F(3,76) = 4.04; p < 0.05). Post hoc Scheffé’s and Bonferroni/Dunn tests indicated that only the thresholds for the base intervals of 75 and 225 msec were significantly different from each other (p < 0.005).

Modality—somatosensory versus auditory

Interval discrimination thresholds with somatosensory and auditory stimuli showed similar temporal precision across the two sensory systems for naive subjects. These data for both modalities obtained from the same set of seven subjects are shown in Figure 2B. A two-way factorial ANOVA with modality (auditory and somatosensory) and interval (50–75, 100–125, and 200–225 msec) as factors revealed statistically significant threshold differences across intervals (F(2,36) = 3.877; p < 0.05), but not across modality (F(1,36) = 0.06; p > 0.5), with no significant interaction (F(2,36) = 1.5; p > 0.1). The thresholds for individual subjects for
comparable base intervals were neither linearly nor rank orderly correlated between the two modalities, indicating idiosyncratic variability in thresholds across conditions.

**Perceptual learning of somatosensory interval discrimination**

The second objective of this study was to determine whether training improved somatosensory interval discrimination. Every subject improved with practice. The individual learning profiles for 12 subjects trained at a base interval of 125 msec are shown in Figure 3A. The symbols indicate the mean thresholds obtained during each training session (open squares) and in the pre- and post-test phases (filled squares). The error bars indicate ± 1 SEM within subjects. Note that each training session consisted of 10–15 threshold estimates, whereas training thresholds were obtained for 15 blocks. B. Mean of all of the subjects trained at a base interval of 125 msec plotted as a function of training days. Here, error bars represent 1 SEM across subjects.

**Figure 3.** Learning curves for training at a base interval of 125 msec. A. Individual subject thresholds, expressed as Weber fractions, plotted as a function of training sessions. Stimuli were delivered to the distal tip of the fourth digit for subjects S1–S8 and to the thenar eminence for subjects S9–S12. Bars are SEM within subjects. The filled symbols indicate pre- and post-test thresholds for each subject. Note that the pre- and post-test thresholds were estimated from five to six blocks of 60 trials, whereas training thresholds were obtained for 15 blocks. B. Mean of all of the subjects trained at a base interval of 125 msec plotted as a function of training days. Here, error bars represent 1 SEM across subjects.
trained at the distal tip of the fourth digit of the left hand. The four panels on the right (S9–S12) show learning for subjects trained on the thenar eminence of the left hand. Reductions in threshold, which indicated improvement, were observed in all of the subjects trained in the study. Some subjects made dramatic improvements (S1–S3), whereas others showed lesser improvements.

Figure 3B shows the mean learning curves for the first 10 d of training for the 12 subjects who worked at the base interval of 125 msec. Performance improved rapidly in the first few days of training and then saturated at approximately the 10th day. Mean thresholds between the pretest and post-test phases changed by 42% (from a Weber fraction of 0.28–0.16). A one-way repeated measures ANOVA with threshold over all of the days as the 42% (from a Weber fraction of 0.28 – 0.16). A one-way repeated thresholds between the pretest and post-test phases changed by training and then saturated at approximately the 10th day. Mean improvements.

The observed improvements were not specific to training at 125 msec. Figure 4A shows the individual learning curves, and Figure 4B shows the mean learning curve for four subjects trained at a base interval of 75 msec. Mean performance improved significantly by 63% from an initial Weber fraction of 0.49 in the pretest to 0.18 in the post-test (F_{(3,11)} = 8.56; p < 0.0001). Again, excluding the pre- and post-test measurements reduced the magnitude of improvement to 42% (from 0.33 to 0.19), which was still significant (F_{(3,9)} = 4.1; p < 0.001).

To confirm that the observed changes were attributable to training, we measured threshold changes for a base interval of 125 msec in the untrained control group across pre- and post-test sessions separated by 10–14 d (see Fig. 5A). Data from the two trained groups and the control group were analyzed by a one-way factorial ANOVA for fractional change, with group as the factor. This analysis revealed a significant effect for group (F_{(3,19)} = 6.53; p < 0.005), and post hoc Scheffé’s and Bonferroni/Dunn tests revealed that there were significant differences between the control group and both training groups (p < 0.01). Furthermore, changes in the control group were not significantly different from zero, as revealed by a Student’s t test on the fractional improvements for subjects in the control group (t_{(5)} = 0.853; p > 0.1).

Finally, to address whether changes attributable to training correlated with pre- or post-test thresholds, fractional changes for individual subjects were plotted against their pretest and post-test thresholds (Fig. 5B). Fractional changes in the trained condition showed a moderate and statistically significant positive correlation with the pretest thresholds (r = 0.56; p < 0.05), but not with the post-test thresholds (right panel). Consistent with this observation, the variability of the thresholds decreased both within and across subjects after training (Fig. 5C).

Generalization of Learning in somatosensory interval discrimination

The third objective of this study was to determine the generalization of learning in somatosensory interval discrimination. Three forms of generalization are described in this section.

Spatial generalization

Learning at the trained location generalized to untrained skin locations. Figure 6A shows fractional changes for the 125 msec base interval at the trained and untrained skin locations for all of the subjects trained at a base interval of 125 msec. Subjects were trained either at the tip of digit 4 of the left hand or to the thenar eminences. Learning in both groups of subjects generalized to untrained contralateral (corresponding positions on the right hand, t_{(5)}; p < 0.05) skin locations. In subjects trained at the tip of digit 4 of the left hand, learning generalized to the adjacent digit (digit 3 of the left hand, t_{(5)} = 4.59; p < 0.005). These generalizations to adjacent and contralateral skin locations were found to be complete. A one-way ANOVA with trained and untrained skin location as the factor revealed no statistically significant differences among the fractional changes between trained and untrained skin locations (F_{(2,20)} = 1.82; p > 0.1).
Temporal generalization

Learning at the trained base interval generalized only partially or not at all to untrained base intervals. To determine the temporal characteristics of generalization, we first examined fractional changes across subjects trained at a base interval of 125 msec, who were tested at untrained base intervals of 75 and 225 msec. For these analyses the fractional changes were pooled across subjects trained at different skin locations for the same base intervals. Figure 7A shows that training at a base interval of 125 msec completely generalized to the untrained interval of 75 msec but showed no generalization to 225 msec. Mean fractional changes showed significant differences from zero at a base interval of 75 msec (t(11) = 4.4; p < 0.005), but not at a base interval of 225 msec (t(11) = 0.08; p > 0.9). Further, a one-way factorial ANOVA performed with base intervals (75, 125, and 225 msec) as the factors showed that mean fractional changes differed across base intervals (F(3,37) = 3; p < 0.05). Post hoc Scheffé’s and Bonferroni/Dunn tests revealed that fractional changes for the base interval of 225 msec differed significantly from those for shorter base intervals (p < 0.01). Surprisingly, however, across subjects the fractional changes at base intervals of 75 msec did not show any statistically significant linear or rank order correlation with fractional changes at a base interval of 125 msec.

Figure 7B shows that training at a base interval of 75 msec only partially generalized to an untrained interval of 125 msec, the only untrained interval tested. Mean fractional changes were significantly different from zero at the variance between pre-test threshold and fractional changes (r = 0.56; p < 0.05) and for <4% of the variance between post-test thresholds and fractional changes (r = −0.2, ns). The variability of thresholds decreases with training both within (left panel) and across subjects (right panel). Within subjects, the SEMs of average pre- and post-test thresholds are shown. Across subjects, the SEMs of the pre-and post-test thresholds are shown.

Modality generalization

Interval discrimination learning in the somatosensory system generalized to the auditory system, but only for an auditory base interval of 125 msec.
Performance of somatosensory interval discrimination in naive subjects

The purpose of this study was to characterize somatosensory interval discrimination by naive subjects and to assess the capacity for perceptual learning and generalization of somesthetic interval discrimination. An important finding of this study was that interval discrimination by naive subjects within the somatosensory system is approximately equivalent to that reported for the auditory system (Wright et al., 1997a) and similar across base intervals, spatial location, and modality. These results suggest that discrimination of timing information across these two sensory systems may operate via similar central timing mechanisms.

The present data revealed few significant linear or rank order correlations between thresholds across different measurement conditions. This observation could result simply from the variability of thresholds in naive subjects. Alternatively, significant correlations or the lack thereof could reflect the mechanisms responsible for task performance. If the latter were true, the observation of a significant correlation between interval discrimination thresholds on adjacent digits would suggest that similar local timing machinery is involved in those discriminations. All of the subjects were right-handed, and no significant differences were observed between thresholds in the right hand and in the left. This lack of correlation of thresholds between contralateral skin locations and of thresholds with handedness would suggest an independence between temporal processing and handedness, consistent with previous reports on haptic processing and handedness (Summers and Lederman, 1990). Furthermore, the data do not reveal any significant correlations between naive thresholds with auditory and somatosensory stimuli. These data would suggest that, although central machinery-representing intervals do not reveal any significant correlations between thresholds across different measurement conditions. This observation could result simply from the variability of thresholds in naive subjects. Alternatively, significant correlations or the lack thereof could reflect the mechanisms responsible for task performance. If the latter were true, the observation of a significant correlation between interval discrimination thresholds on adjacent digits would suggest that similar local timing machinery is involved in those discriminations. All of the subjects were right-handed, and no significant differences were observed between thresholds in the right hand and in the left. This lack of correlation of thresholds between contralateral skin locations and of thresholds with handedness would suggest an independence between temporal processing and handedness, consistent with previous reports on haptic processing and handedness (Summers and Lederman, 1990). Furthermore, the data do not reveal any significant correlations between naive thresholds with auditory and somatosensory stimuli. These data would suggest that, although central machinery-representing intervals are similar, they operate independently across modality and spatially distinct skin locations.

Nontemporal cues and somatosensory interval discrimination

Previous auditory studies have shown that nontemporal cues (e.g., perceptual effects on intensity, frequency, and bandwidth) are not used for duration discrimination with suprathreshold stimuli (Di- venyi and Danner, 1977). Stimulus interactions, such as masking, suppression, or enhancement, do generate perceptual effects with somatosensory stimuli (Verillo and Gescheider, 1975; Gescheider and Migel, 1995). Several studies of Gescheider and colleagues have demonstrated masking interactions on detection thresholds up to 12 dB re 1 μm, which last up to 125 msec. However, clearly suprathreshold displacements were used in this study, so masking effects probably did not play a role in processing. With comparable stimuli, Verrillo et al. (1975) have shown that the perceived intensity of a stimulus pair (summation effect) or the subjective magnitude of the second stimulus of a pair (enhancement effect) were <3 dB re 1 μm displacements, as compared with the perceived intensity of a stimulus in isolation. Moreover, and
at a base interval of 75 msec (indicated by the fractional change at base intervals of 75 and 125 msec for subjects trained to a similar asymptote. These performance limits may indicate the ultimate capacities and constraints for interval or duration estimation mechanisms in normal humans.

An earlier study that recorded no learning effects for interval discrimination concluded that a clock or timing mechanism that was affected by various internal or external factors would not be a very reliable clock (Rammsayer, 1994). In these studies the subjects were trained only on 50 trials per session. By contrast, the subjects in the present study were trained with 900 trials per session. Differences in training intensity, schedule, and trial numbers easily could account for differences in recorded improvements resulting from practice. The learning results reported here provide further evidence that, like many other cortical functions, timing mechanisms can be modified via training.

Generalization of somatosensory interval discrimination

Learning of somatosensory interval discrimination at the trained base interval generalizes completely to untrained skin locations. This finding is consistent with results obtained for interval discrimination that used auditory stimuli, in which training effects generalized across at least two octaves in the frequency dimension for the trained base interval (Wright et al., 1997a). However, it should be remembered that only nearby skin locations on either hand and corresponding skin locations across hands were examined in these experiments. The topographic specificity of inter-hemispheric cortical connections necessitates a cautionary interpretation of widespread spatial generalization. These results are also consistent with other studies on somatosensory perceptual learning that do not involve purely temporal tasks. For example, training on grating discrimination showed widespread spatial generalization but was highly specific to the trained task (Sathian and Zangaladze, 1997).

Somatosensory interval discrimination learning shows partial generalization to base intervals that are similar to the trained one and no generalization to farther base intervals. This temporal specificity is in contrast to auditory interval discrimination in which learning at a base interval of 100 msec did not generalize to base intervals of 50 and 200 msec (Wright et al., 1997a). The broader temporal generalization in the somatosensory system is consistent with the fact that other temporal interactions, such as masking, exhibit longer time constants in the somatosensory than in the auditory system (Gescheider and Migel, 1995). These results also support the notion that learning in temporal tasks is specific to the temporal information in stimuli, analogous to learning in spatial tasks, which is specific to the spatial aspects in stimuli (Karni and Sagi, 1991, 1993).

Remarkably, the observed temporal specificity for base interval extends to a second (auditory) modality. These results corroborate that the subjects in this study did not use nontemporal cues for task performance, because such a possibility could not account for the observed temporal specificity with auditory stimuli. The cross-modal generalization reported here is consistent with other reports on symmetric transfer of improvements in temporal discrimination accuracy between audition and vision attributable to training in audition (Warm et al., 1975; Rousseau et al., 1983). Such cross-modal generalization is also consistent with other perceptual learning experiments involving spatial discrimination tasks with vibrotactile patterns that transfer to vision (Epstein et al., 1989; Hughes et al., 1990). These previous and present examples of cross-modal generalization provide supportive evidence for “sensory integration training” (Ottenbacher, 1982).

It is also remarkable that there is a significant correlation
between improvements on a trained somatosensory condition and an untrained auditory condition at a comparable base interval (see Fig. 8). This correlation between fractional changes is not the consequence of a correlation between performance in pre- or post-test measurements, because there was no significant cross-modal correlation of performance on either of those conditions separately, and only the fractional change was correlated. Such generalization of the mean fractional changes across modality (to audition) also suggests that learning may occur via central or shared timing mechanisms, representing intervals that are independent of modality.

**Models for temporal processing**

Our findings, and those of a previous study (Wright et al., 1997a), provide evidence that challenges previous models of temporal processing. Both studies have found specificity in learning to the trained intervals, and both have found spatial transfer. Transfer to different frequencies in the auditory task is analogous to spatial transfer in somesthesia. Whatever the mechanisms that underlie temporal processing in the CNS, they must be specific for interval length but less specific spatially.

Although several models have been proposed for perceptual learning and associated neural plasticity for spatial tasks, there are no widely accepted models for perceptual learning of temporal tasks because of the lack of information on the characteristics of learning associated with temporal information processing. Extensive studies on interval discrimination performance in experienced subjects have contributed to the formulation of several models of performance on temporal tasks.

One dominant model for temporal processing that is consistent with numerous psychophysical studies is the “internal clock” hypothesis. According to this hypothesis, a pacemaker generates pulses, and the number of pulses occurring during a given time period is recorded by an accumulator. The neurobiological bases for these pacemakers and accumulators currently are unknown, although cerebral oscillations have been argued to participate in
such processing (Treisman, 1984, 1990, 1994). Internal clock models predict that the clock or timing mechanisms would be unaffected by external influences. Such models require significant modification if they are to account for the observed learning in interval discrimination.

An alternative model for interval discrimination is the interval measure hypothesis. Ivry and others have postulated a spatial representation of interval information in the brain that could be used in timing tasks (Ivry, 1996). They argue that increased Weber fractions for stimuli delivered across modalities could not be accounted for by internal clock models. Biologically plausible implementations of interval measure models usually assume the presence of a temporal-to-spatial transformation resulting from deterministic or stochastic “delay lines.” Deterministic delay line models assume a range of time constants that represent intervals. Such models have been successful to a certain extent in implementing temporal tasks (Tank and Hopfield, 1987; Grossberg and Schmajuk, 1989). Stochastic delay line models do not assume a range of time constants. Rather, they postulate that time-dependent neural and synaptic properties, such as short-term synaptic plasticity and slow inhibitory processes, participate in the emergent representation of intervals in the time scale of 50–500 msec (Buonomano and Merzenich, 1995). Recently, experimental evidence for the role of time-dependent neural properties on the representation of interval and duration has been reported (Casseday et al., 1994; Buonomano et al., 1997). Preliminary attempts at determining synaptic learning rules for the processing of temporally complex inputs have brought forth the realization that simplistic Hebbian principles need to be redefined in the context of complex time structure in sensory input (Buonomano et al., 1997; Markram et al., 1997a).

Our results and those of Wright et al. (1997a) showing temporal specificity and spatial generalization indicate that both the internal clock models and interval measure models must be modified significantly, because these models in their current forms would predict neither interval discrimination learning nor the characteristics of generalization. Moreover, both the internal clock and interval measure models assume a representation of absolute time intervals in contrast to the characteristics of relative time discrimination reported in this paper. Therefore, biologically realistic models for interval discrimination require the integration of the characteristics of learning reported here and a greater understanding of the neurophysiological and psychophysical rules governing plasticity in the neural representation of temporal information.

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