Exp Brain Res (1988) 73: 459–469

Experimental Brain Research

Somatosensory evoked potential correlates of psychophysical magnitude estimations for tactile air-puff stimulation in man

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Summary. Brief air-puff stimuli were applied to the volar surface of the right hand to obtain both psychophysical and neurophysiological responses. The detection threshold (So) was first determined ($0.56\ kg \cdot cm^{-2} \pm 0.20\ kg \cdot cm^{-2}$, mean ± SD) and six levels of the stimulus intensities ($So + 0.25\ kg \cdot cm^{-2}$, $So + 1.25\ kg \cdot cm^{-2}$, $So + 2.50\ kg \cdot cm^{-2}$, $So + 3.75\ kg \cdot cm^{-2}$, $So + 5.00\ kg \cdot cm^{-2}$, and $So + 6.25\ kg \cdot cm^{-2}$) were employed for magnitude estimation using the stimulus level of $So + 2.50\ kg \cdot cm^{-2}$ as the standard stimulus. The subject was asked to estimate numerically the series of stimulus intensities randomly presented. Cortical SEPs were recorded over the hand sensory area in response to a set of 120 air-puffs at the identical intensity level. Thus SEPs for six sets of stimulus intensities given in a random order were obtained from each subject. Six components (N20, P27, N35, P45, N60, and P75) were recorded within 100 ms following stimulation. It was seen that a simple power function with an exponent of 0.81 could be an adequate description of the stimulus-response function for magnitude estimation, as was also revealed by the high correlation coefficient ($r = 0.98$). Similarly, stimulus-amplitude functions of different SEP components were well represented by straight lines in double logarithmic plots. The function of the early P27-N35 had the highest exponent (0.56) and also the highest correlation coefficient ($r = 0.91$). Plotting subjective magnitude on the abscissa produced power functions similar to the stimulus-amplitude functions. However, higher correlations were observed for later components. The amplitudes of the four earlier components correlated with stimulus intensity when the effect of subjective magnitudes was removed. In contrast, the correlation between amplitudes and subjective magnitudes with stimulus intensity held constant was positive and significant for the later three components. These results may indicate that early SEP components represent neural coding of physical intensity while later components are more closely related to the subjective judgment of the stimulus.

Key words: Tactile air-puff stimulation – Human skin sensation – Stimulus intensity – Psychophysical magnitude estimations – Somatosensory evoked potentials

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Introduction

During the last two decades, several attempts to relate tactile skin sensation magnitude to somatosensory evoked potentials (SEPs) have been reported, and power function relationships were demonstrated between stimulus intensity and SEP amplitudes and also between sensation magnitude and SEP amplitudes (Franzén and Offenloch 1969; Johnson et al. 1975; Murayama 1985). In those experiments either electric shock or vibration was used as a stimulus modality. The disadvantage of electrical stimulation is the lack of specificity with regard to the types of fibers activated within a nerve trunk, thus confounding SEPs from skin receptors with those from underlying deeper tissue receptors. The problem with vibratory stimulation is the purely mechanical spread of the percussion wave in every direction from the stimulus, activating receptors located both proximal and distal to the area of stimulation (Gandevia et al. 1983). Moreover it is extremely difficult to maintain a constant intensity of vibrotactile stimulation within and across experimental sessions mainly due to skin movements with pulsation and respiration (Westling et al. 1976; Johansson and Vallbo 1979).

Air-puffs have been shown to elicit more selectively activity of skin receptors within a circumscribed area without direct touch or steady pressure on the skin. Thus this mode of stimulation provides a more pertinent means for the study of natural skin sensation (Schieppati and Ducati 1984; Gardner et al. 1984). However, the method has the disadvantage of rather slow rise and decay times (5–13 ms) and long duration (10–60 ms) as a result of the electromechanical opening and closing of valves (Matsumiya and Mostofsky 1971; Gardner and Costanzo 1980; Schieppati and Ducati 1984). Thus, air-puffs have two specific limitations; first, uncertainty about the timing relationship between stimulus onset and activation of cutaneous receptors and, second, the prolonged rise and fall times presumably can activate receptors with different thresholds resulting in a temporal dispersion of the response. The present study employed a new high-speed air control system which provides air-puffs with fast rise (1 ms) and fall (1 ms) times and a total duration of 2 ms to elicit SEPs, permitting reasonably accurate time locking for averaging of SEPs.

We have conducted simultaneous psychophysical and neurophysiological studies on normal subjects, using this brief air-puff. The experiments were designed to allow analysis of quantitative relationships among stimulus intensity, subjective magnitude of the stimulus and SEPs for equivalent stimulus conditions.

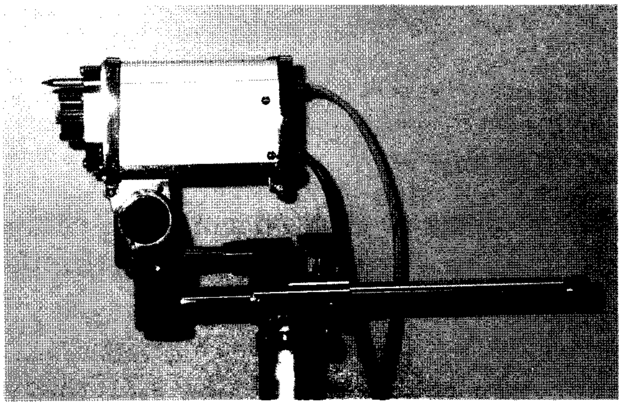


Fig. 1. The air control system for generating fast rise-time air-puffs. A rotating disc driven by a synchronous electric motor and a photo-diode circuit pulsed with each passage of the disc opening were used to control the delivery and duration of the air-puff. The rotating disc, motor and electronics were encased in a sound-damped metal box mounted on a heavy mechanical manipulator, allowing free positioning of the stimulator perpendicular to and above any desired area over the skin surface. A nozzle placed 1 cm from and perpendicular to the volar surface of the right hand delivers the air-puff

Methods

Two different sets of experimental data were collected: the psychophysical magnitude estimations and the SEPs to the identical tactile stimuli on the glabrous skin of the human hand. Experiments were performed on 31 healthy students, 21 females and 10 males following accepted informed consent practices. The subjects were between 16 and 34 years old (22.65 ± 3.67, Mean ± SD). During the experiments they lay supine on a couch with his or her right upper arm extended laterally. The subjects had no experience of psychophysical or electrophysiological tests prior to the experiments. Each subject took part in both psychophysical and neurophysiological experiments on the same day. They were instructed to pay attention to the air-puff stimuli delivered to the skin of their hands. Continuous white noise was delivered bilaterally through insert earphones at a level sufficient to mask any noise from the air control system as well as the sound of air passing through the nozzle when air-puffs were delivered.

Air-puff stimulation

Air-puffs were delivered perpendicular to the volar surface of the right hand at the base of the index finger through a nozzle with a 0.6 mm diameter orifice placed 1 cm from the skin. The most sensitive target point over the skin area was determined manually with a small blunt probe using near-threshold gentle strokings and was marked on the skin. The palm of the right hand was maintained lightly with adhesive plaster against the smoothly curved surface of a semi-circular plastic mold. Thus there was no active muscle contraction to keep the position. The plastic mold had 3 vertical parallel slits, 1 cm in width, for stimulus delivery. In this manner, the distance between the nozzle and target skin could be kept fairly constant throughout an experimental session.

The high-speed air-puff stimulator (Fig. 1) was used. The mechanical characteristics of the air-puff have been described in previous reports (Hashimoto 1987a, b, 1988). Briefly, the rotating disc with a small hole driven by a synchronous electric motor was used to control the delivery and duration of air flow from a compressed air source. A photo-diode circuit, pulsed with each passage of the disc opening, was used to control the stimulus frequency while stimulus duration was kept constant. The rotating disc, motor and electronics were encased in a sound-damped metal box. The time lag between the electric signal from the photo-diode and arrival of the air-puff at the skin surface was monitored with a condenser microphone. This delay was compensated for by the one-shot multi-circuit used to trigger an averaging system (Nicolet Pathfinder II). The stimulation device was mounted on a heavy mechanical manipulator rigidly fixed on the supporting shaft with casters, allowing free-positioning of the stimulator perpendicular to and above any desired area over the skin surface.

The surface area activated by the air-puff is a function of the distance between the exit nozzle and the skin surface (Fig. 2A). The diameter and cross sectional area of the air-puff at a distance of 1 cm where the target skin was in focus were 1.8 mm and 2.5 mm^2 respectively.

The pressure waveform produced by the air-puff varied as a function of the regulated air pressure feeding the source as shown in Fig. 2C. With an initial pressure of 1.0 $kg \cdot cm^{-2}$ or less the rise and fall times of the stimuli were extended. However, a sharp air-puff with a rise time of 1 ms and a total duration of 2 ms was easily achieved with a pressure of 1.5 $kg \cdot cm^{-2}$ or more. The duration of the pressure waveforms did not vary at pressures above

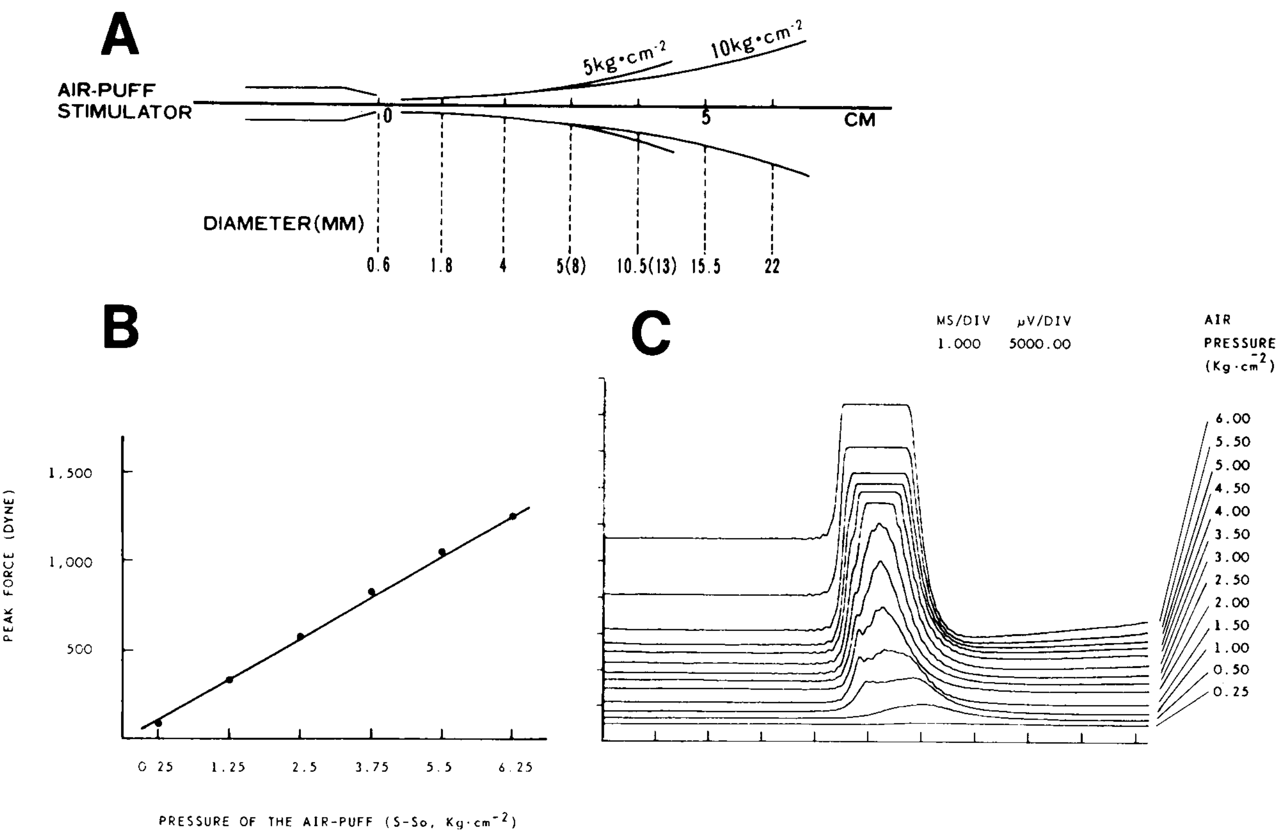


Fig. 2. **A** Jet-beam of the air-puff from the nozzle. The diameter and cross-sectional area of the jet-beam are relatively small up to 3 cm from the nozzle and fan out exponentially beyond. **B** Relationship between pressure (kg · cm^{-2}) and peak force (dyne). Peak force increases linearly with successive elevations of the pressure within the stimulus range used in the experiments. **C** Pressure waveforms of the air-puffs as recorded with a condenser microphone located 1 cm from the nozzle. A sharp peak appears abruptly at a pressure of 1.5 kg · cm^{-2} with no further changes in the rise-time and duration of the curve with increasing pressure. The plots show saturation above a pressure of 3.5 kg · cm^{-2}. The analysis time is 10 ms and the voltage calibration is 5 mV per division.

2.0 kg · cm^{-2} and only peak force increased linearly with successive elevations of the pressure. Overall, the relationship between peak force and air pressure applied to the source was a linear function over the stimulus range employed in the experiments (Fig. 2B).

The air-puffs with a maximal peak force did not produce visible skin indentation at the volar surface of the palm but did produce skin indentation over the face. Within the intensity range, the temperature of the air-puff at 1 cm from the nozzle was 0.2° C or less below that of the room air and the sensation of temperature change associated with the brief cooling of the skin during the air-puff was very weak and much less prominent than the sensation of mechanical skin deformation and thus appeared negligible.

Psychophysical experiments

At the beginning of an experiment a short period was spent on training to acquaint the subject with the procedure. The psychophysical method of limits was adopted to measure the detection threshold (So); the stimulus intensity varied in 0.25 kg · cm^{-2} steps in ascending and descending orders until the minimal intensity was reached which elicited barely perceptible skin sensation. Then the detection probability was assessed by giving the stimulus at random intervals and asking the subjects to count the number of the detected stimuli. Thus the detection threshold was defined as the minimal intensity with a detection probability of more than 90% but less than 100% of presentations.

The thresholds were symmetrically and narrowly distributed around the mean value of 0.56 kg · cm^{-2} with standard deviations as small as 0.20 kg · cm^{-2}.

Six levels of stimulus intensity above the thresholds employed in the present study were the following: So + 0.25 kg · cm^{-2}, So + 1.25 kg · cm^{-2}, So + 2.50 kg · cm^{-2}, So + 3.75 kg · cm^{-2}, So + 5.00 kg · cm^{-2}, and So + 6.25 kg · cm^{-2}. These stimulus intensities elicited skin sensation ranging from light tapping to mild pressure. The scales of apparent intensity were obtained by the method of magnitude estimation (Stevens and Mack 1959). Using the stimulus level of So + 2.50 kg · cm^{-2} as the standard stimulus and assigning the number 10 to this stimulus level, the subject was asked to estimate numerically a series of stimulus intensities in such a way that the number was proportional to the subjective magnitude of the stimulus intensity. Every stimulus intensity occurred once in a random order including the standard itself. This experimental procedure was repeated three times for each subject and the mean values of the reported magnitudes were used for data analysis.

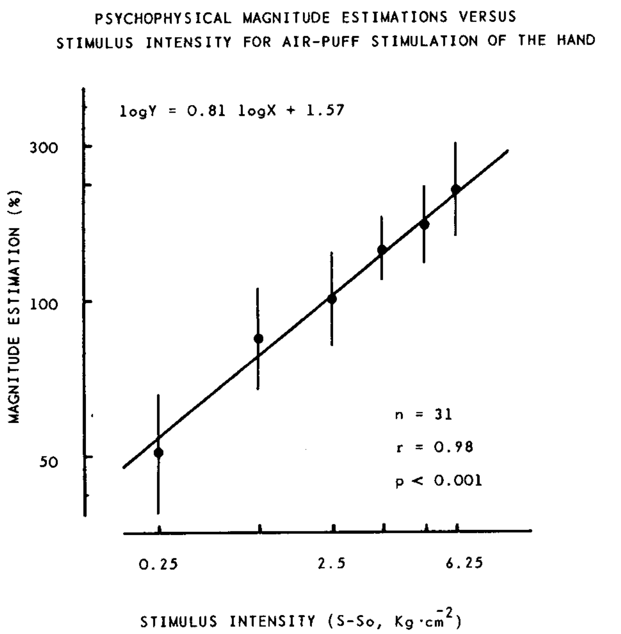


Fig. 3. Log-log plot of normalized magnitude estimations against stimulus intensity. To facilitate a direct comparison with the results of neurophysiological experiments, magnitude estimations at different stimulus levels were transformed into normalized values (%), using magnitude estimation at the standard stimulus level of So + 2.50 kg · cm^{-2} as 100%. Grand means and one S.D. of data from 31 subjects are shown in the plot. The regression line is derived from the individual data

Neurophysiological experiments

SEPs were recorded from a disc electrode over the contralateral (left) hand sensory area referenced to a frontal electrode (Fz). The frontal reference was chosen to reduce the contribution from extracranial and subcortical sources although this montage may pick up concurrent frontal field potentials. Interelectrode impedances were maintained below 3 kΩ and readings generally were in the 1–2 kΩ range. Signals were amplified (gain of 10^5), filtered (15 Hz–250 Hz, 12 dB · oct^{-1} roll-off), and fed to the averaging system. This filtering did not affect waveform of the early 6 cortical components (N20, P27, N35, P45, N60 and P75) but significantly attenuated later components. A sampling period of 200 ms (0.4 ms dwell time, 512 points) was used to average a set of 120 artifact-free responses to air-puffs at the same stimulus intensity level. Thus SEPs for each set of 6 stimulus intensities given in a random order were obtained from each subject. The computer automatically rejected any trial in which the amplifier was loaded with extraneous artifacts generated by eyeblinks, eye movements or excess muscle potentials. Averaged potentials were displayed on an X-Y plotter (relative negativity at the active electrode resulted in an upward deflection) and stored for off-line cursor analysis of amplitudes and latencies. Amplitudes of SEP components were measured from the negative or positive peak to the immediately following peak of opposite polarity (peak-to-peak). Peak latencies were measured from onset of air-puffs hitting the skin surface to peaks of various components. EEG was continuously monitored on the oscilloscope during the experiments and the data were taken from a fairly uniform EEG pattern; averaging was terminated during drowsiness or sleep.

Statistical analysis

Both psychophysical and neurophysiological data were all subjected to analysis of variance (Eisenhart 1947) and trend analysis (Edwards 1972). The correlation analysis of the psychophysical data was based on the mean values of three trials from the individual subject. For the neurophysiological data analysis, original data from the individual tests were used. Thus all plots in the figures in the present study were derived from the individual data. Partial correlation analysis was used to assess the relationships between stimulus intensity level, peak-to-peak amplitudes of SEP components and subjective magnitude estimations (Timm and Carlson 1976). The analysis was made on the individual data as in that of variance. We have chosen this approach to arrive at a true correlation between two variables when there is a third variable that correlates with both as in the present experiments. The statistical significance of differences between two populations was assessed using the Tukey's q-test (Ryan 1960). Comparison of the slopes/exponents of the regression lines, in particular, was made according to Snedecor and Cochran (1967). The level of probability selected as significant was a value of $P < 0.05$ (two-tailed test).

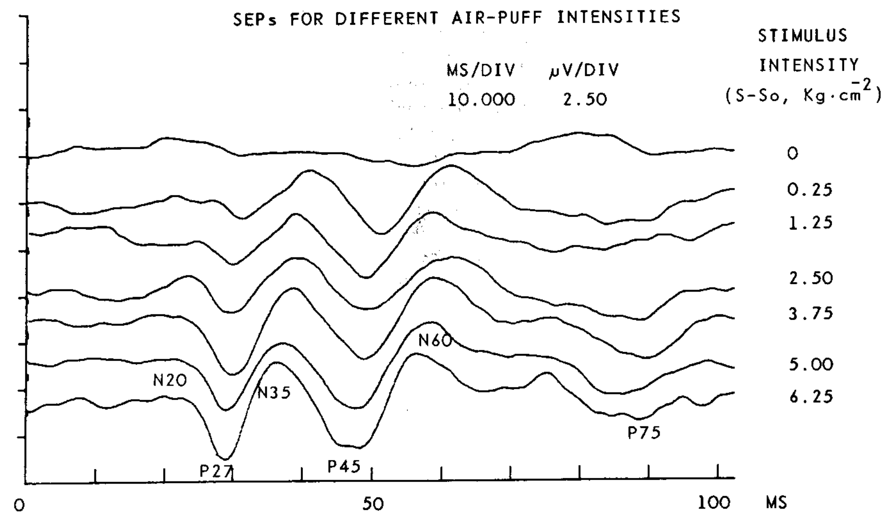


Fig. 4. Somatosensory evoked potentials (SEPs) at varying stimulus intensities. SEPs were recorded from the contralateral hand sensory area in response to a set of 120 air-puff stimuli at the same stimulus intensity. Thus recordings for each set of 6 stimulus intensities given in a random order were obtained from each subject. Peak-to-peak amplitudes increased and peak latencies decreased monotonically with increasing stimulus intensity. The analysis time is 100 ms and the voltage calibration is 2.5 μV per division

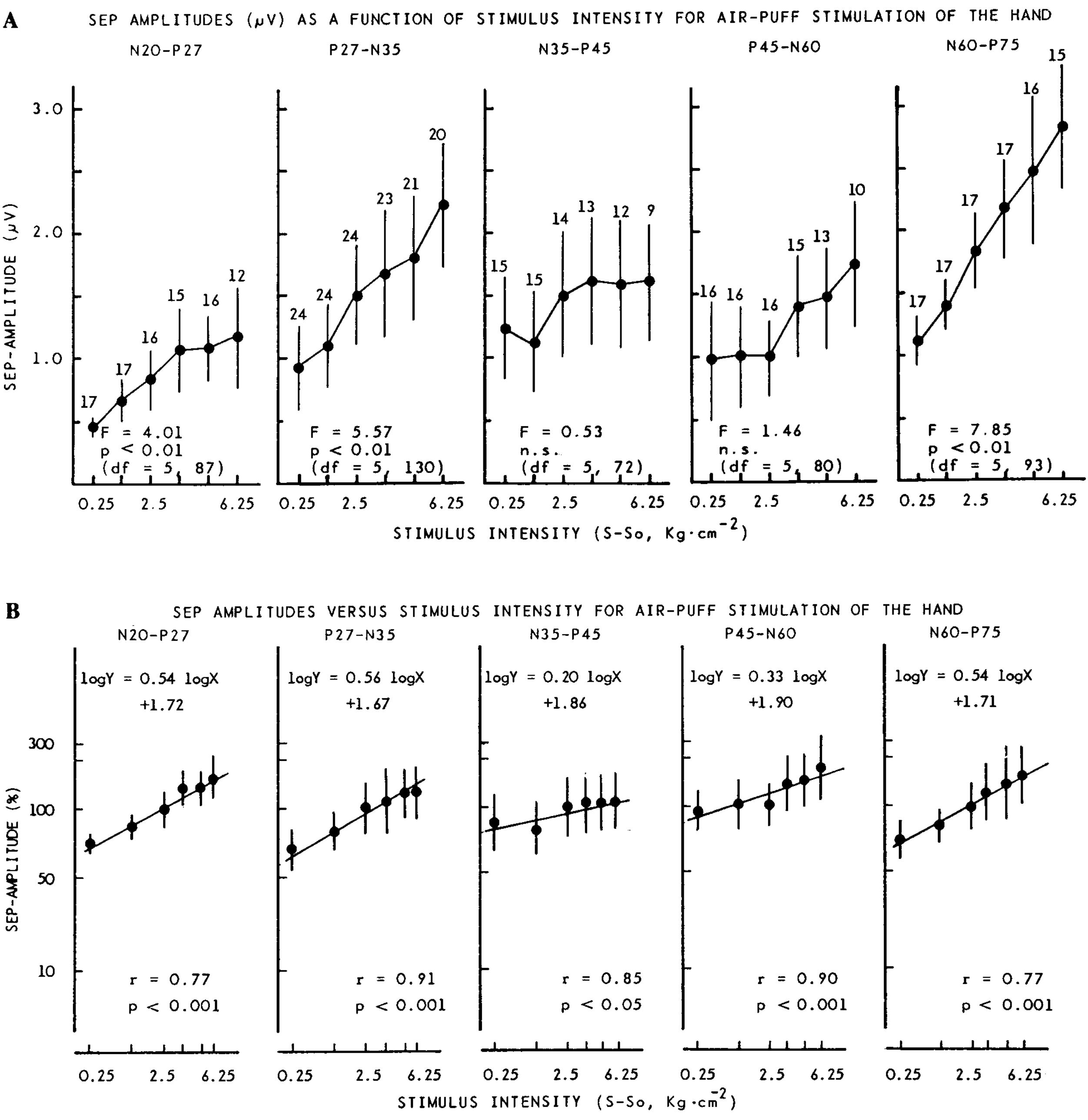
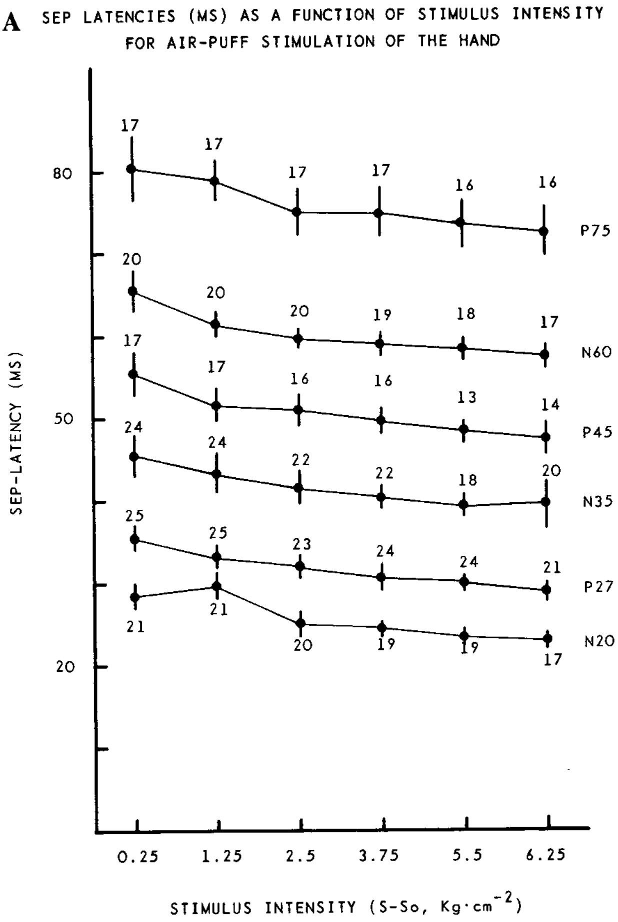


Fig. 5. A Relation between SEP amplitudes (μV) and stimulus intensity in linear plots. Solid circles and vertical bars indicate means and one S.D. Numerals above the bars give the number of SEP tests underlying the distributions. Statistical significance across levels for each SEP component is given at the bottom of the plot. **B** Log-log plots of normalized SEP amplitudes against stimulus intensity. To facilitate a direct comparison between different components and also with the results of psychophysical experiments, amplitude values (μV) at different stimulus levels were converted into normalized values (%) using amplitudes at the standard stimulus level (So + 2.50 kg · cm^{-2}) as 100%. Solid circles and vertical bars indicate means and one S.D. Regression lines are derived from the individual data

Results

Subjective assessment of stimulus intensities

The normalized values of subjective magnitudes were plotted as a function of stimulus intensity on double logarithmic coordinates (Fig. 3). Analysis of variance revealed significant differences in the mean subjective magnitude across stimulus intensities ($F(5,184) = 107.06$, $P < 0.001$). A test for linear trend also yielded statistical significance ($F(1,184) = 25.39$, $P<0.001$). The exponent of the power function was 0.81 and a strong correlation was observed between stimulus intensity and subjective assessment of the



stimulus ($r = 0.98$, $P < 0.001$). It is clear from these results that subjective estimations of the stimulus intensities in skin sensation follow a simple power function as in other sensory modalities (Stevens 1971).

Relationship of SEP amplitudes to stimulus intensities

Samples of cortical SEPs at successively increasing stimulus intensity are illustrated in Fig. 4. On the whole, the cortical responses exhibited a W-shaped morphology and comprised a series of 3 negative and 3 positive components. It is clear from the records that peak-to-peak amplitudes increased in a monotonic fashion with increasing stimulus intensity. It was further demonstrated in analysis of variance that the amplitudes increased significantly with stimulus intensity for N20–P27, P27–N35 and N60–P75 components (Fig. 5A). Trend analysis also revealed significant linearity in amplitudes with respect to stimulus intensity levels for each component except N35–P45. To facilitate a direct comparison between different components and also with the results of psychophysical experiments, amplitude values at different stimulus levels were converted into a new set of normalized values (%) in which amplitudes at the standard stimulus level of So + 2.50 kg · cm^{-2} were adjusted to 100%. In Fig. 5B these relative amplitude values for different SEP components were

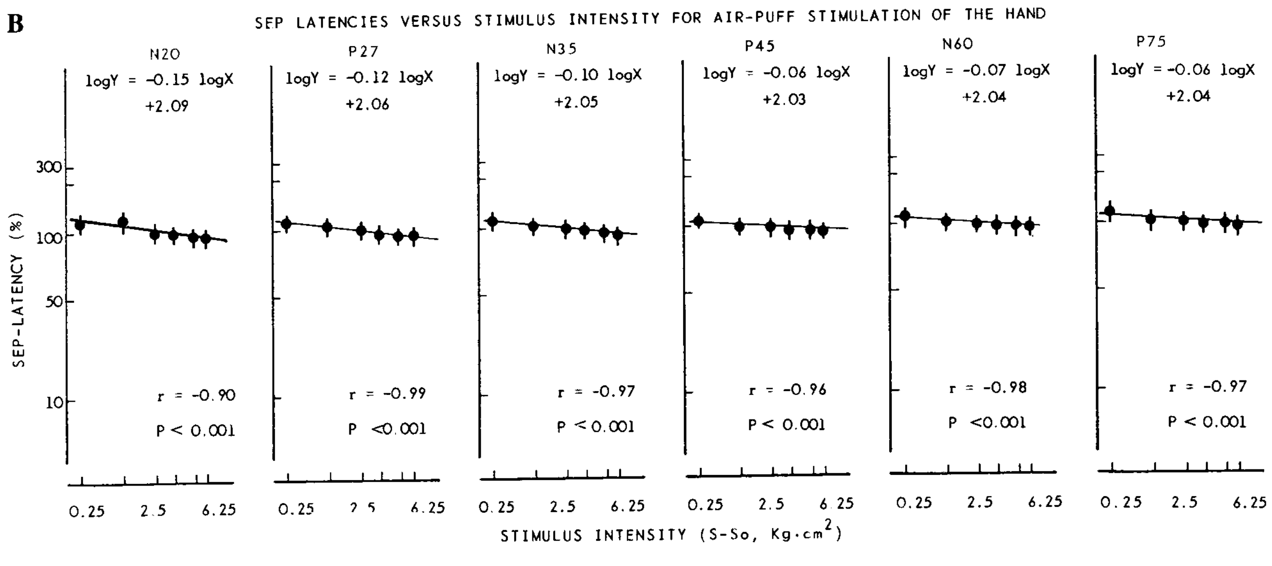


Fig. 6. A Relation between SEP latencies (ms) and stimulus intensity in linear plots. Solid circles and vertical bars indicate means and one S.D. Numerals above the bars give the number of SEP tests underlying the distributions. The differences in latencies across stimulus levels were statistically significant for N20, P27, N35, P45, and N60 ($P < 0.001$), and for P75 ($P < 0.01$). Tests for linearity also yield significance for all components ($P < 0.001$). **B** Log-log plots of normalized SEP latencies against stimulus intensity. Latency values (ms) were transformed into relative values (%) in which latencies at the standard stimulus level of So + 2.50 kg · cm^{-2} were adjusted to 100%. Solid circles and vertical bars indicate means and one S.D. Regression lines are derived from the individual data

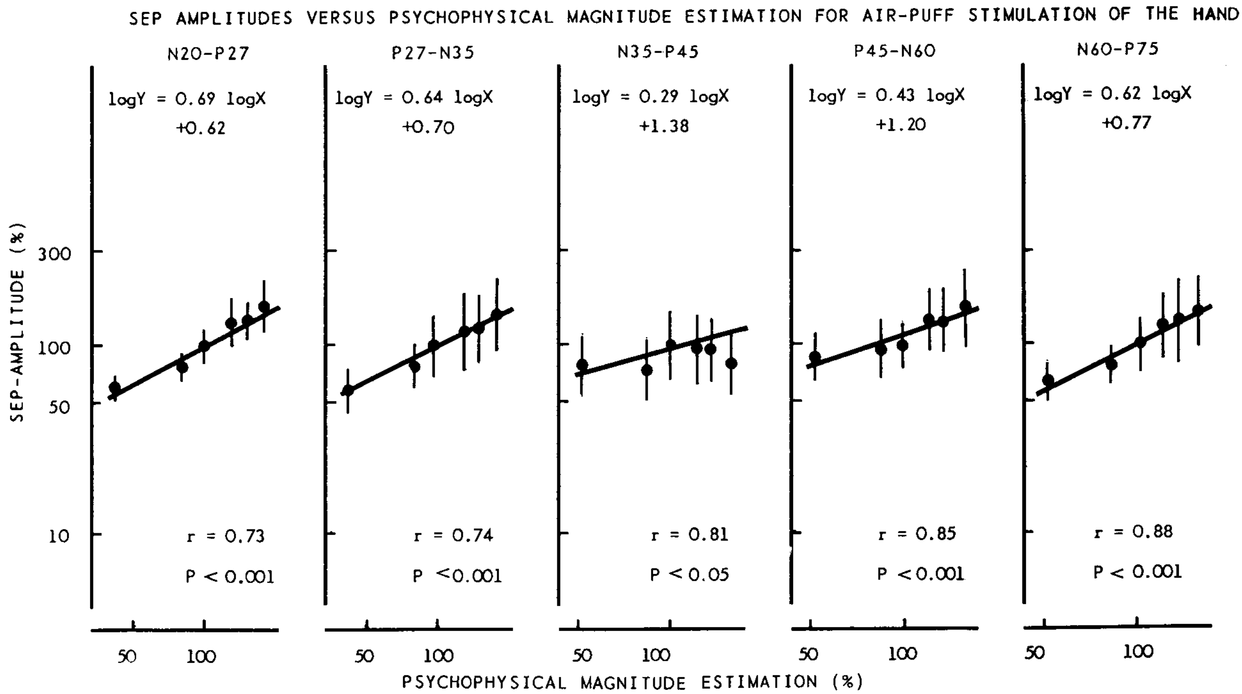


Fig. 7. Log-log plots of normalized SEP amplitudes against psychophysical magnitude estimation. Both amplitude values and magnitude estimations were converted into a new set of normalized values (%) in which amplitudes and magnitude estimation at the standard stimulus level of So + 2.50 kg · cm^{-2} were adjusted to 100%. Solid circles and vertical bars indicate means and one S.D. Regression lines are directly derived from the original data and not from the grand means shown in Figs. 3 and 5B

plotted against stimulus strength on log-log coordinates. The data were well represented by straight lines with different slopes for different components. These differences in slopes, however, were not statistically significant ($P > 0.05$). The function of the early P27–N35 component had the largest exponent (0.56) and showed the highest correlation with the stimulus intensity ($r = 0.91$). Similarly, correlation analysis revealed a significant correlation between amplitude and stimulus intensity for other components as well ($P < 0.05$).

Relationship of SEP latencies to stimulus intensities

As can be clearly seen in Fig. 4, peak latencies of SEP components exhibit a gradual decrease with increasing stimulus intensity. Figure 6A illustrates the mean peak latencies across stimulus levels. Analysis of variance revealed significant differences in the mean latencies across stimulus intensities for all components. Trend analysis also demonstrated significant linearity in latencies over stimulus levels for all components ($P < 0.001$). These latency values were transformed into relative values (%) using latencies at the standard stimulus level (So + 2,50 kg · cm^{-2}) as 100%. Then these relative latency values of each SEP component were plotted against stimulus levels on log-log coordinates (Fig. 6B). The data gave linear plots with negative slopes and the differences between the slopes did not reach statistical significance ($P > 0.05$).

Relationship of SEP amplitudes to subjective magnitudes

Plotting psychophysical magnitude estimations instead of stimulus intensity on the abscissa produced similar power functions (Fig. 7). The plottings were derived from the original data and the regression lines were not the composite functions deduced from the plots described in Figs. 3 and 5B. The N20–P27, P27–N35 and N60–P75 components had higher exponents than other components but the differences were not statistically significant ($P > 0.05$). Subjective magnitude correlated positively and significantly with the amplitudes of SEP components, and the amplitude of N60–P75 components showed the highest correlation with the subjective magnitude ($r = 0.88$). Under the identical experimental conditions stimulus intensity has already been shown to be correlated with SEP amplitudes. Thus physical intensity of the stimulus and subjective judgement of the

Table 1. Coefficients of correlation between SEP amplitude, air-puff intensity and subjective magnitude

Correlation	Coefficients				
	N20–P27	P27–N35	N35–P45	P45–N60	N60–P75
SEP amplitude – stimulus intensity	0.77***	0.91***	0.85*	0.90***	0.77***
SEP amplitude – subjective magnitude	0.73***	0.74***	0.81*	0.85***	0.88***
Subjective magnitude – stimulus intensity	0.86***	0.86***	0.84***	0.85***	0.79***
SEP amplitude – stimulus intensity (Subjective magnitude was partialed out)	0.41***	0.79***	0.53***	0.62***	0.25
SEP amplitude – subjective magnitude (Stimulus intensity was partialed out)	0.20	–0.20	0.34**	0.38**	0.71***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

stimulus were both related to cortical activities represented by amplitudes of SEPs. However, their relative contributions in eliciting the cortical activities were unknown.

In order to determine whether the amplitude of each component reflected primarily physical intensity or perceived magnitude of the stimulus, partial correlation analysis was used. When subjective magnitude was partialed out, significant positive correlations were observed between stimulus intensity and amplitudes for all SEP components except N60–P75 (Table 1). In contrast, the correlation between subjective magnitude and SEP amplitudes with stimulus intensity partialed out was significant for later N35–P45, P45–N60 and N60–P75 components and non-significant for early N20–P27 and P27–N35 components. These results indicate that the earlier SEP waves are closely related to the physical intensity of the stimulus, while later waves are more correlated with the subjective judgment of the stimulus.

Discussion

Topographic distributions of the cortical SEPs

Previous topographic mapping studies on SEPs elicited by mechanical stimulation of the hand have demonstrated that a series of 6 components recorded within 100 ms after stimulation were largest over the contralateral hand sensory area (Franzén and Offenloch 1969; Ishiko et al. 1980; Kakigi and Shibasaki 1984; Hashimoto 1987b).

SEPs evoked by electrical stimulation of the median nerve at the wrist or the index finger also revealed a similar potential distribution although the late P75 component, which probably corresponds to Goff's P80, had a wider and more posteriorly displaced distribution than the earlier components (Goff et al. 1977; Murayama 1985). The results of recordings from the exposed cortex in man support the view that these earlier waves are generated from the primary sensory cortex (Allison et al. 1980; Goff et al. 1980; Papakostopoulos and Crow 1980). Since SEPs are a summation of spatially and temporally overlapping potentials that may have separate origins, it has not been clear which components of the SEPs should correlate with either stimulus intensity or perceived magnitude.

Stimulus-amplitude functions of cortical SEPs

By measuring the amplitude difference between the largest positive (P27 or P45) and negative deflections (N60), Franzén and Offenloch (1969) indicated that the increase in response to vibrotactile stimulation of a finger tip was a power function of the stimulus intensity. Murayama (1985) measured the amplitude of P27 from the baseline and the power relationship was also demonstrated for the SEPs to electrical stimulation of the finger. The exponents obtained by the above authors were 0.47 (Franzén and Offenloch 1969) and 0.54 (Murayama 1985) respectively. We observed similar intensity relations for all SEP components over the range of intensities employed. The exponent for the early P27–N35 component had the largest value (0.56). Furthermore, the amplitude of this component best correlated with stimulus intensity ($r = 0.91$). It is reasonable to assume that the documented similarity in the exponents may result from activation of similar populations of receptors in spite of differences in stimulation methods.

Stimulus-latency functions of cortical SEPs

With electrical stimulation of either the median nerve at the wrist or the digital nerves of the index finger, latencies of SEPs have been shown to remain invariant with different stimulus strength (Lesser et al. 1979; Murayama 1985). In contrast, with mechanical stimulation of the skin, Franzén and Offenloch (1969) documented a decrease in SEP latencies with increasing stimulus intensity. The data of the present study clearly demonstrate power function relationships between stimulus strength and latencies with negative slopes and are in concordance with the previous study using mechanical stimulation (Franzén and Offenloch 1969). The neurophysiological mechanism underlying the discrepancy in intensity-latency functions between electrical and mechanical stimulation is of interest and merits further study.

Comparison of psychophysical and neurophysiological functions

Results of psychophysical experiments performed under the identical stimulus conditions as in the recordings of cortical SEPs confirmed that the subjective perception of increased magnitude as a function of stimulus intensity could be adequately described by a power function with the exponent of 0.81. A similar result was obtained by Franzén and Offenloch (1969) who applied pulses of vibrotactile stimulation to the skin. However, the exponent reported in their experiments was 0.56, a figure somewhat at variance with the value obtained in the present study.

Nevertheless, it is the common finding that the exponents for psychophysical studies are significantly larger than those obtained in evoked potential studies, results which agree with previous studies in somatosensory as well as other sensory systems (Rosner and Goff 1967; Stevens 1971; Murayama 1985). This suggests that subjective magnitude estimations are not a simple linear function of neurophysiological responses.

Relationships between the stimulus-response functions and psychophysical magnitude estimation function for cutaneous mechanoreceptive units have also attracted a great attention and the assumption of close parallelism between the two functions was emphasized (Werner and Mountcastle 1965; Mountcastle 1967; Harrington and Merzenich 1970; Järvilehto et al. 1981). Knibestöl and Vallbo (1980), however, documented a significant difference between the two functions for slowly adapting units in human subject with the average power function exponents of 0.7 and 1.0 respectively. The power exponents from the individual subjects in their study had a large range of variation; 0.3–2.0 for both neural and psychophysical functions. Moreover, when data from individual subjects were compared, there were considerable discrepancies between the exponents of neural and psychophysical functions. From these results, they suggested that the central nervous system plays the major role in producing the psychophysical functions as opposed to the traditional view which places the primary afferent fibers as the site of psychophysical functions (Werner and Mountcastle 1965; Mountcastle 1967; Harrington and Merzenich 1970).

The air-puff used in this study is by far the shortest stimulus (2 ms duration) ever used for eliciting either the cortical SEPs or the sensation of subjective magnitudes. As a result, the neural activity elicited by the air-puffs is probably dominated by rapidly adapting mechanoreceptors (Knibestöl 1973; Johansson and Vallbo 1979). It would be surprising therefore that subjects are able to estimate the magnitude of such a brief stimulus as was demonstrated in this study, if only the number of impulses per se is responsible for magnitude estimation. On the other hand, if the assumption that intensity coding of the skin afferents are not so dependent on the impulse frequency in individual fibers is true, as has been indicated in slowly adapting afferents, it naturally follows that the successive recruitment of many fibers with increasing stimulus intensity may undoubtedly play a more decisive role in the magnitude estimations of the intensity (Kruger and Kenton 1973; Johansson and Vallbo 1980; Knibestöl and Vallbo 1980; Gardner and Costanzo 1980; Ochoa and Torebjörk 1983; Vallbo et al. 1984). However, no direct evidence for this conjecture has been provided so far. Moreover, the complexity of processing at various levels in the central nervous system precludes a simplistic generalization of either the linear or non-linear transformation hypothesis (Kruger and Kenton 1973; Knibestöl and Vallbo 1980).

The cortical SEPs are the net results of summed and averaged activity of neuronal populations of the primary sensory cortex in response to the peripheral inputs whatever the intervening transfer functions are. Thus, a closer relationship between the neural (cortical SEPs) and psychophysical functions might reasonably be expected. However, comparison of these two functions should be made with caution because psychophysical data have to be collected separately from the series of stimuli that generate the SEPs and a trial to trial analysis of perceived magnitude and evoked potential magnitude is usually not possible. Thus, the SEPs are inevitably evoked in a situation which to some extent may produce habituation and may discourage rigid attention to the sensory magnitude.

Because of these limitations in the experimental approach, one may argue that the relation between the neural and the psychophysical data thus obtained are not comparable. For statistical analysis of these data, we have chosen to use the partial correlation analysis to elucidate more directly the causal relationships between neural activity and psychophysical findings. The assumption in applying this statistical analysis has been that the real correlation will emerge between the neural and the psychophysical data, if it exists, after the effect of stimulus intensity is removed. Partial correlation analysis revealed that SEP components reflect both the physical parameters of stimulus intensity and subjective judgment of the stimulus. The early four (N20–P27, P27–N35, N35–P45, and P45–N60) components correlated with stimulus intensity and appeared to reflect coding of physical stimulus intensity in which P27–N35 showed the highest correlation. On the other hand, three later components (N35–P45, P45–N60, and N60–P75) were related to subjective estimation of stimulus intensity in which the amplitude of the N60–P75 component was strongly correlated with subjective magnitude estimation.

In conjunction with topographic evidence that the P75 originates from the association cortex (Goff et al. 1977), the N60–P75 components may primarily reflect cognitive processes involved in subjective evaluation of the stimulus intensity.

Acknowledgements. The authors thank Prof. J.S. Buchwald, Associate Director, Brain Research Institute, University of California, Los Angeles, for providing valuable critical analysis of the manuscript, and Dr. T. Koike, Tokyo Gakugei University, and Dr. T. Yoshida, Tsukuba University, for helpful suggestions during the initial stage of the experiments. This study was supported by grants from the Tokyo Metropolitan Government and the Marine and Fire Insurance Association of Japan, Incorporated.

References

Allison T, Goff WR, Williamson PD, VanGilder JC (1980) On the neural origin of early components of the human somatosensory evoked potential. In: Desmedt JE (ed) Clinical uses of cerebral, brainstem and spinal somatosensory evoked potentials. Progress in clinical neurophysiology, Vol 7. Karger, Basel, pp 51–68

Edwards AL (1972) Experimental design in psychological research. Holt Rinehart and Winston, New York, pp 330–362

Eisenhart C (1947) The assumptions underlying the analysis of variance. Biometrics 3: 1–21

Franzén O, Offenloch K (1969) Evoked response correlates of psychophysical magnitude estimates for tactile stimulation in man. Exp Brain Res 8: 1–18

Gandevia SC, Burke D, McKeon BB (1983) Convergence in the somatosensory pathway between cutaneous afferents from the index and middle fingers in man. Exp Brain Res 50: 415–425

Gardner EP, Costanzo RM (1980) Spatial integration of multiple-point stimuli in primary somatosensory cortical receptive fields of alert monkeys. J Neurophysiol 43: 420–443

Gardner EP, Hämäläinen HA, Warren S, Davis J, Young W (1984) Somatosensory evoked potentials (SEPs) and cortical single unit responses elicited by mechanical tactile stimuli in awake monkeys. Electroenceph Clin Neurophysiol 58: 537–552

Goff GD, Matsumiya J, Allison T, Goff WR (1977) The scalp topography of human somatosensory and auditory evoked potentials. Electroenceph Clin Neurophysiol 42: 57–76

Goff WR, Williamson PD, VanGilder JC, Allison T, Fisher TC (1980) Neural origin of long latency evoked potentials recorded from the depth and from the cortical surface of the brain in man. In: Desmedt JE (ed) Clinical uses of cerebral, brainstem and spinal somatosensory evoked potentials. Progress in clinical neurophysiology, Vol 7. Karger, Basel, pp 126–145

Harrington T, Merzenich MH (1970) Neural coding in the sense of touch: human sensations of skin indentation compared with the response of slowly adapting mechanoreceptive afferents innervating the hairy skin of monkeys. Exp Brain Res 10: 251–264

Hashimoto I (1987a) Somatosensory evoked potentials elicited by sharp-fronted air-puff stimuli in man. Electroenceph Clin Neurophysiol 66: 93p

Hashimoto I (1987b) Somatosensory evoked potentials elicited by air-puff stimuli generated by a new high-speed air control system. Electroenceph Clin Neurophysiol 67: 231–237

Hashimoto I (1988) Trigeminal evoked potentials following brief air puff: enhanced signal-to-noise ratio. Ann Neurol 23: 332–338

Ishiko N, Hanamori T, Murayama N (1980) Spatial distribution of somatosensory responses evoked by tapping the tongue and finger in man. Electroenceph Clin Neurophysiol 58: 1–10

Järvilehto T, Hämäläinen H, Soininen K (1981) Peripheral neural basis of tactile sensations in man. II. Characteristics of human mechanoreceptors in the hairy skin and correlations of their activity with tactile sensations. Brain Res 219: 13–27

Johansson RS, Vallbo ÅB (1979) Detection of tactile stimuli. Thresholds of afferent units related to psychophysical threshold in the human hand. J Physiol 297: 405–422

Johnson D, Jürgens R, Kongehl G, Kornhuber HH (1975) Somatosensory evoked potentials and magnitude of perception. Exp Brain Res 22: 231–234

Kakigi R, Shibasaki H (1984) Scalp topography of mechanically and electrically evoked somatosensory potentials in man. Electroenceph Clin Neurophysiol 59: 44–56

Knibestöl M (1973) Stimulus-response functions of rapidly adapting mechano-receptors in the human glabrous skin area. J Physiol 232: 427–452

Knibestöl M, Vallbo ÅB (1980) Intensity of sensation related to activity of slowly adapting mechanoreceptive units in the human hand. J Physiol 300: 251–267

Kruger L, Kenton B (1973) Quantitative neural and psychophysical data for cutaneous mechanoreceptor function. Brain Res 49: 1–24

Lesser RP, Koehle R, Lueders H (1979) Effect of stimulus intensity on short latency somatosensory evoked potentials. Electroenceph Clin Neurophysiol 47: 377–382

Matsumiya Y, Mostofsky DI (1972) Somatosensory evoked responses elicited by corneal and nostril air puff stimulation. Electroenceph Clin Neurophysiol 33: 225–227

Mountcastle VB (1967) The problem of sensing and the neural coding of sensory events. In: Quarton GC, Melnechuk T, Schmitt FO (eds) The neurosciences. Rockefeller Univ Press, New York, pp 393–408

Murayama N (1985) Correlation of subjective assessments with somatosensory evoked potentials to electrical stimulation of finger in man. Physiol Soc Jpn 47: 171–181 (in Japanese)

Ochoa J, Torebjörk E (1983) Sensations evoked by intraneural microstimulation of single mechanoreceptor units innervating the human hand. J Physiol 342: 663–654
Papakostopoulos D, Crow HJ (1980) Direct recording of the somatosensory evoked potentials from the cerebral cortex of man and the difference between precentral and postcentral potentials. In: Desmedt JE (ed) Clinical uses of cerebral, brainstem and spinal somatosensory evoked potentials. Progress in clinical neurophysiology, Vol 7. Karger, Basel, pp 15–26
Rosner BS, Goff WR (1967) Electrical response of the nervous system and subjective scales of intensity. In: Neff WD (ed) Contribution to sensory physiology, Vol 2. Academic Press, London, pp 169–221
Ryan TA (1960) Significance tests for multiple comparison of proportions, variances, and other statistics. Psychol Bull 57: 318–328
Schieppati M, Ducati A (1984) Short latency cortical potentials evoked by tactile air-jet stimulation of body and face in man. Electroenceph Clin Neurophysiol 58: 418–425
Snedecor GW, Cochran WG (1967) Statistical methods, 6th edn. The Iowa State University Press, Ames Iowa, pp 432–436
Stevens JC, Mack JD (1959) Scales of apparent force. J Exp Psychol 58: 405–413
Stevens SS (1971) Sensory power functions and neural events. In: Lowenstein WR (ed) Handbook of sensory physiology, Vol 1. Springer, Berlin, pp 226–242
Timm NH, Carlson JE (1976) Part and bipartial canonical correlation analysis. Psychometrika 41: 159–176
Vallbo ÅB, Olsson KÅ, Westberg KG, Clark FJ (1984) Microstimulation of single tactile afferents from the human hand. Sensory attributes related to unit type and properties of receptive fields. Brain 104: 727–749
Werner G, Mountcastle VB (1965) Neuronal activity in mechanoreceptive cutaneous afferents: stimulus-response relations, Weber functions, and information transmission. J Neurophysiol 28: 359–397
Westling G, Johansson R, Vallbo ÅB (1976) A method for mechanical stimulation of skin receptors. In: Zotterman Y (ed) Sensory function of the skin in primates. Pergamon, Oxford, pp 151–158

Received October 16, 1987 / Accepted May 13, 1988