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Sensory nerve action potentials elicited by mechanical air-puff stimulation of the index finger in man

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Summary Brief air-puff stimuli were applied to the tip of the index finger to record propagating sensory nerve action potentials (APs) from pairs of surface electrodes at successive sites over the median nerve of the distal forearm. Within 10 msec, air-puff stimulation elicited 2–4 separate waves lasting 3–6 msec, in contrast to a single triphasic wave evoked by electrical stimulation. Amplitudes of air-puff evoked APs were much smaller than those of electrically induced APs. However, the amplitude ratio of the initial negative wave (P1-N1) of electrically evoked APs to that of air-puff induced APs declined linearly as a function of recording points along the ascending median nerve. Similarly, the duration ratio of the same component (N1) increased progressively in the proximal direction along the nerve. These results suggest that air-puff evoked afferent volleys undergo considerably less temporal dispersion than those induced by electrical stimulation. Thus, each peak of air-puff evoked APs represents a relatively homogeneous afferent fiber population. The initial P1, N1 and P2 peaks of air-puff evoked APs occurred later than those of electrical induced APs, and the latency included the time of skin indentation and receptor transduction in response to mechanical stimulation. Proximal conduction velocities were faster than distal conduction velocities due to cancellation of the extra delay at the skin mechanoreceptors as well as a true increase in the proximal direction. There were no significant differences between the interelectrode conduction velocities of the fastest fibers activated by the air-puffs and by electrical stimulation. Interelectrode propagation velocities of the different peaks from the same segments had no significant differences for air-puff evoked APs. The presence of multiple peaks may not be the result of temporal dispersion due to difference in conduction velocity of skin afferents but primarily due to a more peripheral receptor mechanism involving transduction and impulse generation.

Key words: Sensory nerve action potentials; Air-puff stimulation; Multiple peaks; Conduction velocities; Temporal dispersion; Mechanoreceptor transduction time

Surface recording of peripheral nerve action potentials (APs) elicited by electrical stimulation has been used routinely to measure conduction velocity and to assess the functional state of peripheral nerves in human. In contrast, there are only two reports describing sensory nerve APs evoked by mechanical stimulation of the human skin (Pratt et al. 1979a; Schieppati and Ducati 1984). Furthermore, the subject of sensory nerve APs in these two studies was only touched upon briefly as a minor part of a more extensive description of somatosensory evoked potentials at various levels along the somatosensory pathway in response to mechanical stimulation. McLeod (1966) recorded extraordinarily large afferent volleys (4–18 μV) elicited by a single tap on the fingernail with an electromechanical stimulator from surface electrodes over the human digital nerves and over the median nerve at the wrist. The recorded potentials, however, were probably an artifact of movement resulting from mechanical spread of the percussion wave (Pratt et al. 1979a; Gandevia et al. 1983). Using the same technique

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of mechanical stimulation but after averaging as many as 1000 sweeps, Pratt et al. (1979a) were able to record low voltage sensory nerve APs (1.5 ± 0.7 μV) over the median nerve at the wrist.

Subsequently, Schieppati and Ducati (1984) used mechanical air-puff stimulation to study peripheral nerve conduction velocity. After averaging 500 responses from needle electrodes inserted close to the median nerve, they obtained much smaller sensory nerve APs (0.20 ± 0.13 μV) with a low signal-to-noise ratio; this probably resulted from the small amplitude of mechanically evoked afferent volleys coupled with a large amplitude myogenic noise (Schieppati and Ducati 1984). Air-puffs can provide constant and reproducible cutaneous stimuli for initiating afferent volleys. Using air-puff stimuli controlled with respect to force to study somatosensory evoked potentials may enable us to circumvent the run-to-run intensity variability of the displacement-controlled electromechanical stimulation caused by oscillating skin movement synchronous with pulsation and respiration; this is because air-puffs are delivered without directly touching the skin (Johansson and Vallbo 1979b). Furthermore, several reports have suggested from studies of sensory transduction that force, rather than displacement per se, might be the critical variable for activation of cutaneous mechanoreceptors (Werner and Mountcastle 1965; Petit and Galifret 1978) and not vice versa (Pubols 1982).

Air-puff stimulation has the disadvantages of a slow rise time (5 msec) and long duration (20–30 msec) as a result of the electromechanical opening and closing of valves (Schieppati and Ducati 1984). Thus, for the study of short latency propagating APs, air-puffs have 2 definite limitations: first, uncertainty about the timing relationship between stimulus onset and activation of skin mechanoreceptors and, secondly, the extended rise and fall times can presumably activate receptors with different thresholds, resulting in considerable temporal dispersion of the afferent volleys (Johansson and Vallbo 1979b; Johansson et al. 1980).

In the present study, we employed a high-speed air control system which provided air-puff stimuli with fast rise (1 msec) and fall (1 msec) times and a total duration of 2 msec, permitting reasonably accurate time locking for averaging of the nerve activity (Hashimoto 1987, 1988; Hashimoto et al. 1988). We compared APs evoked by air-puff stimulation with those elicited by traditional electrical stimulation at the same skin locus over the index finger. We have confirmed in another series of experiments (unpublished data) that the recorded potentials are not movement artifact and are certainly of neural origin on the basis of transient attenuation and loss of the potentials by temporary ischemia and nerve blockade and recovery of the potentials afterwards.

Methods

Experiments were conducted on 22 healthy students (14 women) who gave informed consent. They were between 19 and 27 years old (21.6 ± 2.3, mean ± S.D.). During experiments, they lay supine on a couch with the right arm extended laterally. Sensory nerve APs from each subject were collected in a single session in response to air-puff and electrical stimulation of the tip of the index finger. Both air-puff and electrical stimuli were delivered at a rate of approximately 1/sec.

Air-puff stimulation

Air-puffs were delivered perpendicular to the volar surface of the distal phalanx of the right 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 finger tip was determined manually with a small cotton wisp using near-threshold gentle strokings and was marked on the skin.

The position of the palm and fingers of the right hand was maintained against the smoothly curved surface of a semi-circular plastic mold, using adhesive plaster; thus, no active muscle contraction was required to hold the position. The plastic mold had 3 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.

A detailed description of the mechanical characteristics of the air-puff method has been given in earlier reports (Hashimoto 1987, 1988; Hashi-

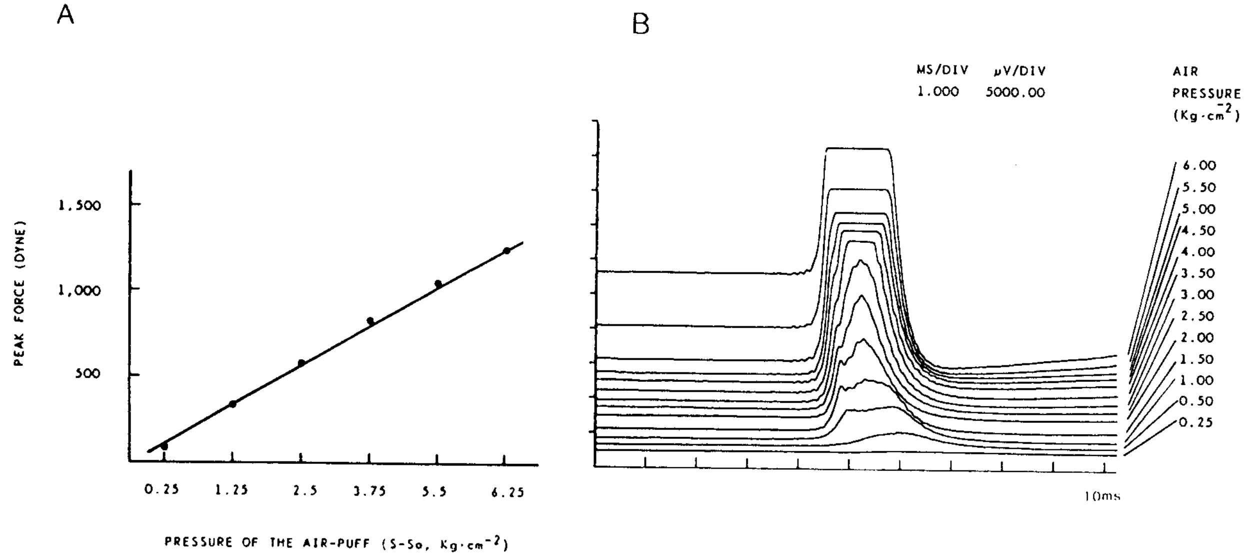

Fig. 1. A: relation between pressure (kg·cm^{-2}) and peak force (dyne). Peak force increases linearly with successive elevations of the pressure up to the stimulus intensity (7 kg·cm^{-2}) used in this study. B: pressure wave forms of the air-puffs at 1 cm from the nozzle of the air-control system. 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 msec and the voltage calibration is 5 mV/div.

moto et al. 1988). Briefly, each air-puff at the distance of 1 cm from the target skin had a diameter of 1.8 mm and a cross-sectional area of 2.5 mm^2. A sharp air-puff with a rise time of 1 msec and a total duration of 2 msec was achieved with a pressure of 1.5 kg · cm^{-2} or more (Fig. 1B). The relationship between peak force and air pressure applied to the stimulator was a linear function over the stimulus range used in this and previous studies (Fig. 1A).

This study employed a single constant pressure of 7 kg · cm^{-2}, resulting in air-puffs with a peak force of 1357 dyne at the skin surface. Although this stimulus intensity produced no visible skin indentation at the volar aspect of the finger, it evoked touch and pressure sensations at the target skin (Sasaki et al. 1988). The skin sensation following air-puff stimulation was considerably weaker than that evoked by the electrical stimulation used in this study (3 times sensory threshold). 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 brief cooling of the skin during the air-puff was very weak and much less prominent than the sensation of touch and pressure.

A photo-diode circuit pulsed with each air-puff was used to trigger an averaging system (Nicolet Pathfinder II) and the time lag between the electrical signal from the photo-diode and arrival of the air-puff at the skin was compensated for by using a one-shot multi-circuit.

Electrical stimulation

Electrical stimuli were delivered through a pair of ring electrodes placed around the distal phalanx of the index finger. The proximal electrode was the cathode and was secured at the level of air-puff stimulation. This allowed a direct comparison of latency and wave form of mechanically and electrically evoked nerve activities. The electrical stimuli were 0.2 msec duration, square-wave pulses of constant current delivered at 3 times sensory threshold.

The subjective sensation evoked by electrical stimulation differed in nature from that elicited by air-puffs and was characterized by its extremely limited intensity range as compared with the natural skin sensation. Conversely, air-puff stimulation at the same multiple of sensory threshold as the electrical stimulation neither elicited comparable skin sensation nor comparable nerve activity. Therefore, we attempted to equalize the intensity of electrical stimulation with that of the air-puff in 6 subjects using a cross-modality matching technique (Stevens 1971). Air-puff and electrical stimuli were given alternately, and the intensity of electrical stimulation was adjusted until it elicited a sensation equal in strength to that of the air-puff (7 $\mathrm{kg \cdot cm^{-2}}$). The intensity of the cross-modality matched electrical stimulation differed considerably from one subject to the next but was usually within 2 times sensory threshold and never exceeded 3 times sensory threshold.

Recording procedures

Sensory nerve potentials were recorded bipolarly from 4 pairs of recording disk electrodes at successive sites over the median nerve of the forearm. We chose to use bipolar recording because AP amplitudes were larger than those obtained with unipolar recording, although the shape of the potentials with bipolar recording varied to some extent, depending on partial cancellation and summation of the 2 time-displaced potentials (Buchthal and Rosenfalck 1966). Five electrodes were placed in 2 cm increments from the distal crease at the wrist to 8 cm proximally along the median nerve, and 2 adjacent leads were connected with input 1 distal to input 2 in each channel. Interelectrode impedances were kept below 3 kΩ. A ground strap was placed around the base of the index finger of the right hand. After amplification (gain 10^5) and filtering (15 Hz–3 kHz), neural activity was averaged for a 10 msec period using an averaging system with automatic artifact rejection. The sampling rate was 50 kHz, and 250 artifact-free sweeps were averaged. Triplicate averages were run routinely to ensure reproducibility of the onset and peaks of the potentials. Averaged potentials were displayed on an X-Y plotter and stored for off-line cursor analysis of amplitude and latency. Negativity at the distal electrode (input 1) relative to the proximal electrode (input 2) resulted in an upward deflection. Amplitude was measured from the positive or negative peak to the immediately following peak of opposite polarity (peak-to-peak). Peak latency was measured either from the air-puff or electrical pulse onset. All measurements were made on the grand average derived from 3 individual averages. We designated peaks of the propagating APs by polarity at input 1 (N or P for negative or positive) and their sequence.

Measurement of nerve conduction velocity

Nerve conduction velocities along the median nerve were determined in 16 subjects by measuring the distance between the stimulus site at the tip of the finger and the distal electrode of each pair of recording electrodes over the wrist and forearm or between adjacent electrode pairs (2 cm apart) and then dividing these distances by the latencies of the peaks or latency differences of the corresponding peaks in the recorded propagating potentials.

Statistical analysis

Analysis of variance was used to assess the statistical significance of differences in amplitudes, latencies, durations and conduction velocities of the corresponding components in the propagating nerve potentials recorded at different locations, or the differences between those of different components recorded at the same electrode locations. Furthermore, the statistical significance of differences between the two populations in the above variables was assessed using Tukey's q test. Otherwise, Student's t test was used to assess the significance of differences between populations. The level of probability selected as significant was a value of $P < 0.05$ (2-tailed test).

Results

General characteristics

Fig. 2 illustrates typical wave forms of the propagated nerve potentials in response to air-puff stimulation of the volar aspect of the finger tip recorded from successive sites along the median nerve at the wrist and forearm. The most prominent feature was that they usually consisted of 2–4 distinct waves lasting 3–6 msec in contrast to

TABLE IA

AP amplitudes (μV, mean ± S.D.) along the median nerve to air-puff stimulation of the index finger. Bipolar records from 4 pairs of electrodes (1, 2, 3 and 4) from distal to proximal locations (2 cm increments) over the median nerve of the distal forearm were simultaneously obtained. Analysis of variance was used to assess the statistical significance between populations in this and the following tables. Numerals in parentheses give the number of individual data underlying the distributions in this and the following tables.

AP component	Recording site				Statistical significance
	1	2	3	4	
P1-N1	0.19 ± 0.07 (16)	0.12 ± 0.04 (16)	0.07 ± 0.02 (15)	0.05 ± 0.03 (8)	$P < 0.01$
N1-P2	0.20 ± 0.08 (13)	0.10 ± 0.05 (13)	0.06 ± 0.02 (11)	0.05 ± 0.02 (4)	$P < 0.01$
P2-N2	0.13 ± 0.07 (12)	0.10 ± 0.07 (10)	0.07 ± 0.02 (6)	0.04 ± 0.02 (3)	n.s.
N2-P3	0.23 ± 0.10 (11)	0.13 ± 0.07 (11)	0.08 ± 0.04 (8)	0.08 ± 0.01 (3)	$P < 0.01$
P3-N3	0.21 ± 0.10 (6)	0.08 ± 0.03 (6)	0.05 ± 0.02 (3)	0.03 ± 0 (1)	$P < 0.01$
N3-P4	0.21 ± 0.16 (6)	0.12 ± 0.05 (5)	0.08 ± 0.04 (4)	0.07 ± 0 (1)	n.s.
P4-N4	0.19 ± 0.01 (3)	0.13 ± 0.03 (3)	0.12 ± 0.05 (2)	0.05 ± 0 (1)	n.s.
Statistical significance	n.s.	n.s.	n.s.	n.s.	

n.s. = not significant ($P > 0.05$) in this and the following tables.

TABLE IB

Comparison of AP amplitudes (mean ± S.D.) along the median nerve to air-puff and electrical stimulation of the index finger. E and A indicate electrical stimulation and air-puff stimulation respectively in this and the following tables.

AP component	Recording site				Statistical significance
	1	2	3	4	
P1-N1					
E (μV)	3.67 ± 1.62 (16)	2.00 ± 0.84 (16)	0.85 ± 0.38 (15)	0.54 ± 0.21 (12)	$P < 0.005$
A (μV)	0.19 ± 0.07 (16)	0.12 ± 0.04 (16)	0.07 ± 0.02 (15)	0.05 ± 0.03 (8)	$P < 0.01$
Amplitude ratio (E/A)	20.32 ± 9.87 (16)	18.64 ± 9.20 (16)	13.85 ± 8.53 (15)	10.64 ± 3.42 (8)	$P < 0.05$
N1-P2					
E (μV)	4.88 ± 1.96 (16)	2.46 ± 1.01 (16)	1.11 ± 0.49 (15)	0.76 ± 0.30 (12)	$P < 0.005$
A (μV)	0.20 ± 0.08 (13)	0.10 ± 0.05 (13)	0.06 ± 0.02 (11)	0.05 ± 0.02 (4)	$P < 0.01$
Amplitude ratio (E/A)	24.87 ± 9.65 (13)	21.59 ± 7.83 (13)	22.11 ± 12.29 (11)	23.32 ± 9.85 (4)	n.s.

the traditional single triphasic wave evoked by electrical stimulation. The amplitudes of air-puff evoked APs were much smaller than those of electrically induced APs (Table IB). It can be seen clearly that the latencies of the potentials to both air-puff and electrical stimulation increased progressively from distal to proximal recording sites (Table IIB).

The electrical stimulus which felt the same as the intensity of air-puff stimulation (7 kg · cm^{-2}) elicited triphasic nerve activities with smaller amplitudes than those elicited by the higher intensity stimulation (3 times sensory threshold). However, there were no significant differences in onset and peak latencies between APs elicited by low and high intensity electrical stimuli. In one subject the low intensity stimulus elicited two separate peaks in the nerve potentials, similar to those described by Buchthal and Rosenfalck (1966) with near-threshold electrical stimulation. They suggested that the separate peaks were the exception in young subjects and were derived from fibers conducting at different velocities. Usually, amplitudes of the APs evoked by electrical stimulation at the

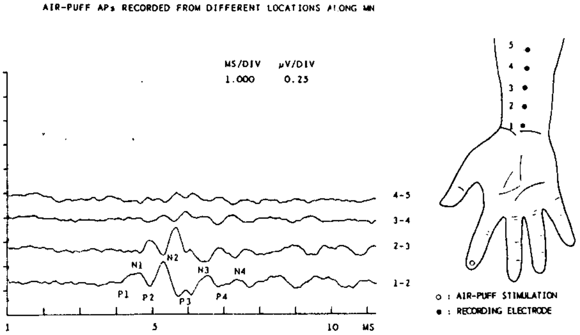

Fig. 2. Propagating sensory nerve action potentials following air-puff stimulation of the finger tip. Potentials are recorded bipolarly from 4 pairs of electrodes at successive sites (2 cm increments) over the median nerve at the wrist and forearm. Two adjacent leads are connected with grid 1 distal to grid 2 in each channel. In contrast to a traditional triphasic wave elicited by electrical stimulation, the air-puff evoked nerve potentials are characterized by a multiphasic wave form with two or more separate components.

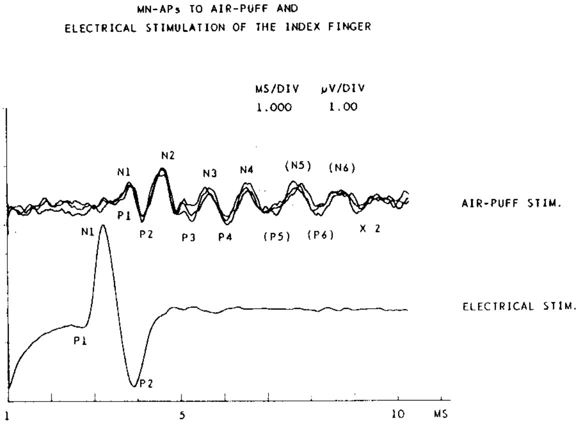

Fig. 3. Sensory nerve action potentials in response to air-puff and electrical stimulation of the finger tip. The early peaks (P1 and N1) of air-puff evoked nerve potentials occur later than those of electrically induced nerve potentials. This latency difference includes the time of skin indentation and receptor transduction in response to mechanical air-puff stimulation. Calibration for air-puff evoked APs is 0.5 µV/div while that for electrically induced APs is 1 µV/div.

matched intensity were relatively larger than those of the initial negativity of air-puff evoked APs.

Comparison of amplitudes of mechanically and electrically evoked afferent volleys

Amplitudes of air-puff evoked APs recorded at the wrist were extremely small, in the nanovolt range (Table IA). Amplitudes of all components were largest at the most distal recording electrode and became progressively smaller proximally. The triphasic APs elicited by electrical stimulation were much larger (Fig. 3) than those mechanically evoked but showed a similar systematic amplitude reduction from distal to proximal electrode locations (Table IB). These decreasing amplitudes toward proximal locations are explained by the temporal dispersion of the afferent volleys along the ascending peripheral nerve, and also by the fact that the median nerve lies superficially and close to the recording electrodes distally at the wrist, whereas it is more deeply situated and at a greater distance from the electrodes at more proximal locations of the forearm.

TABLE IIA

AP latencies (msec, mean ± S.D.) along the median nerve to air-puff stimulation of the index finger.

AP component	Recording site				Statistical significance
	1	2	3	4	
P1	4.26 ± 0.51 (16)	4.54 ± 0.48 (16)	4.85 ± 0.58 (15)	5.33 ± 0.51 (9)	$P < 0.01$
N1	4.79 ± 0.56 (16)	5.08 ± 0.56 (16)	5.40 ± 0.57 (14)	5.68 ± 0.72 (6)	$P < 0.05$
P2	5.23 ± 0.59 (16)	5.55 ± 0.66 (15)	5.85 ± 0.70 (10)	6.19 ± 0.71 (5)	$P < 0.05$
N2	5.55 ± 0.61 (13)	5.87 ± 0.63 (13)	6.21 ± 0.68 (8)	6.48 ± 0.79 (3)	n.s.
P3	6.04 ± 0.66 (12)	6.36 ± 0.68 (12)	6.69 ± 0.55 (10)	6.90 ± 0.43 (4)	n.s.
N3	6.51 ± 0.77 (7)	6.81 ± 0.86 (7)	6.96 ± 1.19 (4)	6.84 ± 0 (1)	n.s.
P4	6.93 ± 1.00 (6)	7.25 ± 1.05 (6)	7.53 ± 1.29 (4)	7.86 ± 1.27 (4)	n.s.
N4	7.21 ± 1.36 (3)	7.59 ± 1.40 (3)	8.43 ± 1.27 (2)	8.54 ± 0 (1)	n.s.
Statistical significance	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$	

TABLE IIB

Comparison of AP latencies (msec, mean ± S.D.) along the median nerve to air-puff and electrical stimulation of the index finger. The symbols in the first lines for different components indicate the significance levels of differences (Student's t test) with regard to latencies of air-puff evoked APs in relation to those of electrically evoked counterparts given in the second lines.

AP component	Recording site				Statistical significance
	1	2	3	4	
P1					
A	4.26 ± 0.51 (16) ***	4.54 ± 0.48 (16) ***	4.85 ± 0.58 (15) ***	5.33 ± 0.51 (9) ***	$P < 0.01$
E	3.07 ± 0.38 (16)	3.33 ± 0.36 (16)	3.55 ± 0.40 (15)	3.74 ± 0.39 (12)	$P < 0.01$
Latency difference (A − E)	1.19 ± 0.35 (16)	1.19 ± 0.32 (16)	1.30 ± 0.30 (15)	1.56 ± 0.33 (9)	n.s.
N1					
A	4.79 ± 0.56 (16) ***	5.08 ± 0.56 (16) ***	5.40 ± 0.57 (14) ***	5.68 ± 0.72 (6) ***	$P < 0.05$
E	3.58 ± 0.43 (16)	3.90 ± 0.45 (16)	4.17 ± 0.47 (15)	4.37 ± 0.50 (12)	$P < 0.01$
Latency difference (A − E)	1.22 ± 0.38 (16)	1.19 ± 0.37 (16)	1.27 ± 0.46 (14)	1.46 ± 0.39 (6)	n.s.
P2					
A	5.23 ± 0.59 (16) ***	5.55 ± 0.66 (15) ***	5.85 ± 0.70 (10) **	6.19 ± 0.71 (5) *	$P < 0.05$
E	4.22 ± 0.48 (16)	4.63 ± 0.52 (16)	4.99 ± 0.55 (15)	5.29 ± 0.61 (12)	$P < 0.01$
Latency difference (A − E)	1.01 ± 0.40 (16)	0.96 ± 0.43 (15)	0.80 ± 0.42 (10)	0.86 ± 0.41 (5)	n.s.

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

The amplitude ratio of the initial negative wave (P1-N1) of electrically evoked APs to that of air-puff induced APs (electrical stimulation/air-puff stimulation) was calculated for each electrode pair from individual subjects (Table IB). The mean amplitude ratio at the distal electrode pair was largest, and this ratio declined linearly at successive recording sites along the median nerve proximally. There was a significant difference between the ratios obtained at the most distal and proximal locations ($P < 0.05$). This decline in amplitude ratios as a function of recording points along the ascending peripheral nerve indicates that in air-puff evoked afferent volleys considerably less temporal dispersion takes place relative to those induced by electrical stimulation. The amplitude ratios for the following N1-P2 component were generally larger than those for P1-N1 component and showed no such systematic changes as were observed in P1-N1 component along the nerve.

Comparison of latencies of mechanically and electrically evoked afferent volleys

The latencies of the early P1, N1 and P2 peaks following air-puff stimulation progressively increased along the median nerve at a rate of 0.28–0.48 msec/2 cm distance; these latency differences were statistically significant (Table IIA). On the other hand, although the latencies of the later peaks showed similar increases in the proximal direction, analysis of variance disclosed no significant difference.

This was unexpected, because we had initially assumed that the multiple peaks were due to differences in the conduction velocities of afferent fibers from various skin mechanoreceptors, and that later peaks reflected conduction at slower velocities (see other section of Results). The latencies of the onset (P1) and negative peak (N1) and the second positive peak (P2) of the triphasic APs induced by electrical stimulation showed a

TABLE IIIA

AP durations (msec, mean ± S.D.) along the median nerve to air-puff stimulation of the index finger.

AP component	Recording site				Statistical significance
	1	2	3	4	
N1	0.97 ± 0.28 (16)	1.00 ± 0.33 (15)	0.93 ± 0.32 (10)	0.85 ± 0.37 (5)	n.s.
N2	0.79 ± 0.26 (12)	0.87 ± 0.38 (12)	0.88 ± 0.20 (6)	0.94 ± 0.32 (2)	n.s.
N3	0.73 ± 0.33 (6)	0.89 ± 0.25 (6)	0.98 ± 0.40 (2)	0.70 ± 0 (1)	n.s.
Statistical significance	n.s.	n.s.	n.s.	n.s.	

TABLE IIIB

Comparison of AP duration (mean ± S.D.) of the initial N1 component recorded along the median nerve to air-puff and electrical stimulation of the index finger. The symbols in the first line indicate the significance levels of differences with regard to durations of electrically evoked APs in relation to those of air-puff elicited APs given in the second line. Tests of significance were made using Student's *t* test.

Stimulus	Recording site				Statistical significance
	1	2	3	4	
E (msec)	1.15 ± 0.21 (16)	1.27 ± 0.22 (16) *	1.44 ± 0.24 (15) ***	1.56 ± 0.31 (12) **	$P < 0.005$
A (msec)	0.97 ± 0.28 (16)	1.00 ± 0.33 (15)	0.93 ± 0.32 (10)	0.85 ± 0.37 (5)	n.s.
Duration ratio (E/A)	1.28 ± 0.40 (16)	1.40 ± 0.42 (15)	1.70 ± 0.64 (10)	2.01 ± 0.77 (5)	$P < 0.05$

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

similar increase at a rate of 0.19–0.41 msec per unit distance along the nerve. The P1, N1 and P2 peaks of air-puff evoked APs invariably occurred later than those of electrically evoked APs (Fig. 3), the mean latency difference between the two ranging from 0.80 msec to 1.56 msec (Table IIB). This

TABLE IVA

Distal conduction velocities * (m/sec, mean ± S.D.) along the median nerve following air-puff stimulation.

AP component	Recording site				Statistical significance
	S1	S2	S3	S4	
P1	39.84 ± 5.08 (16)	41.67 ± 4.57 (16)	43.66 ± 5.28 (14)	43.66 ± 4.63 (9)	n.s.
N1	35.37 ± 4.48 (16)	37.28 ± 4.47 (16)	39.08 ± 4.50 (13)	40.67 ± 4.26 (7)	n.s.
P2	32.42 ± 4.12 (16)	34.54 ± 4.52 (15)	36.43 ± 4.91 (9)	36.84 ± 4.02 (5)	n.s.
N2	30.59 ± 3.71 (13)	32.40 ± 3.90 (13)	33.69 ± 4.29 (8)	34.84 ± 3.77 (4)	n.s.
P3	28.09 ± 3.38 (12)	29.91 ± 3.55 (12)	31.89 ± 4.06 (10)	34.80 ± 0.57 (3)	$P < 0.05$
N3	26.02 ± 3.80 (7)	27.93 ± 4.26 (7)	29.98 ± 5.82 (4)	33.92 ± 0 (1)	n.s.
P4	24.32 ± 4.21 (6)	26.08 ± 4.42 (6)	27.79 ± 4.33 (4)	27.07 ± 4.17 (3)	n.s.
N4	23.44 ± 4.96 (3)	24.96 ± 5.08 (3)	25.52 ± 5.93 (2)	30.77 ± 0 (1)	n.s.
Statistical significance	$P < 0.005$	$P < 0.005$	$P < 0.005$	$P < 0.005$	

* Distal conduction velocities were calculated between the stimulus site (S) at the finger tip and the distal electrode of each pair of recording electrodes over the forearm (1, 2, 3 and 4) in this and the following Table IVC.

TABLE IVB

Proximal conduction velocities * (m/sec, mean ± S.D.) along the median nerve following air-puff stimulation.

AP component	Recording site			Statistical significance
	1–2	2–3	3–4	
P1	64.28 ± 18.09 (11)	51.86 ± 24.00 (8)	55.51 ± 19.90 (8)	n.s.
N1	67.68 ± 17.91 (13)	64.91 ± 21.20 (9)	48.37 ± 12.91 (4)	n.s.
P2	67.08 ± 15.75 (14)	62.54 ± 18.49 (6)	47.02 ± 10.60 (4)	n.s.
N2	59.08 ± 14.92 (10)	55.74 ± 9.86 (5)	47.22 ± 2.78 (2)	n.s.
P3	54.02 ± 11.51 (8)	57.78 ± 13.03 (5)	54.80 ± 0.75 (2)	n.s.
N3	55.80 ± 15.09 (4)	41.25 ± 4.21 (2)	52.63 ± 0 (1)	n.s.
P4	58.89 ± 10.47 (5)	68.11 ± 6.11 (3)	62.50 ± 20.83 (2)	n.s.
N4	53.63 ± 5.21 (3)	66.67 ± 0 (1)	52.63 ± 0 (1)	n.s.
Statistical significance	n.s.	n.s.	n.s.	

* Proximal conduction velocities along the median nerve were calculated between adjacent electrode pairs (2 cm increments).

TABLE IVC

Comparison of distal conduction velocities (m/sec, mean ± S.D.) along the median nerve to air-puff and electrical stimulation of the index finger. The symbols in the first lines for different components indicate the significance levels of difference (Student's *t* test) with regard to conduction velocities of air-puff evoked APs (A) in relation to those of electrically elicited counterparts (E) given in the second lines in this and the following table.

AP component	Recording site				Statistical significance
	S1	S2	S3	S4	
P1					
A	39.84 ± 5.08 (16) **	41.67 ± 4.57 (16) **	43.66 ± 5.28 (14) **	43.66 ± 4.63 (9) **	n.s.
E	54.97 ± 6.33 (16)	56.49 ± 5.87 (16)	58.78 ± 6.25 (15)	62.35 ± 5.28 (11)	$P < 0.05$
N1					
A	35.37 ± 4.48 (16) **	37.28 ± 4.47 (16) **	39.08 ± 4.50 (13) **	40.67 ± 4.26 (7) **	n.s.
E	47.13 ± 5.41 (16)	48.43 ± 5.52 (16)	50.31 ± 5.82 (15)	53.43 ± 4.89 (11)	$P < 0.05$
P2					
A	32.42 ± 4.12 (16) **	34.54 ± 4.52 (15) **	36.42 ± 4.91 (9) *	36.84 ± 4.02 (5) *	n.s.
E	40.14 ± 4.20 (16)	40.77 ± 4.39 (16)	41.78 ± 4.41 (15)	43.46 ± 4.49 (12)	n.s.

* $P < 0.05$; ** $P < 0.001$.

TABLE IVD

Comparison of proximal conduction velocities (m/sec, mean ± S.D.) along the median nerve to air-puff and electrical stimulation of the index finger.

AP component	Recording site			Statistical significance
	1–2	2–3	3–4	
P1				
A	64.28 ± 18.09 (11)	51.86 ± 24.00 (8) *	55.51 ± 19.90 (8)	n.s.
E	65.75 ± 14.54 (10)	80.59 ± 8.95 (8)	78.09 ± 10.48 (5)	n.s.
N1				
A	67.68 ± 17.91 (13)	64.91 ± 21.20 (9)	48.37 ± 12.91 (4)	n.s.
E	62.09 ± 12.57 (14)	71.41 ± 12.35 (10)	73.61 ± 16.84 (7)	$P < 0.05$
P2				
A	67.08 ± 15.75 (14) *	62.54 ± 18.49 (6)	47.02 ± 10.60 (4) *	n.s.
E	52.04 ± 14.89 (15)	59.41 ± 11.55 (12)	68.18 ± 12.24 (10)	$P < 0.05$

* $P < 0.05$.

delay includes the time of skin indentation and receptor transduction in response to mechanical stimulation.

Comparison of durations of the initial negative peaks of mechanically and electrically evoked afferent volleys

The durations of the early 3 negative waves in mechanically evoked APs, defined as latency differences between P1 and P2 (N1), P2 and P3 (N2) and P3 and P4 (N3) were significantly shorter than those of electrically induced triphasic APs (Table IIIA, B). The duration of electrically induced APs (N1) increased linearly in a proximal direction along the median nerve ($P < 0.005$), while that of air-puff evoked APs remained invariant. Thus, it is clear from Table IIIB that the duration ratio of the electrically evoked N1 component to its air-puff induced counterpart increased along the ascending median nerve, suggesting differential temporal dispersion of the volleys elicited by the two modes of stimulation. This is in accord with results obtained from comparison of amplitudes of the same component in the propagating volleys in response to air-puff and electrical stimulation.

Comparison of conduction velocities of mechanically and electrically evoked afferent volleys

Table IV shows conduction velocities of the median nerve, measured for the finger tip-distal forearm segments (Table IVA) and for each 2 cm segment over the wrist and distal forearm (Table IVB). When measured to the onset (P1) of the first negative wave of the APs there was a successive increase in conduction velocity of the median nerve from distal (39.85 ± 5.08 m/sec) to proximal (43.66 ± 4.63 m/sec) location. Similarly, propagation velocities of the later peaks increased linearly in the distal-to-proximal direction. These differences in conduction velocities as a function of recording site did not reach statistical significance except for that of P3. On the other hand, these distal conduction velocities derived from the different peaks recorded at the same segments showed a gradual decrease with successively later peaks, and the differences were statistically significant for all recording derivations ($P < 0.05$).

Proximal conduction velocities calculated over the unit distance between adjacent electrode pairs were much greater than the distal conduction velocities determined from the finger tip to the distal forearm, primarily due to cancellation of the extra delay at the skin mechanoreceptors (Table IVB).

Distal propagation velocities of the electrically evoked APs derived from P1 and N1 showed a linear increase in the proximal direction and the differences were significant ($P < 0.05$, Table IVC). These values were significantly greater than those obtained from the same segments after air-puff stimulation ($P < 0.001$).

In contrast, comparing interelectrode propagation velocities of the onset (P1) and initial negative peak (N1) between nerve volleys at the same segments following air-puffs and electrical stimulation, the differences were significant only for 1 out of 6 segments ($P < 0.05$, Table IVD). Conversely, there were no significant differences between the conduction velocities of the fastest fibers activated by air-puffs and electrical stimulation for five-sixths of the nerve segments. The results suggest that there are no appreciable differences, if any, between the fastest volleys elicited by the two modes of stimulation. In this connection, attention should be given to the fact that segment to segment variations in the proximal conduction velocities were greater than those in the distal conduction velocities, probably due to errors in electrode placements. A 2 mm displacement for instance, gives an uncertainty of 1.3% for a distal segment of 15 cm, while this gives an error of as much as 10% on the 2 cm proximal segment.

Discussion

The results of this study show that air-puff stimulation of the finger tip evokes a series of propagating AP waves along the median nerve at the wrist and forearm. Early pioneering studies by Sears (1959), Bannister and Sears (1962) and McLeod (1966) on mechanically evoked digital nerve potentials were recently reproduced, and it has been unfortunately shown that their recorded potentials were not of neural origin but rather movement artifacts caused by the fingernail tapping (Pratt et al. 1979a). Thus, these authors were the first to record mechanically evoked nerve potentials using surface electrodes over the median nerve at the wrist. The wave forms illustrated in their report were biphasic and similar to those evoked by electrical stimulation.

This is in sharp contrast with wave forms of air-puff elicited afferent nerve volleys, which had several separate peaks. Using similar tapping stimuli and surface recording techniques, Nakanishi et al. (1973) were also able to register mechanically induced peripheral nerve activity. However, the morphology of their recorded APs was neither illustrated nor described.

Schieppati and Ducati (1984) recorded air-puff induced compound nerve activity directly with needle electrodes and found a much smaller potential with an average amplitude of 0.2 μV compared to the potential (1.5 μV) following fingernail tapping (Pratt et al. 1979a). This discrepancy probably resulted from air-puff activation of mechanoreceptors exclusively in the small area of target skin, whereas finger tapping recruits a larger population of skin as well as deep receptors within a relatively larger area.

In contrast, in our study stimulation with sharp air-puffs elicited nerve potentials with well defined and reproducible multiple peaks, although their amplitudes were almost the same as those reported by Schieppati and Ducati (1984). The multiplicity of peaks in summed and averaged APs following mechanical stimulation has not been described previously. Studies on single unit impulses of cutaneous afferents have suggested that these separate peaks are due to sequential activation of various types of mechanoreceptor (Knibestöl 1973, 1975; Johansson and Vallbo 1979a, b; Johansson et al. 1980). First, force thresholds of individual mechanoreceptors in the glabrous skin area of the human hand, as determined with von Frey hairs, are distributed over a wide intensity range from 10 to 1000 dynes (Johansson et al. 1980). Secondly, median thresholds of two types of rapidly adapting mechanoreceptors, the rapidly adapting (RA) and pacinian corpuscle (PC), were as low as 58 and 54 dynes, whereas those of slowly adapting mechanoreceptors, the type I slowly adapting (SA I) and type II slowly adapting (SA II), were much higher (130 and 750 dynes respectively) (Johansson et al. 1980). Extrapolation from these data indicates that all skin mechanoreceptors can be recruited by the air-puffs we used (1357 dynes). Moreover, there is a possibility that deep receptors were also activated, but we have no available evidence so far to test this conjecture. Thus, the multiple peaks in the compound APs registered in this study presumably reflect sequential excitation of mechanoreceptors with different thresholds. In this connection, Johansson and Vallbo (1979b) documented that the human finger tip is densely innervated by RA and SA I mechanoreceptors but PC and SA II receptors are more evenly distributed over the fingers and palm. Moreover, the RA and SA I afferents have small and well defined cutaneous receptive fields of relatively uniform sensitivity. In contrast, the PC and SA II afferents are characterized by large receptive fields sensitive to remote stimuli. Thus, the PC and SA II might also be activated with a delay introduced by the traveling time of the percussion wave from the stimulus point to the location of these receptors. It seems reasonable, therefore, to assume that these low threshold RA, PC and SA I cutaneous afferents contribute substantially to early peaks of the summed and averaged nerve activity. It is not possible, however, to deduce from the present work the detailed temporal relationship between each peak of the compound APs and afferent volleys from a certain type of skin receptors. Alternatively, it may be argued that the separate peaks after air-puff stimulation are the product of differences in conduction velocities of afferent fibers from different receptors, as was suggested by electrically evoked APs (Buchthal and Rosenfalck 1966). However, a comparison of interelectrode propagation velocities of the different peaks from the same segments did not demonstrate any significant difference for air-puff evoked APs. This is compatible with data from human microneurographic studies that single afferents from 4 types of receptor had mean conduction velocities (hand to elbow) of 59, 55, 47 and 45 m/sec for SA I, RA, PC and SA II mechanoreceptors respectively, and although the PC and SA II afferents tended to conduct at slightly lower velocities than the other two types, no significant difference could be demonstrated between the 4 types of receptor (Knibestöl 1973, 1975). From this type of evidence, it appears unlikely that the separate peaks in air-puff evoked APs are the result of temporal dispersion due to differences in conduction velocities of skin afferents. Therefore, we conclude that these multiple peaks are due to a more peripheral receptor mechanism involving transduction and impulse generation; that is, to differences in rise-time of the depolarizing generator potentials and/or differences in activation threshold among the 4 types of mechanoreceptor.

Proximal conduction velocities (wrist to elbow) similar to those we measured were reported by Nakanishi et al. (1973) (54 and 57 m/sec for 2 subjects) and Schieppati and Ducati (1984) (54 m/sec for 10 subjects) using either mechanical tapping or air-puff stimulation on the finger tip. On the other hand, distal conduction velocities from the finger tip to the wrist were consistently slower than the proximal conduction velocities by 10–20 m/sec, i.e., a fairly close agreement with the values (40–47 m/sec) obtained in rapidly adapting and slowly adapting mechanoreceptive afferents recorded from the median nerve at the wrist (Hagbarth et al. 1970). This abrupt increase in conduction velocities from distal to proximal segments involves (1) a true increase in the proximal direction as well as (2) removal of transduction delay in the calculation of interelectrode proximal conduction velocities (Buchthal and Rosenfalck 1966; Pratt et al. 1979b).

Transduction delays, as determined by the latency differences of early peaks (P1, N1 and P2) between the median nerve potentials evoked by the air-puffs and those induced by electrical stimulation, have mean values ranging between 0.80 and 1.56 msec. When only the mean transduction delays for N1 are considered, they are more narrowly distributed, ranging from 1.18 to 1.31 msec. These values are smaller than those measured for N1 by Schieppati and Ducati (1984) using air-puffs (1.9 msec) and by Pratt et al. (1979b) using electromechanical stimulation (3.0 msec), probably reflecting the shorter rise-time of the air-puff we employed. Recently, Pratt and Starr (1986) used this latency difference to evaluate the function of receptors and sensory nerve terminals in peripheral neuropathies caused by diabetes, uremia and mercury poisoning. They suggested that the latency difference was significantly prolonged in uremic neuropathy and mercury poisoning but was normal in diabetic neuropathy. These results indicate that measurement of this latency difference may be useful in evaluating receptors and sensory nerve terminals in health and disease.

Based on the systematic decrease in the P1-N1 amplitude ratio of electrically elicited APs to air-puff evoked APs recorded along the ascending median nerve, neural elements activated by electrical stimulation of the digital nerves appear to be more diverse than after air-puff stimulation of the skin. Conversely, the corresponding component of air-puff evoked APs may originate from a more uniform afferent fiber population. This is supported by the increasing ratio of the duration of N1 of the electrical APs relative to the air-puff APs in the proximal direction along the nerve.

In conjunction with the previous single unit data (Knibestöl 1973, 1975; Johansson and Vallbo 1979a, b; Johansson et al. 1980), the results of the present study suggest that mechanical air-puff stimulation elicits a series of peripheral nerve AP peaks in which each peak represents a relatively homogenous population of skin mechanoreceptors.

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