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# PHASE COHERENCE IN VIBRATION-INDUCED RESPONSES OF TACTILE FIBRES ASSOCIATED WITH PACINIAN CORPUSCLE RECEPTORS IN THE CAT

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## SUMMARY

1. In pentobarbitone-anaesthetized cats, responses were recorded in peripheral nerves or cervical dorsal columns from sensory fibres associated with Pacinian corpuscle (P.c.) receptors in the forelimb footpads. Factors affecting the phase of response to cutaneous vibration in individual P.c. fibres, and the extent of phase coherence in the responses of different P.c. fibres were examined when sinusoidal vibratory stimuli at 100–400 Hz were delivered using a 1 mm diameter probe.

2. Increases in vibration amplitude from the absolute to the 1 : 1 threshold for the P.c. fibre led to phase advances in the response, often of about 60 deg, in over 85 % of fibres tested at 200 and 300 Hz, but further increases had little effect.

3. Variations in stimulus position within the receptive field led to unpredictable changes in the response phase that ranged from minimal change to shifts of 180 deg. As the response phase was unrelated to the distance from the point of peak sensitivity it is likely that at high vibration frequencies ($\geqslant$ 100 Hz) the recruited population of P.c. fibres will respond over the whole range of phase angles.

4. The calculated phase of spike initiation in different pairs of P.c. fibres that shared coincident points of best sensitivity on the skin ranged from near synchrony to maximum asynchrony indicating that there is little phase coherence even in the subpopulation of somatotopically related P.c. fibres recruited by high-frequency cutaneous vibration.

5. Paired recordings from P.c. fibres within the cervical dorsal columns revealed a broad range of phase discrepancies in the responses of P.c. fibres to vibration at 200 and 300 Hz.

6. Several hypotheses are considered to explain the known presence of phase-locked responses to high-frequency ($\geqslant$ 100 Hz) vibration in the central neurones of dorsal column nuclei.

## INTRODUCTION

Cutaneous vibration sensitivity covers a band width from about 5 to 1000 Hz (Newman, Doupe & Wilkins, 1939; Verrillo, 1962; Goff, 1967) with the major part of the range, from approximately 80 to 1000 Hz, being mediated by Pacinian corpuscle (P.c.) receptors and their associated P.c. sensory fibres (Jänig, Schmidt &

Zimmermann, 1968; Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968; Iggo & Ogawa, 1977; Ferrington & Rowe, 1980*b*). Over their whole frequency range, the P.c. fibres respond to vibration with tightly phase-locked impulse trains whose metronome-like regularity reflects precisely the periodicity of the applied vibration (Talbot *et al.* 1968; Ferrington & Rowe, 1980*b*; Ferrington, Hora & Rowe, 1984).

However, despite this reliable signal of vibration frequency within the impulse patterns of individual P.c. sensory fibres, the subjective capacity for recognition and discrimination of vibration frequencies declines markedly at frequencies above 100 Hz (von Bekesy, 1962; Goff, 1967; Rothenberg, Verrillo, Zahorian, Brachman & Bolanowski, 1977).

It appears, therefore, that the reliable information about vibration frequency encoded in the impulse patterns of individual P.c. fibres is not retained within the central pathways. This may be related to the known deterioration in the precision of impulse patterning in the course of central transmission (Douglas, Ferrington & Rowe, 1978; Ferrington & Rowe, 1982; Connor, Ferrington & Rowe, 1984; Rowe, Ferrington, Fisher & Freeman, 1985). The deterioration may arise because the central neurones receive convergent, phase-discrepant inputs from different P.c. fibres.

In the present experiments we have investigated, first, the factors influencing the phase of vibration-induced responses within individual P.c. fibres, in particular, the effects of changes in vibration amplitude and in stimulator probe position within the fibre's receptive field. Secondly, we have examined the extent to which variations in these parameters, or in conduction velocity of different P.c. fibres, influence phase coherence in the responses across the P.c. fibre population.

## METHODS

### *Animal preparation*

Experiments were performed on thirty-one adult cats anaesthetized with sodium pentobarbitone (45 mg $kg^{-1}$; intraperitoneal) and maintained with intravenous (I.V.) supplements. After shaving the skin around the footpads the distal forelimb was fixed, pads uppermost, in paraffin wax to permit accurate positioning of the mechanical stimulator. The median or ulnar nerve was exposed in the forearm, freed from surrounding tissue and cut near the elbow. The perineural sheath was opened to free the component nerve bundles and the nerve covered with liquid paraffin in a pool formed by the skin flaps and held at 32–34 °C. Thin nerve strands were isolated by microdissection and draped over the recording electrodes.

For experiments in which recordings were made from primary fibres within the spinal dorsal columns a laminectomy was performed in the upper cervical segments and the spinal cord covered with a 4 % w/v agar gel to minimize cardiac and respiratory pulsations. Positive-pressure ventilation was used to maintain an end-tidal $P_{CO_2}$ of $4{\cdot}0 \pm 0{\cdot}5$ %. Anaesthesia was maintained by a continuous infusion of sodium pentobarbitone (3 mg $kg^{-1}$ $h^{-1}$; I.V.) in a 5 % w/v solution of dextrose, usually in combination with gallamine triethiodide (5 mg $kg^{-1}$ $h^{-1}$) to eliminate any spontaneous movements. Rectal temperature was held at $38 \pm 0{\cdot}5$ °C in all experiments. At the termination of experiments an overdose of pentobarbitone was given.

### *Recording and stimulation procedures*

Activity was recorded from peripheral nerve strands using stainless-steel or platinum hook electrodes and from the dorsal columns using tungsten micro-electrodes. Recorded signals were amplified and displayed using conventional techniques. They could also be fed to a magnetic tape recorder and a discriminator unit whose output pulses were relayed to a laboratory computer.

P.c. fibres selected for study at both the peripheral and central recording sites had receptive fields with their most sensitive points on the forelimb footpads.

Stimuli were delivered normal to the skin surface using a circular probe, 1 mm in diameter, driven

by a feed-back-controlled mechanical stimulator (Douglas *et al.* 1978; Bennett, Ferrington & Rowe, 1980; Ferrington & Rowe, 1980*a*,*b*). The stimuli consisted of 1 s trains of sinusoidal vibration that were superimposed on a 400 $\mu$m step indentation of 1·6 s duration that started 300 ms prior to the vibration. During periods of analysis the repetition rate for the stimulus pattern was one per nine seconds.

The region of peak sensitivity within the receptive field of each P.c. fibre was defined either as the point at which the threshold for a response to 200 or 300 Hz vibration was lowest or, in some cases, the point of maximum sensitivity as assessed with a von Frey hair.

Peripheral conduction velocity estimates were obtained for some P.c. fibres after measuring conduction distance and conduction time to the recording site following electrical stimulation using needle electrodes inserted into the skin at the site of maximum sensitivity within the fibre's receptive field.

*Analysis of phase of response to vibration*

Cycle histograms were constructed using the laboratory computer to examine the temporal relations between impulse activity and the vibration wave form (Rose, Brugge, Anderson & Hind, 1967; Talbot *et al.* 1968; Mountcastle, Talbot, Sakata & Hyvärinen, 1969; Douglas *et al.* 1978; Bennett *et al.* 1980; Ferrington & Rowe, 1980*a*,*b*; Rowe *et al.* 1985). The cycle histograms use a pulse associated with the onset of each vibration cycle as the stimulus marker and display the probability of an impulse occurring at different times throughout the period of the vibration cycle (see Fig. 1). The analysis period for the cycle histogram corresponds to the cycle period for the vibration and was divided into a number (from twenty-four to ninety-nine) of time segments or addresses. The histograms were constructed from the impulse activity recorded in response to 500–2000 cycles of vibration delivered in trains lasting 1 s.

Two procedures were performed on the cycle histogram distributions for the statistical analysis of the phase relations in the responses to vibration. First, the mean phase of response was calculated and, where paired recordings were made, the difference in mean phase of response, in degrees, was obtained for the fibre pair. Because the cycle histogram distributions for P.c. fibre responses are confined to a narrow segment of the histogram, the calculation of mean phase of response was usually satisfactory using linear statistics for the mean and standard deviation. However, a more appropriate statistic for analysing information about phase relations in cyclic events is the directional or angular statistic (Mardia, 1972), particularly when the impulse distribution extends beyond the bounds of the histogram in its linear form. For the directional statistic the distribution is arranged in a circle so that 0 and 360 deg are congruent (Goldberg & Brown, 1969; Mardia, 1972) and the contents of each address in the histogram radiate in a column whose height reflects the number of impulse occurrences within that address (Fig. 5). The measure obtained using the cyclic statistic was the *resultant* ($R$), which is a measure of phase coherence in the distribution and is inversely related to the dispersion in the impulse occurrences around the mean phase of the response. In the case of paired distributions for two P.c. fibres (see Fig. 5), values of $R$ could range from 1 for complete phase synchrony to 0 for symmetrical distributions separated by a 180 deg phase-difference.

In previous applications of the cyclic statistic in sensory physiology, for measuring the degree of synchronization or *vector strength* in the responses of auditory neurones to tonal stimuli, values of $R$ below 0·3 were taken to indicate little or no phase-locking, values from 0·3 to 0·7 as moderate phase-locking and 0·7 to 1·0 as a high degree of phase-locking (Lavine, 1971; Bledsoe, Rupert & Moushegian, 1982). However, in the present study a different criterion was chosen, as $R$ values were obtained for pairs of P.c. fibres sampled from a population. If there was complete phase incoherence in the responses of the population then the phase discrepancies found for different pairs of fibres would range from 0 to 180 deg. The predicted mean value of $R$ for P.c. fibre pairs sampled from such a population is 0·63. This was obtained from a series of $R$ values derived for two P.c. fibres, each with typical phase-locked responses, when the phase difference between their paired distributions was systematically varied between 0 and 180 deg. Therefore, for P.c. fibre pairs to be drawn from a population with phase-coherent responses requires that, for most pairs sampled the mean phase difference should be $< 90$ deg and the $R$ value $> 0{\cdot}63$.

In the present analyses it was uncertain from the histograms whether some of the observed changes in the mean phase angle represented advances or retardations. For example, a 100 deg advance could also represent a 260 deg retardation in the mean phase-angle. However, as the

analyses were concerned with phase relations and the extent of coherence the directions of shifts were not crucial for the analysis.

## RESULTS

All fibres selected for study from either peripheral nerves or cervical dorsal columns displayed rapidly adapting responses to a step indentation of the skin. They were most sensitive to vibration in the range 200–500 Hz and at their 'best' frequency had thresholds that were usually < 1–2 $\mu$m from the most sensitive point within the

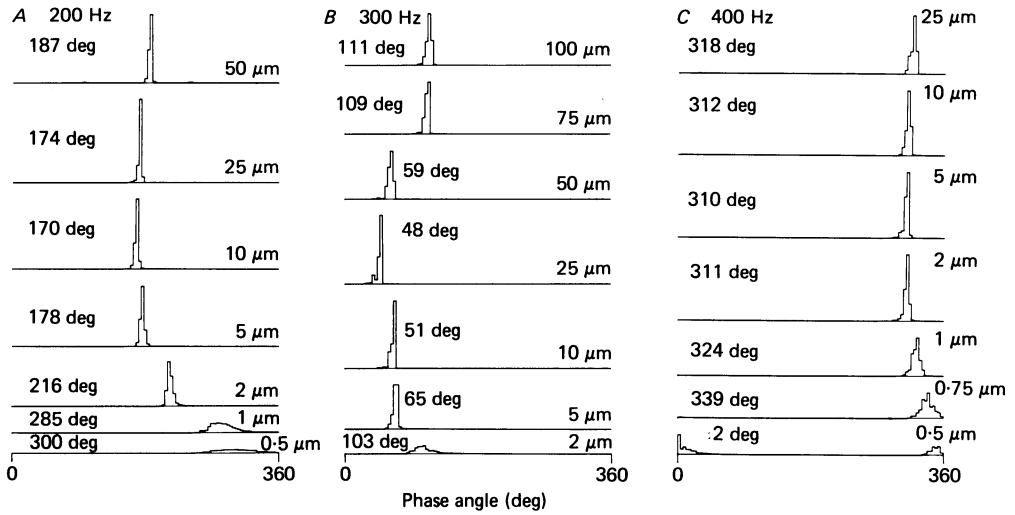


Fig. 1. Effect of changes in vibration amplitude on the phase of response in P.c. sensory fibres. The cycle histograms were constructed from responses of three different P.c. fibres to vibration at three frequencies and at a series of amplitudes (increasing from lowest amplitude at the bottom of each set). At each frequency the major changes in response phase occurred at the lowest vibration amplitudes where the response level had not reached a regular 1 : 1 pattern. At these lower levels of response the phase locking was less tight as reflected in the broader distribution of impulse occurrences. The abscissa for each cycle histogram is scaled from 0 to 360 deg as the analysis time corresponds to one cycle period at each frequency. It therefore represents 5 ms in *A*, 3·3 ms in *B* and 2·5 ms in *C*. On each histogram the phase angle of response is indicated. All histograms within each of the three sets share the same vertical gain; the highest column in the top histogram in *A* contains 610 impulse counts, in *B*, 530 counts and in *C*, 540 counts. The histograms were constructed from responses accumulated during 1000 cycles of vibration in *A*, 1200 in *B* and 1600 in *C*, in each case delivered in 1 s trains.

receptive field on the footpads. They were therefore identifiable as P.c. sensory fibres that are associated with P.c. receptors (Hunt & McIntyre, 1960; Hunt, 1961; Lindblom & Lund, 1966; Jänig *et al.* 1968; Talbot *et al.* 1968; Lynn, 1969, 1971; Ferrington & Rowe, 1980*b*; Ferrington *et al.* 1984). The mean peripheral conduction velocity measured for seventeen fibres was $54 \pm 8$ m s$^{-1}$ (S.D.) with a range of 40–75 m s$^{-1}$.

The sensitivity and responsiveness of P.c. fibres at a fixed vibration frequency were quantified by constructing stimulus–response relations in which the mean response (impulses s$^{-1}$) was plotted against vibration amplitude. At frequencies of 100–500 Hz these relations rose steeply to a plateau that was maintained over a broad range of

amplitudes and corresponded to a response level of one impulse per vibration cycle, that is, a 1 : 1 pattern of response, as described in previous reports (Talbot *et al.* 1968; Ferrington & Rowe, 1980*b*).

The phase of response to vibration was examined for fifty-one P.c. fibres recorded in the peripheral nerves and for twenty-five recorded in cervical dorsal columns.

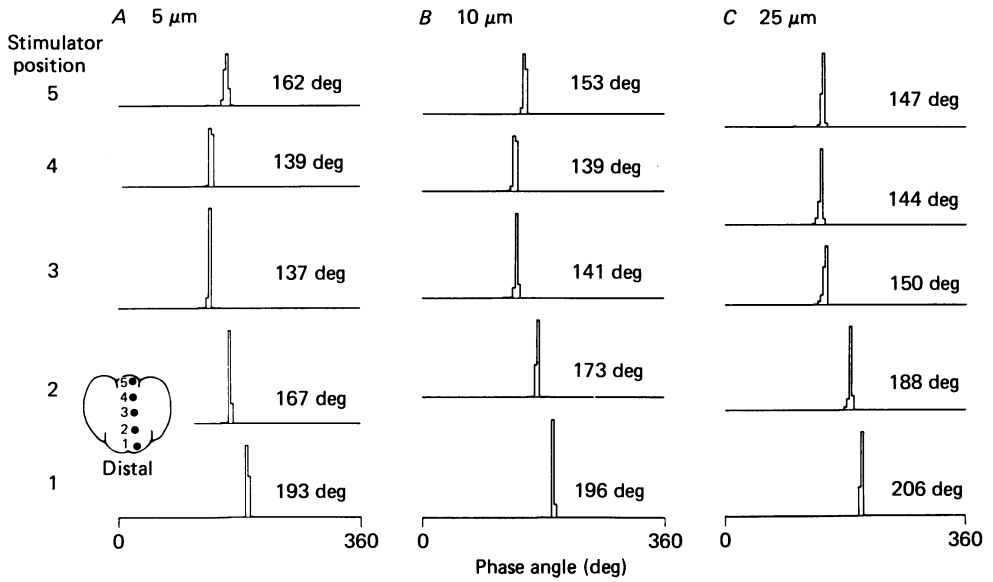


Fig. 2. Influence of changes in stimulus location on the phase of response of P.c. fibres. The cycle histograms in *A*, *B* and *C* were constructed from the responses of a P.c. fibre to 200 Hz vibration at five different positions (1–5) in a single plane running across the central footpad, indicated in the inset in *A*. The histograms show the probability of impulse occurrence throughout the vibration cycle period at each of these locations for three different vibration amplitudes: 5 μm (*A*), 10 μm (*B*) and 25 μm (*C*). The phase angle of the response is indicated next to each distribution. For each histogram the abscissa is scaled from 0 to 360 deg and corresponds to the cycle period of 5 ms for the 200 Hz vibration. All histograms within each of the three sets share the same vertical gain; the highest column in the top histogram in *A* contains 540 impulse counts, in *B*, 520 counts, and in *C*, 630 counts.

*The influence of vibration amplitude on the response phase of P.c. afferent fibres*

In almost all P.c. fibres, the preferred phase of response to vibration showed some advance with increases in vibration amplitude above the absolute threshold (Fig. 1). This was seen in twenty-two out of twenty-six fibres (85 %) tested at 200 Hz and in sixteen out of eighteen fibres (89 %) at 300 Hz. The phase advance was often approximately 60 deg, or one-sixth of the cycle period, and was most marked at low vibration amplitudes, in the range between the absolute and 1 : 1 threshold for the fibre as seen in Fig. 1. In Fig. 1*A*, the major phase advance in the response occurred with changes in vibration amplitude from 0·5 to 2 μm. For the fibre whose cycle histogram distributions are plotted in Fig. 1*B*, the 1 : 1 threshold at 300 Hz was between 2 and 5 μm, and for the fibre in *C* it was approximately 1 μm at 400 Hz. In most fibres, little change occurred in the phase of response with increases in

vibration amplitude beyond the 1:1 threshold for the fibre (Fig. 1*A*, *B* and *C*), although with quite intense vibration a phase retardation was seen in some fibres (Fig. 1*B*).

*Effect of stimulus position on the phase of responses*

The distribution of P.c. receptors activated by vibration will extend for some distance from the site of stimulation on the skin because of the high vibration

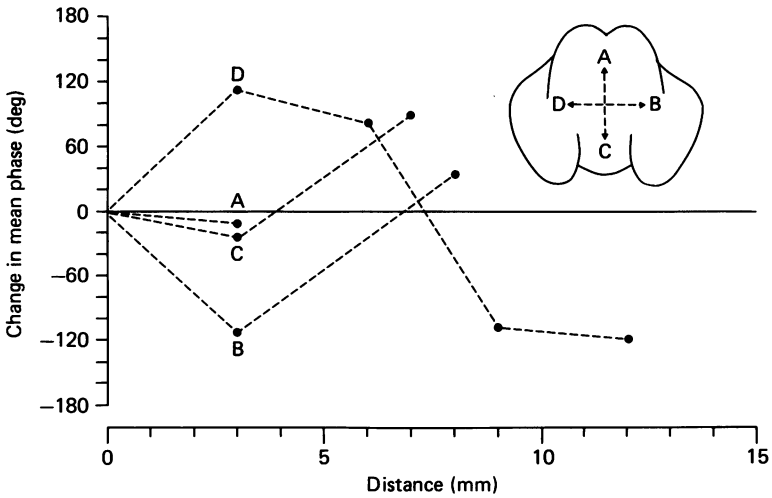


Fig. 3. Shifts in the phase of response to vibration (200 Hz, 30 $\mu$m) associated with changes in stimulus position. The graphs show the change in mean phase of response (derived from cycle histogram distributions) for a P.c. fibre as the stimulus probe position was moved along four orthogonal radii away from the central point of the footpad (inset) which corresponded to the most sensitive point in the receptive field for this fibre. The mean phase of response at this central position was assigned a phase angle of zero for the purposes of the present graph. Points on a common radius are connected by interrupted lines (A–D). On radius D, one stimulus point was beyond the footpad. Apparent phase advances are given negative values of phase change and retardations positive values.

sensitivity of these receptors and the very effective spread of vibration through the skin at 100–500 Hz (Moore, 1970). Variation in the distance between the probe tip and an individual receptor may contribute to phase changes in the receptor response, first, because of differences in the effective intensity of the vibration (although, as seen above, this influence on the phase of response is minor except at very low levels of response) and secondly, because of variability in the propagation time through the intervening tissue for the vibratory disturbance.

Changes in stimulus location had quite variable effects on the phase of response in different P.c. fibres. The phase changes extended up to 180 deg and were not systematically related to the distance of the probe from the most sensitive point in the receptive field. The effect of both probe location and vibration intensity on the response phase for one fibre is seen in Fig. 2 where five different points were stimulated along the proximo-distal axis of the central footpad as indicated in the inset in *A*. The central point, position 3, was the point of maximum sensitivity. Each column

of cycle histogram in Fig. 2 shows that the phase of response (indicated in degrees on each histogram) to 200 Hz vibration differed by up to about 60 deg at the five stimulus positions. In contrast, comparison of the three cycle histograms within a given row at a fixed stimulus position (1–5) reveals a change in response phase of only 5–21 deg with changes in vibration amplitude from 5 $\mu$m (which exceeded the 1 : 1 threshold for this fibre) to 25 $\mu$m.

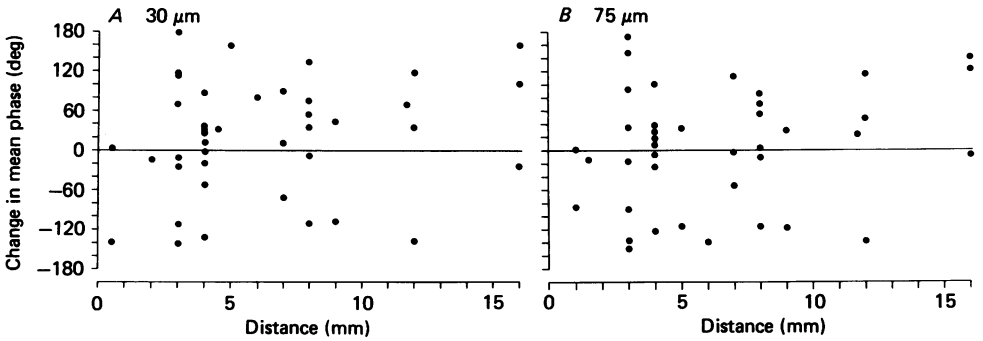


Fig. 4. Absence of a systematic relation between the phase of response to vibration and the distance separating the stimulus position and the point of peak sensitivity within the receptive field of P.c. fibres. Data pooled from eight P.c. fibres studied using 200 Hz vibration at an amplitude of 30 $\mu$m (*A*) and 75 $\mu$m (*B*). The mean phase of response of each fibre at the point of peak sensitivity within the receptive field was assigned a value of 0 and the change in mean phase of response (derived from cycle histogram distributions) moving away from this position has been plotted as in Fig. 3.

More substantial shifts in response phase with changes in stimulator position are seen for a different P.c. fibre in Fig. 3 where the changes in response phase with distance along four orthogonal radial lines (A–D) from the point of maximum sensitivity on the central footpad are plotted for 200 Hz stimulation when the amplitude was 30 $\mu$m. In this graph the phase of response at the point of peak sensitivity was allocated a phase angle of 0 on the ordinate and the change in phase at other positions expressed in relation to this reference position. There was no consistent relation between the response phase and the distance from the point of peak sensitivity. Nor did the changes along different radii reveal any particular consistency in their form.

The unpredictable effects of probe position on response phase were seen for eight P.c. fibres studied as shown by the pooled data in Fig. 4 for 200 Hz stimulation at amplitudes of 30 and 75 $\mu$m in *A* and *B* respectively. Phase discrepancies up to the maximum of 180 deg were found between the reference position and other locations, but the magnitude of the discrepancy appeared unrelated to the distance from the reference point.

In order to verify that the phase angle of response at different locations was a function of location and not attributable to variability in the way the stimulus probe was positioned at each location, or to the time intervals between analyses at different locations, we examined the influence of these factors on the phase of response at a fixed location. Repositioning of the stimulus probe normal to the skin surface at its original location produced changes in response phase of $< 10$ deg ($< 3\%$ of the cycle

period) in seven tests on three P.c. fibres. When the placement angle departed from normal by up to 45 deg the phase shifts were < 15 % of the cycle period. The response phase was re-examined at different intervals in the one location in twenty-four tests carried out on twelve P.c. fibres. At intervals of < 1 h the mean phase shift was $6 \pm 3{\cdot}5$ deg ($n = 13$) and at $\geqslant 1$ h the shift was $9 \pm 6$ deg ($n = 11$).

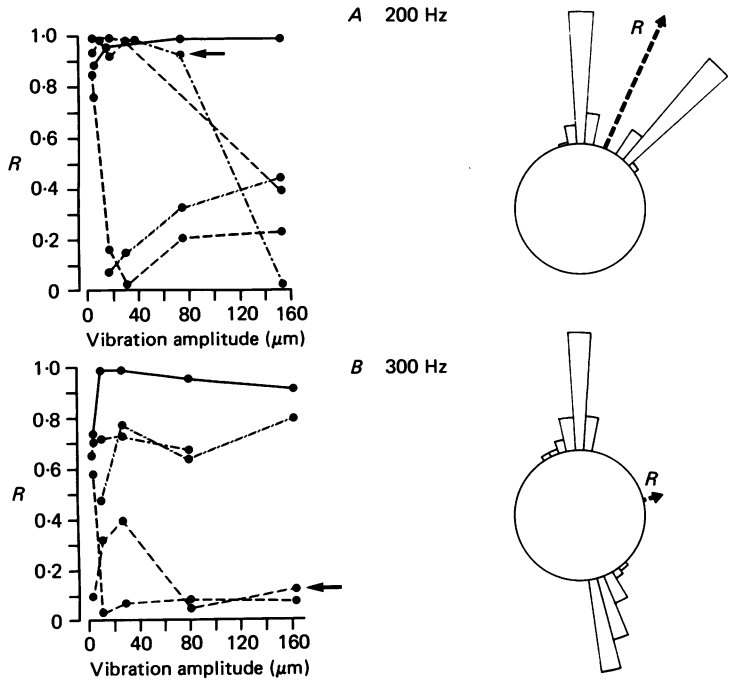


Fig. 5. Extent of coherence in the phase of response initiation for simultaneously recorded pairs of P.c. fibres. Phase coherence for each pair has been quantified by calculating $R$ using circular statistics (see Methods) from the circular histograms of the type shown on the right-hand side in $A$ and $B$. The value of $R$ can range from 0 to 1; for the distribution shown in $A$ it was 0·93, and for that in $B$ it was 0·12. These values are indicated in the graphs of $A$ and $B$ by the arrows. For each of five pairs of P.c. fibres $R$ was obtained at a series of vibration amplitudes at 200 and 300 Hz and the values plotted in $A$ and $B$, respectively. The connected points within each graph were obtained for a particular pair of fibres. Before calculating $R$ for the paired responses, the phase of spike initiation at the receptor was obtained for each fibre by subtracting the conduction time, calculated from the fibre's conduction velocity and the distance from the point of peak sensitivity on the footpad to the recording site in the peripheral nerve.

*Variability in phase of response initiation in P.c. receptors*

Peripheral nerve recordings were also carried out to determine whether there was synchrony in the phase of spike initiation in different P.c. receptors when both vibration amplitude and stimulus location were fixed. These observations were made on pairs of P.c. fibres whose most sensitive points on the central footpad were coincident. The phase of spike initiation in each fibre was obtained by adjusting the phase angle of the recorded responses by an amount corresponding to the conduction time from the skin to the forelimb recording site. The phase coherence of spike

initiation for the fibre pairs was then assessed from the adjusted cycle histograms either by measuring the difference between the mean phase of response or by calculating $R$ (see Methods) from the combined cycle histograms (Fig. 5). Values for both measures in the different pairs sampled ranged from almost complete synchrony in the phase of initiation (phase difference $< 10$ deg, and $R > 0{\cdot}99$), to maximum

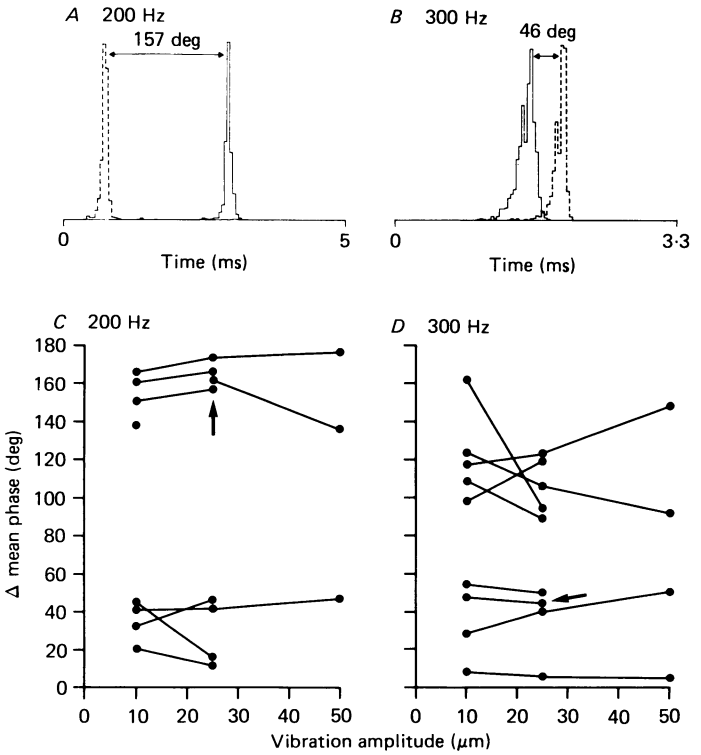


Fig. 6. The extent of phase coherence in the vibration-induced responses of pairs of P.c. fibres was recorded in cervical dorsal columns near the entry zone of the cuneate nucleus. The cycle histograms constructed from responses of fibre pairs to 200 and 300 Hz vibration in *A* and *B*, respectively, show in *A*, a marked discrepancy (157 deg) in the mean phase of response but in *B*, only a small discrepancy (46 deg). These differences in mean phase of response (Δ mean phase) are plotted in *C* and *D* (indicated by the arrows) along with those obtained at different vibration amplitudes for all nine fibre pairs recorded centrally.

incoherence (for example, a phase difference of 176 deg, and $R$ of 0·04). The circular histograms on the right-hand side in Fig. 5 show paired response distributions for two fibres with similar phases of spike initiation following 200 Hz vibration (*A*) and for two different fibres with widely discrepant phases of spike initiation in response to 300 Hz (*B*). The graphs on the left-hand side of Fig. 5 plot $R$ for five pairs of fibres at a series of vibration amplitudes at 200 (*A*) and 300 Hz (*B*).

*Variability in response phase for pairs of P.c. fibres recorded centrally*

The extent of phase coherence in the responses of P.c. fibres near their entry point to the dorsal column nuclei was assessed directly by recording at the first cervical

segment from P.c. fibre pairs whose most sensitive points were coincident or nearly coincident on the central footpad. Fibres studied had stimulus–response relations and band widths of vibration sensitivity similar to those of peripherally recorded P.c. fibres. They also responded to high-frequency (> 200 Hz) vibration with a regular 1 : 1 impulse pattern over a broad range of vibration amplitudes. They therefore had all the attributes of primary P.c. fibres and were unlikely to be post-synaptic units of the dorsal columns (Brown, Brown, Fyffe & Pubols, 1983). The observed phase relations displayed a wide range, from coherent to incoherent, as seen in Fig. 6 for nine pairs studied at 200 and 300 Hz. The phase discrepancies were determined from the cycle histogram distributions obtained at a fixed vibration frequency and amplitude and are plotted in Fig. 6 as the difference between the mean response phase for each fibre of the pair.

The data at 200 Hz in Fig. 6*C* include four pairs with coherent responses (< 50 deg discrepancy in mean phase) and five with widely discrepant phase relations. At 300 Hz (Fig. 6*D*) there was a more even scatter of phase discrepancies but over a similar broad range. The histogram pairs shown in Fig. 6*A* and *B* had mean phase discrepancies of 157 and 46 deg respectively, these values being indicated in *C* and *D* by the arrows.

*R* values calculated for the paired cycle histograms from the centrally recorded P.c. fibres also confirmed the variability in phase coherence apparent in the mean-phase differences of Fig. 6. The broad range of phase discrepancies indicates that the pairs were sampled from P.c. fibre populations in which the whole range of phase relations occurs.

## DISCUSSION

The phase of P.c. fibre responses to cutaneous vibration varied with changes in both vibration amplitude and the position of the stimulator probe within the receptive field of the fibre. However, the changes in vibration amplitude when the stimulus probe was in a fixed location had little effect on the response phase except at very low vibration amplitudes (below the 1 : 1 threshold of the fibre; Fig. 1), as was also observed (Johnson, 1974) for the class of tactile fibres (designated r.a. or q.a. fibres) that signal vibration information in the range 5 to about 80 Hz (Jänig *et al.* 1968; Talbot *et al.* 1968; Johnson, 1974; Mountcastle, 1975; Iggo & Ogawa, 1977; Ferrington & Rowe, 1980*b*).

The phase advance observed at 100–400 Hz in the responses of most P.c. fibres going from the absolute to the 1 : 1 threshold level was about 60 deg which is similar to the shift observed in the response phase of r.a. fibres at 40 Hz when vibration amplitude is changed from their absolute to their 1 : 1 threshold level (Johnson, 1974). While this phase advance represents about 4 ms at 40 Hz where the cycle period is 25 ms, it corresponds to a shift of only 0·55 ms for the P.c. fibre response at 300 Hz.

As the predominant effects of amplitude changes on the phase of response occur at low response levels for both P.c. and r.a. fibres, these effects will occur principally when the fibre's contribution to over-all input activity is comparatively low. Therefore, except for those fibres weakly activated by vibration, most will show only minor phase shifts in their response over a broad range of vibration intensities.

*Stimulus probe position and phase of response*

Changes in stimulus probe position from the point of maximum sensitivity within the receptive field of P.c. fibres led to changes in response phase that were not readily predictable as a function of distance, whether in the medio-lateral or proximo-distal dimension from the most sensitive point on the footpad. This behaviour contrasts with that of r.a. fibres (Johnson, 1974) which in response to 40 Hz vibration display more consistent and predictable alterations in response phase with changes in stimulus position. Johnson (1974) observed that with increasing separation between the stimulus position and the point of peak sensitivity for the r.a. fibre there is a progressive phase retardation of approximately 25 deg $mm^{-1}$ in the response to 40 Hz vibration. Amplitude effects contribute to this phase retardation in r.a. responses as the effective intensity of the vibration falls with distance. For most P.c. fibres, however, the effects of amplitude on response phase were small in comparison with the effects of stimulus position. Presumably the major and less predictable effects of probe position are attributable to the time taken for mechanical spread of the vibration from the stimulus site to the receptors. The unpredictability of these effects probably reflects some heterogeneity in the mechanical properties of the skin and underlying tissues of the footpads.

*Phase coherence in the vibration-induced responses of P.c. fibres*

The observations on the phase relations between responses of P.c. fibre pairs recorded both at the periphery and within the cervical dorsal columns indicate that there is an absence of coherence in the profile of incoming activity in response to vibration at 100–400 Hz. The principal factors contributing to this lack of coherence are, first, discrepancies in the phase of spike initiation that, in part, are related to variable and unpredictable effects of probe position on the phase of response and, secondly, conduction-velocity differences among different P.c. fibres. These differences can allow phase discrepancies to arise between fibres that display some synchrony at the periphery, or, in the case of those with asynchrony at the periphery, they presumably make no systematic contribution to an enhancement of synchrony over the conduction path to the nuclei (Fig. 6).

The results therefore demonstrate that across the P.c. afferent population arising in the footpads, the responses to high-frequency vibration can occur across the whole range of phase angles, in contrast to the coherence seen for r.a. fibre responses to 40 Hz vibration, where responses occur within 180 deg, or half-cycle segment of the cycle period (see Figs. 8 and 9, Johnson, 1974).

*Phase relations in P.c. fibre responses to vibration: implications for central processing of information about vibration frequency*

Despite the lack of obvious coherence in the population response of P.c. afferent fibres, their target neurones within dorsal column nuclei retain phase-locked responses up to vibration frequencies of $\geqslant 400$ Hz (Douglas *et al.* 1978; Ferrington & Rowe, 1982; Connor *et al.* 1984; Rowe *et al.* 1985). Mechanisms that might account for this include first, a non-convergent, 1 : 1 linkage between primary fibre and central neurone; secondly, integration by individual central neurones of inputs from a

convergent subset of P.c. fibres that retain some net phase preference in their response to vibration; and thirdly, functional domination of an individual neurone by just one of its convergent P.c. fibres (Ferrington, Horniblow & Rowe, 1987; Ferrington, Rowe & Tarvin, 1987*a*, *b*).

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