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A THEORETICAL FRAMEWORK TO REPRESENT AND PREDICT THE RESPONSES OF CUTANEOUS MECHANORECEPTORS

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1. INTRODUCTION

It is well known that mechanoreceptors are activated only when the skin is distorted and not when there is distortion-free translation or rotation (i.e., "rigid body" motion) of the region of the skin around the receptor. We are, therefore naturally led to the hypothesis that the receptor response is related to the strains generated by the stimulus. Furthermore, the farther the stimulation region is from the receptor site, the weaker are the strains at the receptor site and responses of the receptor. Therefore, it seems reasonable to expect the strains in the immediate neighborhood of a receptor to be the cause of its response. A slightly more general form of this hypothesis is to include stresses, and can be represented by the block diagram shown in Figure 1:

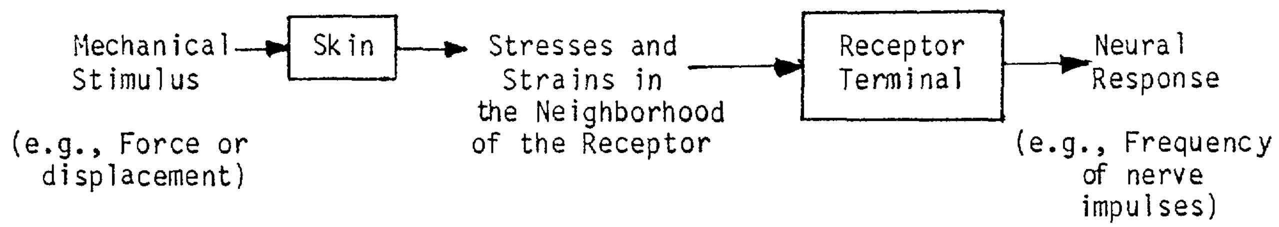

Figure 1

Ideally, a direct experimental investigation of the various aspects of the system represented above would involve the actual observation of the distortions at a receptor site caused by a known stimulus, while recording the response of that receptor. However, such an experiment is not possible at the present time. First of all, the receptors are imbedded approximately 1mm below the skin surface (Figure 2, from Darian-Smith, 1984) and, hence, cannot be directly observed.

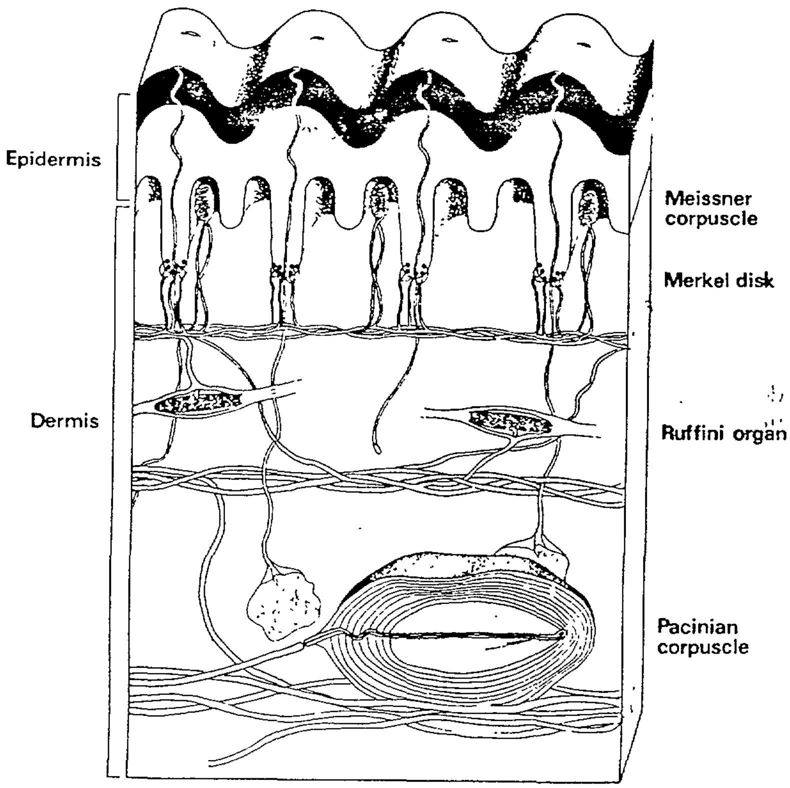

Figure 2

Even with a video technique such as the one used by Cohen and Vierck (1983), where the skin can be cut and viewed in cross section, we do not have high enough resolution or the means of recording from the receptor that is being observed. Except for the Pacinian corpuscle, which is about 1mm in diameter, mechanoreceptors are small (only 5 to 100 um, Darian-Smith, 1984) and, at present, we have no means of measuring all the strain components in soft tissue at such small length scales. In fact, at these length scales, the skin can be seen to consist of irregular interconnections of collagen and elastic fibers together with blood vessels, nerves and lymphatics (Gibson and Kenedi, 1968). On the other hand, at the molecular level, even though the basic processes of impulse generation and propagation are well understood (Katz 1961), and there is some information concerning their relation to the stretching of the nerve membrane (Guharay and Sachs, 1984), the quantitative relationship between a general mechanical stimulus and the molecular processes of transduction is not well understood.

From a theoretical viewpoint, the representation shown in Figure 1 implies that the response to any given stimulus can be predicted if we have the following:

(1) A mechanical model of the skin and the substrate materials which can be used to calculate reliably the stresses and strains at each point in the skin for a given stimulus.

(2) A model of the receptor that provides the relationship between the relevant stimulus (a particular combination of stresses and strains in the neighborhood of the receptor) and the measure of the response that is of interest, say, the frequency of nerve impulses.

For simplicity, even if we neglect the details of the fiber network that make up the skin and assume the skin to be a continuum, deducing a mechanical model of the skin and the substrate materials from a strict application of the principles of continuum mechanics is a complex problem. Experiments conducted on soft biological tissues in general and skin in particular (Gibson and Kenedi, 1968, Fung, 1981) show that they exhibit inhomogeneity, anisotropy, rate and time dependence.

In the case of the fingertip, even if we assume it to be linear elastic, it is three dimensional, curved and composed of layers of soft material (which cannot be tested easily under realistic conditions). The three specifications fundamental to a mechanical analysis, namely, (i) the mathematical description of the geometry of the structure, (ii) constitutive equation for the material behavior, and, (iii) taking into account the large deformations therefore pose formidable problems.

2. A Model Proposed by Phillips and Johnson.

The first step in simplifying the problem on all three counts mentioned above and in postulating a receptor model has been taken by Phillips and Johnson (1981b). They constructed a mechanical model to predict the spatial response profiles of mechanoreceptors to gratings stepped across their receptive fields. The fingertip was assumed to be mechanically equivalent to a semi-infinite, homogeneous, isotropic, incompressible elastic medium with a plane surface and in a state of plane stress or strain under infinitesimal deformations. In such a case, the Boussinesque solution (Timoshenko and Goodier, 1970) for a line load is applicable except in the vicinity of the load where it predicts extremely large vertical deflections. This difficulty is eliminated by Phillips and Johnson - more or less arbitrarily - by abandoning the Boussinesque solution at locations up to a distance of 25um from the load and assuming the deflection to be constant in that region. By using the predicted surface deflection profile under a line load and the principle of superposition, inverse calculations are performed, where for a known depth of indentation under the bars of the gratings used in the experiments, the force distribution necessary to cause the indentation is inferred. This force distribution is then used to calculate the strain fields at the receptor site.

On the basis of the observation that under a range of aperiodic gratings, the profiles of the predicted maximum compressive strain were quite close to the spatial impulse rate profiles of slowly adapting mechanoreceptors (SA) during the steady part of the vertical indentation experiments, it was proposed that the slowly-adapting (SA) mechanoreceptors respond to maximum compressive strain*. In the model, three SA receptor characteristics - its depth, sensitivity and threshold, were determined by matching the maximum compressive strain profiles with the spatial discharge rate profiles using the method of least squares.

It is indeed remarkable how well the maximum compressive strain profiles match the receptor responses for all the gratings, in spite of the fact that the three parameters (receptor depth, sensitivity and threshold) were adjusted over all the responses for each fiber only once. However, the main drawback of this model is that it is in terms of variables that are not empirically

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*Similarly, maximum tensile strain was postulated as the relevant stimulus for rapidly adapting (RA) mechanoreceptors. Since under steady indentation, maximum tensile strain is present (and constant, according to the model) while there is no RA response, a direct relationship between them is incorrect. Maximum tensile strain <u>rate</u> is perhaps more appropriate, but the comments made next regarding the drawbacks of this approach hold for RAs, too.

verifiable at present. We have no means of measuring the depth of the receptor whose responses are being recorded, the compressive strain at a certain depth in the finger or even the force profile under the gratings. In addition, it is not obvious as to how the approach has to be modified in order to predict the responses under a given stimulus.

One possibility is to indent the most sensitive spot with line loads corresponding to various depths of indentation and record the responses to the static phase. For an assumed receptor depth (average obtained empirically), we can calculate the compressive strain at the receptor site for various depths of indentation using the Boussinesque solution. Threshold and sensitivity could then be obtained from a plot of calculated compressive strain vs. response for various depths of indentation. These values could then be used in predictions. However, the confidence in such calculated results would not be high because they are unverifiable.

In spite of these difficulties, results obtained by Phillips and Johnson establish a strong prima facie case that the compressive strain is the relevant stimulus to the SAs. Clearly, it explains two major characteristics of SAs under steady indentations: a greater response with greater depths of indentation and an exquisite sensitivity to the edges of the indenting object. (However complex the actual materials that make up the fingertip may be, compressive strain must certainly be higher under an edge than under the flat portion of the bar in the grating.)

3. A New Approach

We shall now try to simplify the problem of determining the quantitative relationship between the mechanical stimulus and the resulting response of a receptor by taking a more gross approach. Since direct empirical verification of receptor characteristics and the local skin mechanics are not possible at present, we shall view them together as a "system." The stimuli applied to the skin surface are the inputs to the system and the resulting sequences of action potentials are the outputs. We know from a large number of experiments that the suprathreshold responses of this system are repeatable to a high degree of accuracy, provided adequate care is taken in stimulus control and the elimination of interstimulus adaptation effects (Pubols, 1982). Therefore, there is hope for a modeling approach that does not explicitly take into account the detailed biomechanics of the skin or the characteristics of the transducer mechanism of the receptor at the molecular level.

The indications from previous studies are that the system response is immediate* and not a strong function of the time history of inputs. It is then possible to predict the responses to a complex stimulus by expressing it as a combination of stimuli to which response is known. If such an approach is successful, we will then have a unified interpretation of the system's

*Since the recording site is at most about 30cm from the receptor, due to finite conduction velocity (30-50m/sec.), there is a delay of about 10 msec between the recorded response and the stimulus that caused it. However, we shall neglect this delay for a first analysis.

behavior under various circumstances, thereby enabling us to have more confidence in hypotheses concerning the actual mechanism of coding. Specific aspects of these hypotheses can then be verified by performing fine experiments along the lines of the video technique developed by Cohen and Vierck (1983) to observe cut skin in cross-section.

Although the mechanoreceptors can be divided into fairly well-defined classes (SA, RA, PC), within each class the units can respond in ways that differ significantly for the same stimulus. It is reasonable to expect that these differences are due to variation in both the local mechanical behavior of the skin in the neighborhood of the receptor and the individual characteristics of the receptor itself. In any of the single unit recording techniques used now, except for the most sensitive spot on the skin surface, no information can be obtained concerning the location and characteristics of the receptor or the skin structure around it. Any features that distinguish the receptor from others of its own class have to be in terms of its response to some standard stimuli. Therefore, <u>any</u> predictive modeling approach must have the following two components to it:

1) A set of "unit identification experiments" consisting of simple stimuli which can be used to characterize the unit response.
2) A theoretical framework with which we can represent both the simple stimuli used in the unit identification experiments and the stimuli for which we wish to predict the responses. This framework should enable us to express the latter as some combination of the former.

Additional desirable features of the stimulus representation are that they should be simple, empirically verifiable and, if possible, directly relatable to the shapes of objects. For example, under a bar in a grating, kinematic variables such as displacement and curvature of the most sensitive spot are usually measurable, while the local force distribution in the neighborhood of that point is not. Hence, from a verification point of view, it is better to specify kinematic variables as the stimulus rather than the force distribution, even though the two are necessarily related.

To summarize, we propose that any quantitative modeling of mechanoreceptors should start with a gross level investigation as follows: Identification of the unit characteristics by recording responses to simple stimuli applied at the skin surface; Prediction of the system response to more complex stimuli by using a theoretical framework to express them in terms of the simple stimuli used earlier; Verification of the appropriateness of the framework by actually applying the complex stimuli and recording the response. If the results match the prediction for various complex stimuli, then we can formulate hypotheses about the receptor mechanisms and perform fine experiments to check the hypotheses . If the predictions are not right, the framework has to be modified.

It should be noted that this kind of gross level approach has been used very successfully in structural mechanics. In analyzing the behavior of a complex structure, the following steps are generally followed: First, the material is "identified" in terms of its gross properties, such as the Young's modulus and Poisson's ratio in the case of an elastic material, by performing simple tests on sample specimen. At this stage, no detailed attention is paid to its actual grain or molecular structure and mechanisms. Then, using a theoretical framework involving laws of material behavior obtained from the simple tests and the laws of equilibrium of internal forces, the response of the complex structure is predicted and later verified by actual experiments. If the predictions do not match, such as the case where elastic material begins to exhibit plastic or viscoelastic behavior, additional experimentally determined "identification" parameters are incorporated into the theoretical framework. This dialogue between experiments and theory is continued until a satisfactory match between the two is achieved. If desired, specific hypotheses concerning finer mechanisms, say, at the grain level, are made such that they are consistent with the gross level results and then tested.

In the next section, we propose a representation for the RAs and later for SAs. As in structural mechanics, the proposed gross study of mechanoreceptors has its limitations. We restrict ourselves to objects and shapes that have "length scales" of the order of millimeters. We rule out fine textures (um length scale), because of the expected importance of miniscule movements of skin, such as local distortions of papillary ridges (LaMotte and Whitehouse, 1985). We also concentrate only on experimental findings that are repeatable and especially on major recurring features.

4. Modeling Responses of Rapidly Adapting Mechanoreceptors

It is known from the experiments performed on humans by Johansson and Vallbo (1983) that at stimulus intensities near threshold, RAs appear to have multiple sensitive spots distributed over a roughly circular area of 2mm diameter on the skin surface. But when the intensity of the stimulus is much greater than the threshold level, the units behave for all practical purposes as if they had only one "most sensitive spot." In the following discussion, we restrict ourselves to this view.*

In order to decide on an appropriate framework for a discussion of RA behavior, we shall now review their responses to the vertical indentations.

4.1 Choice of input-output variables

In a typical vertical indentation experiment , a lucite probe of 1mm diameter, rounded to a one-third sphere, is placed onto the most sensitive spot in the RA's receptive field. The skin is then vertically indented by 1mm, as shown in Figure 3 (Pubols, 1980). By definition, all RAs respond only when the velocity of the skin is non-zero.

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* Such an assumption is not absolutely necessary for this approach. But it simplifies the discussion.

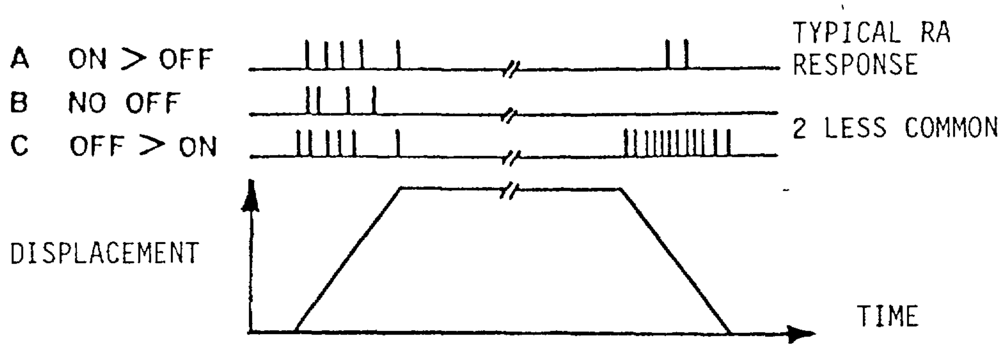


Figure 3

We see that the responses of RAs differ in many ways: the number of impulses during ON and OFF phases vary, the interspike interval may remain constant or increase during ON ramp and the number of impulses during ON may be greater or lesser than that during OFF. In addition, the threshold or minimal displacement required to evoke a minimal response varies from RA to RA. Any input-output representation of RAs should be capable of handling these diverse behaviors.

(a) Output variable

Even though the response of a unit is a sequence of impulses and therefore discrete, it would be desirable to have a measure of the output that is continuously varying in time so as to relate it one-to-one with continuous measures of the input. Therefore, we choose to represent the output in terms of "instantaneous frequency." A continuous graph of instantaneous frequency vs. time for a given train of impulses is obtained by plotting the reciprocal of interspike interval at the midpoints of the interval and joining the successive points by straight lines or a smooth curve.

(b) Input variables

We know that the farther the stimulation region is from the most sensitive spot, the kinematic variables (displacement, velocity, acceleration, etc.) at the most sensitive spot as well as the response of the unit are smaller. Also, since the kinematic variables are usually empirically verifiable, it is reasonable to use their values at the most sensitive spot to describe the effective stimulus.

Instantaneous frequency is a function of the velocity of vertical indentations (e.g., Pubols and Pubols, 1976; Knibestol, 1973; Mountcastle *et al*, 1983). Indentation velocity is therefore chosen as an input variable. In addition, it is also known that for some RAs, the instantaneous frequency decreases during a constant velocity ramp (adaptation). Traditionally, this is viewed as a characteristic of the receptor. Alternatively, we can look for a quantity that varies during the ramp that may be thought of as the cause of such a decrease in frequency. Two possible candidates are force and displacement at the most sensitive spot. In the case of indentation with, say, a sharp probe, force at the most sensitive spot is zero when stimulation is at a neighboring location, while both the instantaneous frequency and the displacement at the most sensitive spot vary during the ramp. Hence, displacement at the most sensitive spot is chosen as the second input variable. We shall see that the choice of displacement (d) and its time derivative, velocity (v) at the most sensitive spot, as inputs are sufficient for our present purpose, though future experiments might make it necessary to consider other variables (section 4.6).

4.2 Input representation

The input to the skin-receptor system is now viewed as a specific variation of d and v with respect to time. A two axes representation of d and v (Figure 4) defines a stimulus plane or "S-plane" which is characteristic for each experiment. Some typical experiments done on RAs are shown in Figure 4 with their respective traces on an S-plane. This representation is known as the "Phase plane representation" in the study of differential equations (Jordan and Smith). Here, time is an implicit parameter that determines the speed at which various portions of a path are traversed.

The variation of displacement of the most sensitive spot with respect to time in a vertical indentation experiment is indicated as (1) in Figure 4A and traces the path OABCDEO on the S-plane. The line AB corresponds to the ramp; the point C represents the steady indentation phase and the line DE represents the retraction of the probe. Sharp corners in Figure 4A indicate discontinuous changes in velocity, and hence, infinite acceleration, implying that the portion OA, BC, CD and EO in the S-plane are traversed instantaneously. In an actual experiment, however, no such sharp corners exist in a strict sense, and if necessary, the path on the S-plane can be easily modified to reflect the realistic conditions by using the input trace used in the experiment.

Let the sinusoidal vibration at the most sensitive spot, superposed on the steady indentation (d_o) in path (2) of Figure 4A, be given by:

$$d(t) = d_o + A\ \mathrm{Sin}\Omega t \qquad (1)$$

Where, A = amplitude of vibration

t = time elasped from the start of vibration

Ω = angular velocity

Therefore, $$v(t) = A\Omega\cos\Omega t \qquad (2)$$

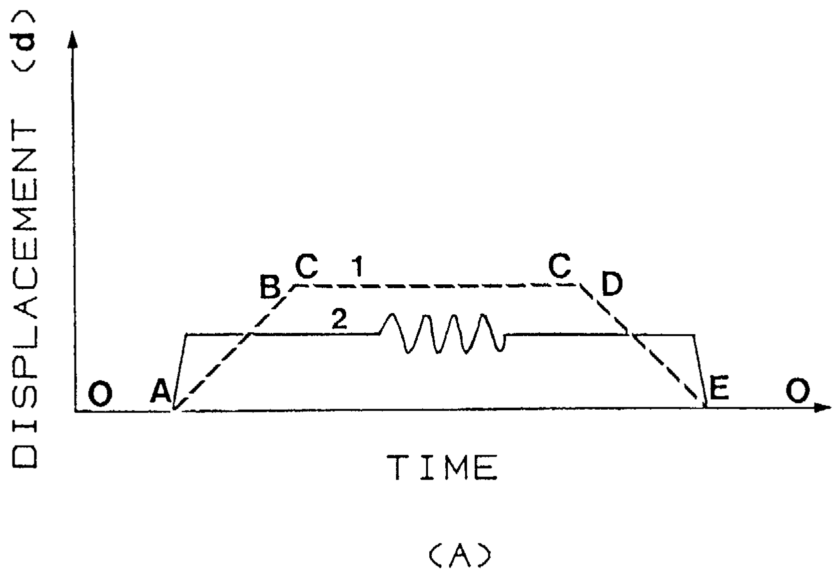
Using the relation $\mathrm{Sin}^2\Omega t + \cos^2\Omega t = 1$, we obtain from (1) and (2):

$$\frac{(d-d_o)^2}{A^2} + \frac{v^2}{A^2\Omega^2} = 1 \qquad (3)$$

which defines the ellipse shown in Figure 4B which is centered at the displacement value d_o.

4.3 Output representation

As mentioned before, we choose the instantaneous frequency of response as the output measure. We shall represent the instantaneous frequency along a response axis or "R-axis" perpendicular to the S-plane, so that together they form the "S-R space." Consider now a sequence of vertical indentation experiments at the most sensitive spot, each of which is entirely repeatable due to proper care in eliminating the effects of interstimulus adaptation (Pubols, 1982). Furthermore, let these experiments be such that the ramp velocity is held constant at a value much greater than threshold, while the


DISPLACEMENT (d)
O
A
B
C
1
2
C
D
E
O
TIME
(A)

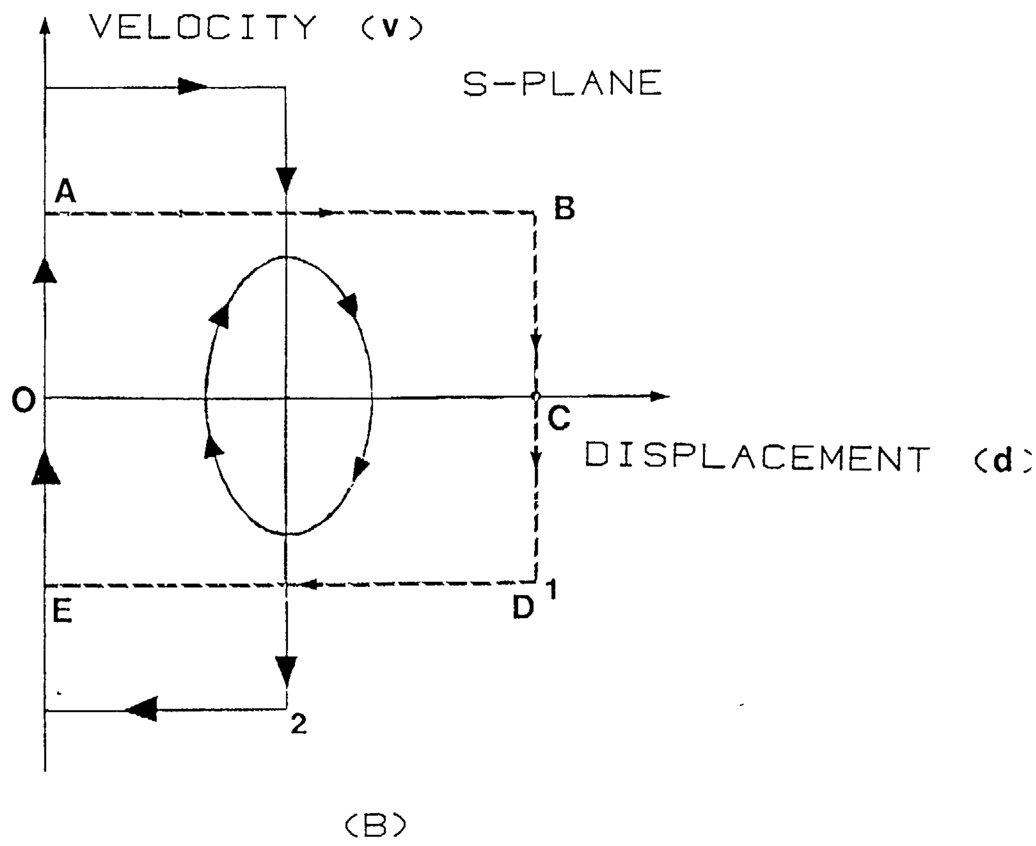

VELOCITY (v)
S-PLANE
A
B
O
C
DISPLACEMENT (d)
E
D
1
2
(B)

Fig. 4

depths of indentation at the end of the ramp are successively increased. Let T_1 be the ramp-time of one experiment and T_2 be that of the next where T_2 is greater than T_1. Since through a proper choice of interstimulus interval, we have ensured repeatability, the response trace of impulse frequency vs. time up to T_1 should be identical in both the experiments. In other words, the unit's response at any instant during the ramp cannot depend on when the experimenter decides to terminate the ramp (which fixes the total depth of indentation). This implies that there is only one impulse frequency for each (d,v) pair.

Since this should be true for all values of v above threshold, we must have a "response surface" that defines the response for each point on the S-plane. We hypothesize that this surface characterizes the unit and remains valid* for any experiment on that unit. Therefore, once the response surface of a unit is known, its response for any stimulus can be predicted as follows. As described earlier, the input in any experiment traces a certain path in the S-plane (Figure 5 - for an RA). The ordinates at each point of this path give the response of the unit for that point in terms of instantaneous frequency. As we integrate these responses over time, whenever the integral increments by unity, an impulse is inferred to have occurred (Figure 5), and therefore the time sequence of impulses can be predicted.

4.4 Explanations of some results of published studies of RAs

A typical response surface for RA is shown in Figure 6 (see also Figure 5). We know that for a unit to respond, the displacement and velocity should

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* Actually, we expect that the dominant part of the response in any experiment can be predicted from the use of the response surface obtained from vertical indentation experiments. Additional factors such as horizontal stretch do affect the response, but we neglect them for a first analysis.

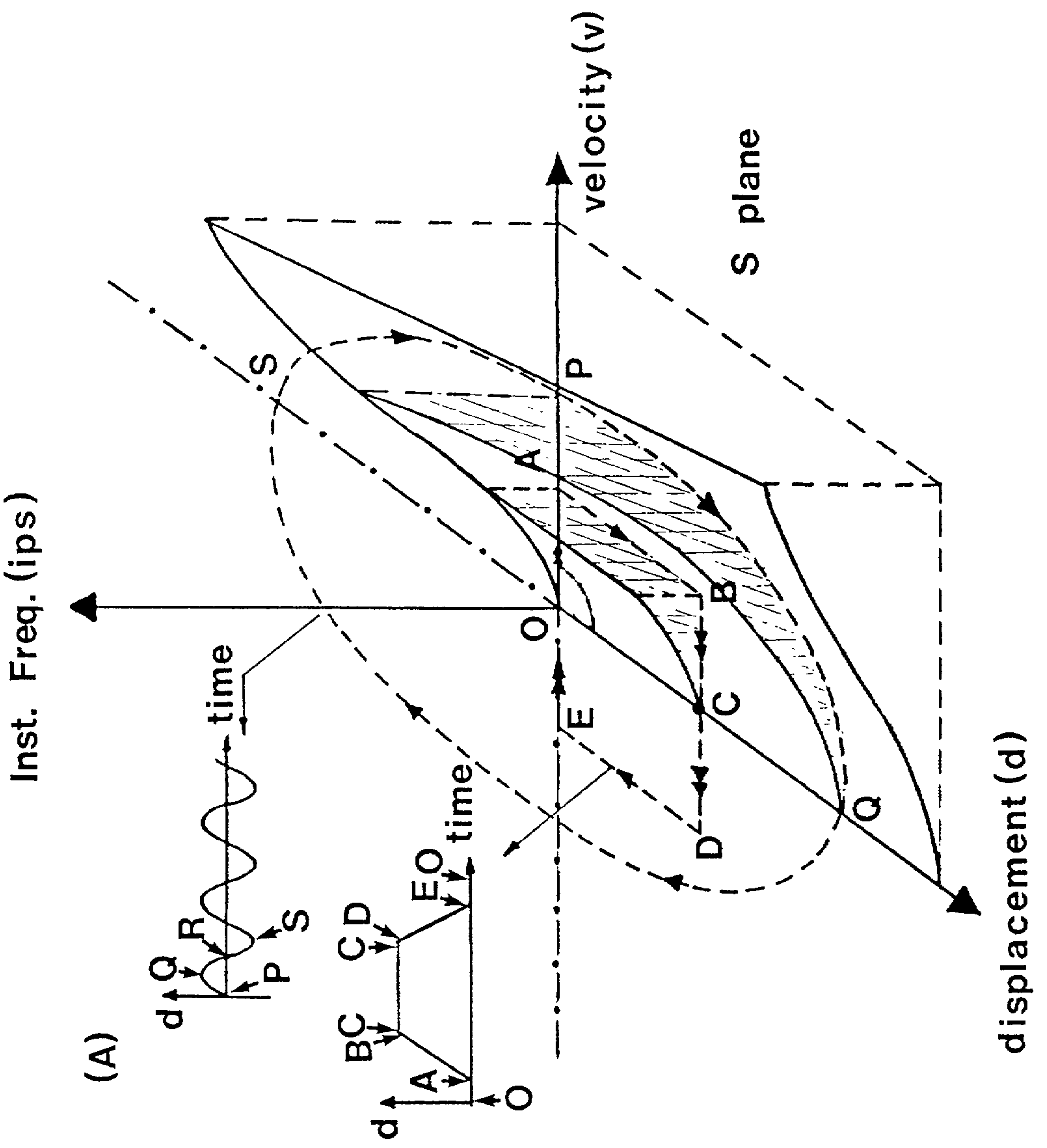

Inst. Freq. (ips)
velocity (v)
S plane
displacement (d)
time
time
time
(A)
d
d
O
A
B
C
D
E
P
Q
R
S
BC
CD
EO

Fig. 5

be above a certain threshold. This can be explained as due to the fact that within the shaded region neighboring the d axis, the time integral of the instantaneous frequency over any experimental input path is less than unity and hence no impulses are emitted.

Shown in Figure 6A are three typical suprathreshold displacement vs. time plots for vertical indentations at the most sensitive spot. The corresponding paths in the S-plane are shown in Figure 6A and the chosen response surface predicts the instantaneous frequency to vary with time as shown in Figure 6C. These results agree with the empirical observations in the literature (Pubols and Pubols, 1976; Knibestol, 1973; Burgess et al, 1983). Asymmetry in the response to ON (loading) and OFF (unloading) ramp described in Section 4.1 can easily be represented by an appropriate response surface that is asymmetrical about the displacement axis. For example, as shown in Figure 6B, if the response surface coincides with the S-plane when the velocity is negative, then the unit will be quiet during the OFF ramp.

A special case is that of a unit which emits impulses at regular time intervals during the ON ramp and whose frequency increases linearly with respect to v. This unit can be considered as a pure velocity detector and can be represented by a plane in the S-R space that intersects the S-plane along the displacement axis. The equation for this plane can be written as

$$r(t) = K\,v\,(t) \qquad (4)$$

where r = instantaneous frequency of discharge

K = constant of proportionality (sensitivity of the unit)

v = velocity of indentation of the most sensitive spot

t = time

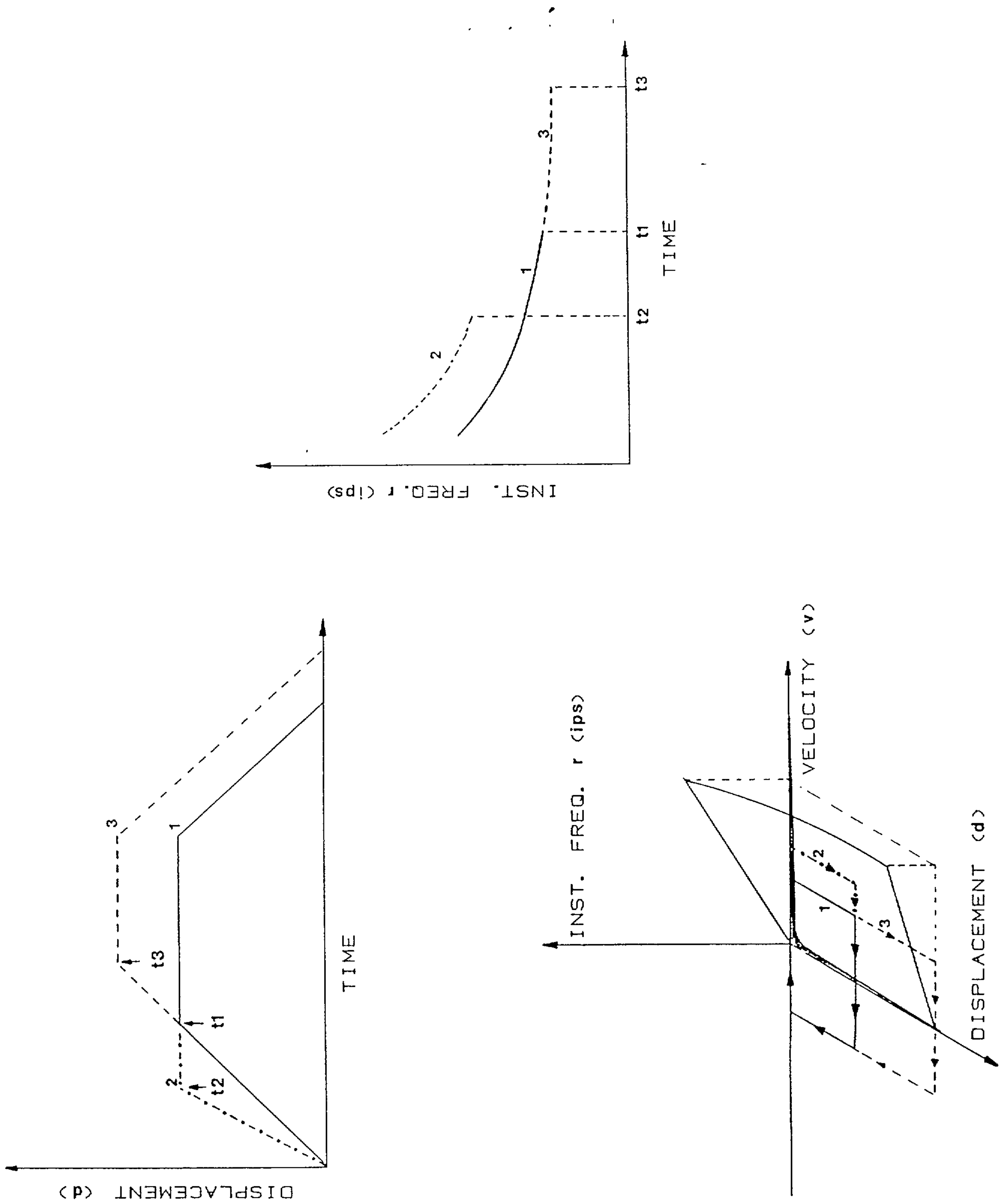


Figure 6

Integrating over time from the beginning to the end of ramp, we obtain

$$N = KD \qquad (5)$$

where N = total number of impulses during the ramp

D = depth of indentation of the most sensitive spot at the end of ramp

Thus, we have the testable implication that the number of impulses during the ramp should be proportional to the total depth of indentation of the most sensitive spot. If this is true, then as we perform the same vertical indentation experiments with a probe along various positions on a line passing through the most sensitive spot, the spatial response profile of impulses during ramp should have the same shape as the skin surface displacement profile resulting from the same probe indenting the most sensitive spot. The skin surface displacement profile perpendicular to the length of the wedge was measured when the fingertip of the monkey was indented up to a depth of 2mm with a line load delivered by a sharp wedge (Srinivasan, 1985). This displacement profile, which should be reasonably close to that under a probe, matched quite well the shape of the spatial response profile under the probe. It was also evident that when the probe indents the skin at a distance greater than or equal to about 3mm, the receptor does not respond since the most sensitive spot does not undergo any displacement. In general, whenever the relation (4) is satisfied, equation (5) implies that the spatial response profile of impulses during the ramp under any object should approximate the skin surface displacement profile under that object. This conclusion is in agreement with the empirical results of Phillips and Johnson (1981a). Thus, if the central nervous system has a simple impulse counter that keeps track of the number of impulses emitted by all the RAs when an object indents the skin and knows their respective locations, it then has a reasonable idea of the deformed shape of the skin surface. The accuracy of this information is dependent on the jitter introduced due to the variation in thresholds and sensitivities of the RAs.

We shall now try to establish the plausibility of explaining the shape of the tuning threshold curve in an experiment with mechanical sinusoids by assuming a specific form of response surface. As explained in Section 4.2, sinusoidal vibration at the most sensitive spot traces an elliptical path in the S-plane (Figure 4B). If we postulate that in evaluating the time integral of the response on this path, the integral has to be initialized to zero at the beginning of each cycle, the phase-locking of impulses becomes a consequence. It is then enough to consider only one typical cycle since both stimulus and response are periodic with the same period.

For the sake of simplicity, take $d_o = o$ in equations (3) and (4), we have,

$$d = A \, \mathrm{Sin}\Omega t \qquad (6)$$

$$v = A\Omega \cos\Omega t$$

Let r denote the response (instantaneous frequency) which is a function of d and v. For simplicity, we choose the response surface defined by:

$$r = 0 \qquad \text{When d or v is negative} \qquad (7a)$$

$$r = C_1 v^a \qquad \text{When d and v are both positive} \qquad (7b)$$

where C_1 and a are constants.

Then only the portion of the paths on that quadrant of S-plane where both d and v are positive (Figure 7) contributes to the response.

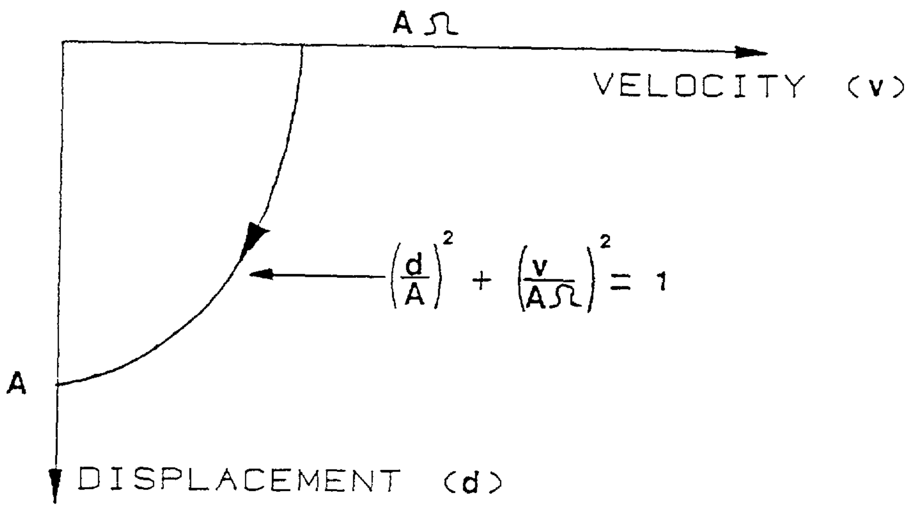


Figure 7

Therefore,

$$n = \text{number of impulses/cycle} = \int_0^{2\pi/\Omega} r\,dt$$

$$= C_1 (A\Omega)^a \int_0^{\pi/2\Omega} (\cos\Omega t)^a dt$$

$$= C_1 \frac{b(A\Omega)^a}{\Omega} \text{ where } b = \int_0^{\pi/2} (\cos\theta)^a d\theta = \text{constant} \qquad (8)$$

The amplitude A_T at tuning threshold for a given Ω is obtained by calculating the value of A in (8) when n = 1. We then obtain:

$$A_T = \frac{1}{(C_1 b)^{1/a} \Omega^{1-1/a}} = \frac{1}{(C_1 b)^{1/a} (2\pi f)^{1-1/a}} \qquad (9)$$

where f = frequency in Hz = $\frac{\Omega}{2\pi}$. The variation of r with respect to v is shown schematically in (Figure 8A) for values of a. We can then obtain the

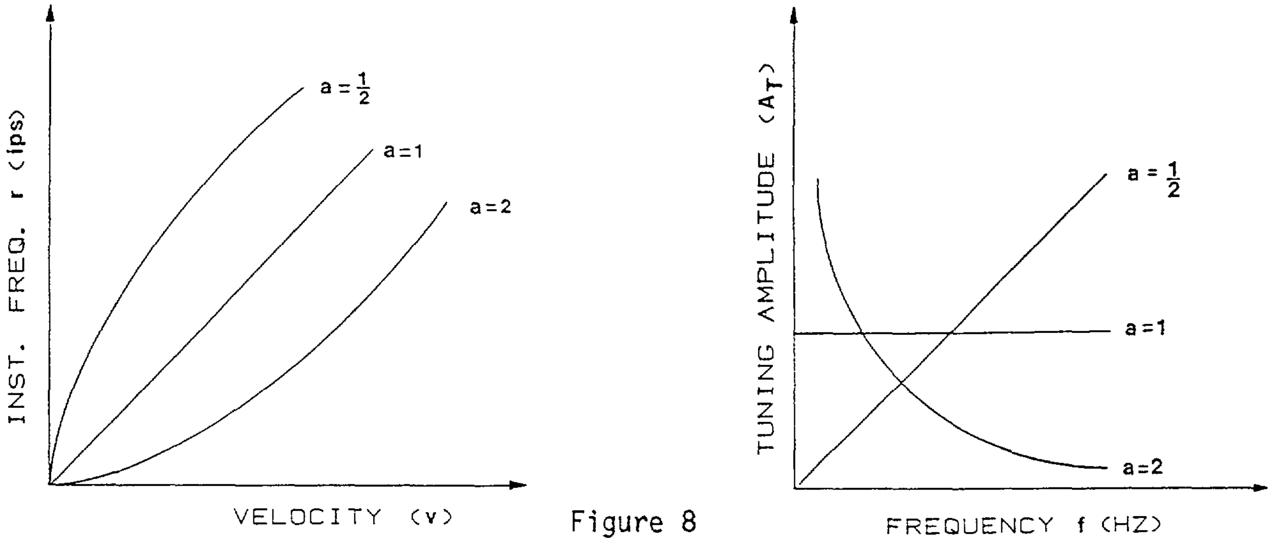


Figure 8

corresponding variation of A_T with respect to f from equation (9) and it is as shown in (Figure 8B). If a typical RA response is as shown in (Figure 9A),

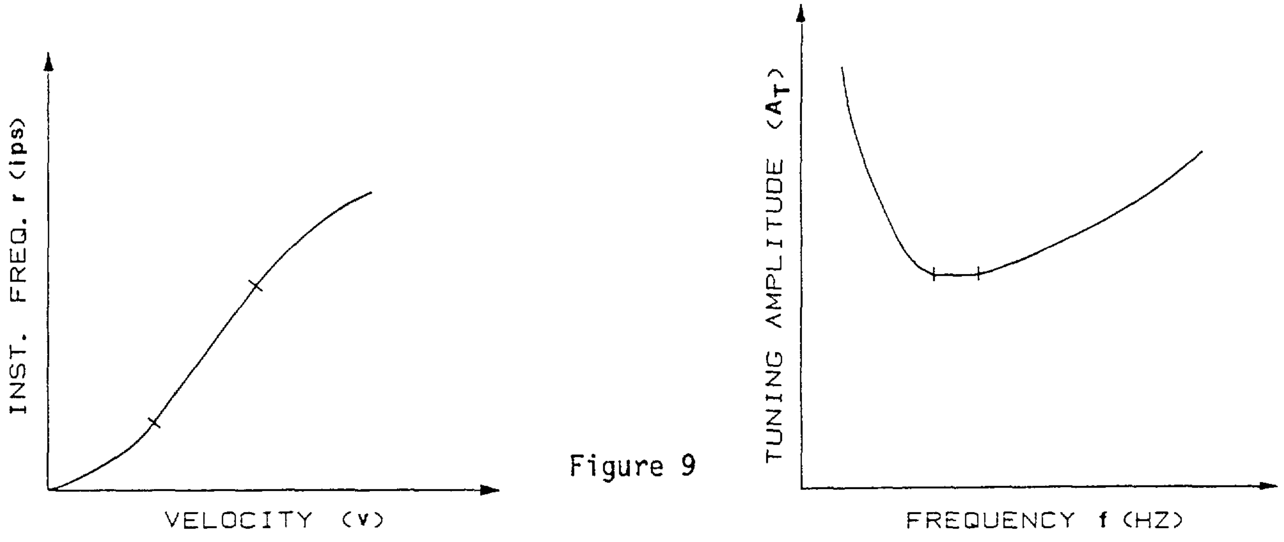


Figure 9

it is plausible that we can obtain a tuning curve as shown in Figure 9B. Obviously, the additional constants required to describe the curve in Figure

9B piece-wise in terms of equation (8) (with a different value of a for each piece) and the dependence of r on Ω can alter the shape of the tuning curve considerably.

We next describe a procedure to test the proposed representation.

4.5 Identification, Prediction and Verification

Identification of the system consisting of both the receptor and the skin structure around it involves the determination of the response surface. A series of vertical indentations are delivered to the most sensitive spot with varying ramp velocities but constant maximum depth of indentation ($\leq$ 2mm maximum should suffice). The variations of instantaneous frequency along a series of lines on the S-plane can then be obtained and suitable interpolation determines the response surface.

As described above, prediction of the response of the identified unit in a different experiment (say, sinusoidal vibration of the most sensitive spot) requires determining the associated path in the S-plane and evaluating the time integral of the ordinates at each point on this path. Integrating from the beginning, whenever the value of this integral increments by unity, an impulse is predicted to occur.

The verification of the predicted response can be accomplished by recording the responses of the same unit to the desired stimulus for which the predictions were made.

4.6 Modification of the representation

If the predicted responses do not agree with the experimental results, then the representation will have to be modified. It is possible that RAs might need acceleration as another input, thereby requiring a three-dimensional "S-space" instead of two dimensional S-plane. Also, it is known that at least some of the RAs are sensitive to sharpness or the curvature of the object used for stimulation (Johansson et al, 1982; Phillips and Johnson, 1981; LaMotte and Srinivasan, 1985). Therefore, for such units, the response surface determined by using a sharp probe cannot be used to predict the responses under a flat object. Their sensitivities to skin curvature may have to be used as an input variable, as we shall see in the case of SAs. At the same time, simplification in determining the response surfaces might be possible if, after determining enough of them in detail, we can confidently approximate them with appropriate planes. Then it is sufficient to experimentally determine this plane's orientation in S-R space, which requires much fewer identification experiments. At the very least, the theoretical framework will enable posing of specific hypotheses (such as the path dependence of responses)so that it is possible to have a unified understanding of the unit behavior under diverse circumstances.

5. Modeling Responses of Slowly Adapting Mechanoreceptors

We retain the assumption that there exists only one most sensitive spot in the receptive field (refer to section 4). It is known that in a vertical indentation experiment with a probe on the most sensitive spot, the frequency of response of SAs increases dramatically during the ramp (Pubols and Pubols, 1976; Phillips, 1980). In the plateau region, however, the response frequency drops with varying rates of adaptation until a steady state is reached. During the OFF ramp, the unit usually is either quiet or gives much fewer impulses than during the ON ramp. An additional complicating factor in representing SAs is their edge sensitivity (Phillips and Johnson, 1981; Johansson et al, 1982) or, more generally, curvature sensitivity. The smaller the curvature of the object that stimulates the most sensitive spot, the greater the response (LaMotte and Srinivasan, 1985). Also, the response seems to depend on the rate of change of skin curvature: an increased response with increasing rates of change of curvature and an absence of response when the curvature is "unloaded" or reduced. Thus, the SA response seems to be a function of displacement (d), vertical velocity (v), change in skin curvature (c) and its rate (r) at the most sensitive spot. When measuring the response in terms of instantaneous frequency as before, we see that the S-R space is five-dimensional. However, we shall explore this space by choosing situations where only two of the input variables are dominant, so that we can continue to adopt some of the geometrical methods used in the case of RAs.

5.1 Explanations of Some Results of Published Studies of SAs

In the case of SAs, a sub-threshold region exists in the neighborhood of the V-axis in the S-space (Figure 10B), where time integral of the response along any path is less than unity, and, hence, no impulses are emitted. The observation of Phillips and Johnson, 1981, that in vertical indentation experiments, SAs did not respond when the stimulus was at least 3mm away from the most sensitive spot, can be interpreted as due to sub-threshold displacement of the most sensitive spot, as explained for RAs in Section 4.4. In the case of SAs, we do not expect the spatial response profile of impulses during ramp to match the skin surface deflection profile. For example, when the edge of an object is on the most sensitive spot, the responses of an SA would be much higher than what would be necessary to match the skin surface deflection profile - because of the sensitivity of the SA to skin curvature.

Three typical supra-threshold displacement vs. time plots for vertical indentations at the most sensitive spot are shown in Figure 10A. Since the skin curvature at the most sensitive spot is equal to that of the indenting object, it remains almost constant during the experiment and, therefore, it is enough to have a two-dimensional S-space defined by axes representing vertical displacement (d) and velocity (v). The paths corresponding to the traces in Figure (10A) are as shown in Figure 10B. The chosen response surface predicts the instantaneous frequency to vary with time as shown in Figure 10C. A typical SA response recorded in indentation experiments with probes (Pubols and Pubols, 1976; Phillips, 1980; Chambers et al, 1972; Knibestol and Vallbo, 1980; Janig et al, 1980) is shown schematically in Figuré (10D). Except for the adaptation behavior of SAs during the initial part of the steady indentation phase, the chosen response surface predicts well the observed responses. Therefore, if we are only interested in the dynamic and static responses of SAs and not in the transition phase, or if the transition phase is short, the proposed representation is adequate. Otherwise, modification is necessary as discussed in Section 5.3.

When an object of varying surface curvature such as the aperiodic grating used by Phillips and Johnson (1981a) indents the skin, it is necessary to define the S-space in terms of all the four variables (d, v, c, r) (Section 5). We shall now try to establish the plausibility of the proposed representation by assuming a reasonable skin surface profile under an

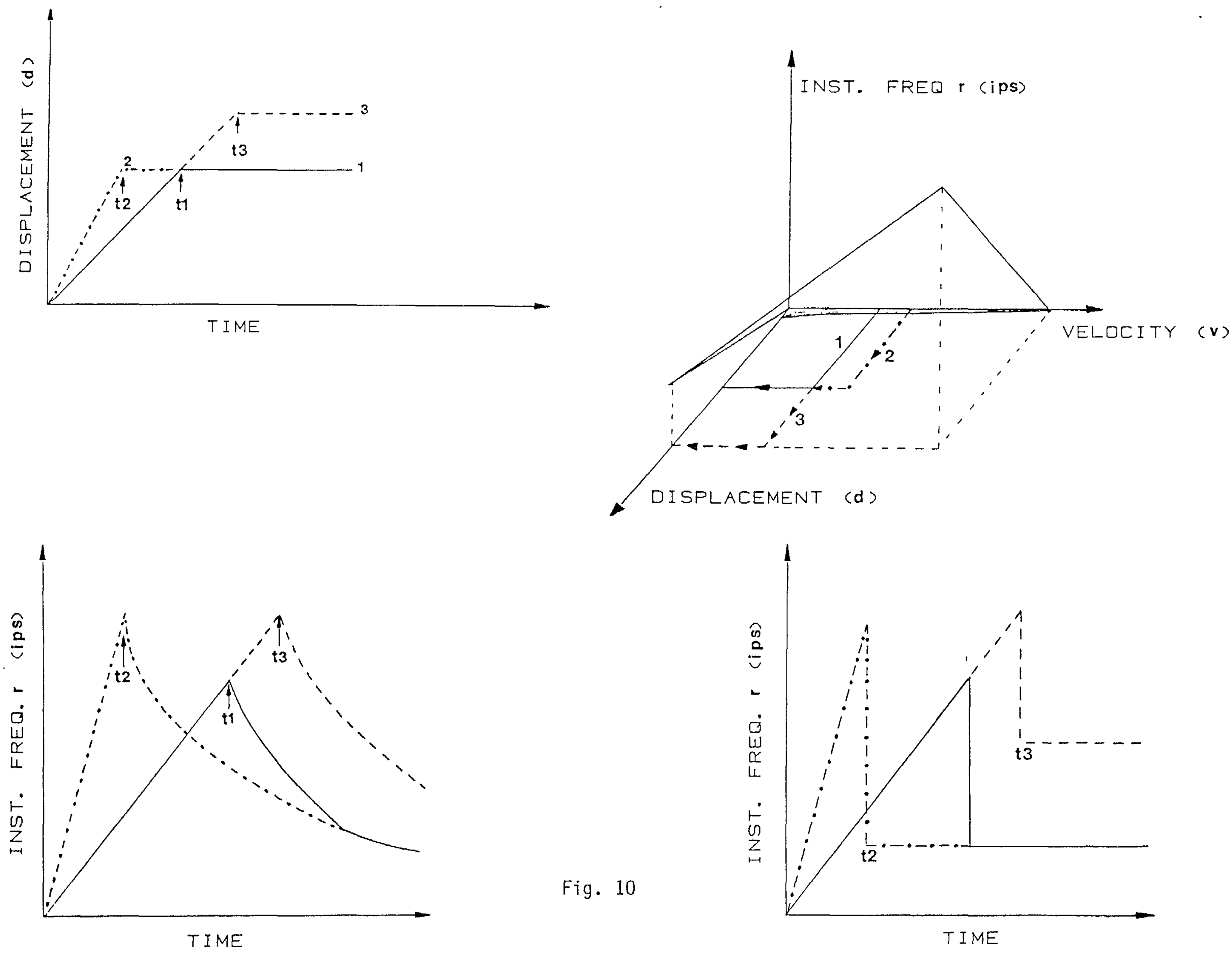

DISPLACEMENT (d)
TIME
INST. FREQ r (ips)
VELOCITY (v)
DISPLACEMENT (d)
INST. FREQ. r (ips)
TIME
INST. FREQ. r (ips)
TIME

Fig. 10

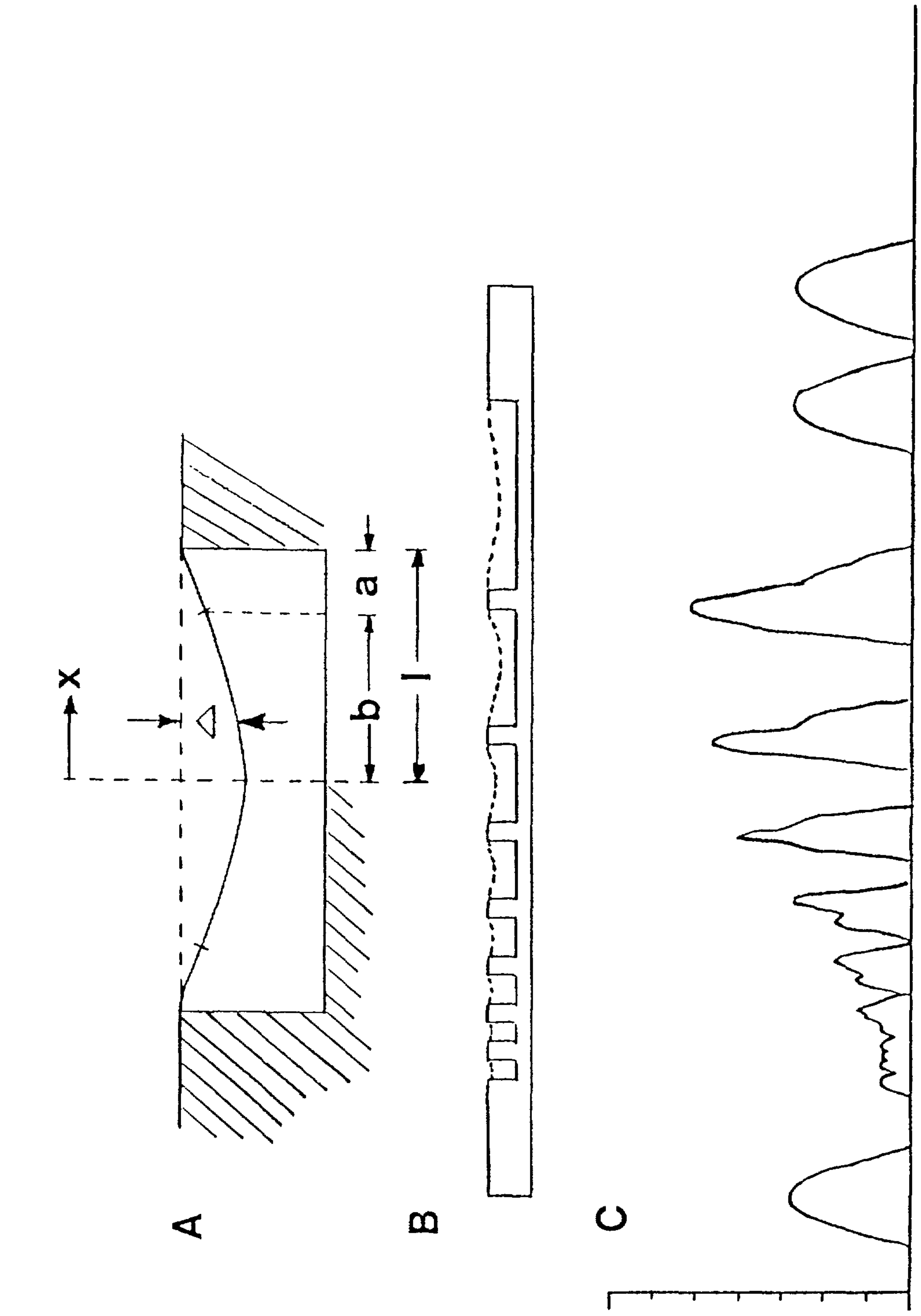


Fig. 11

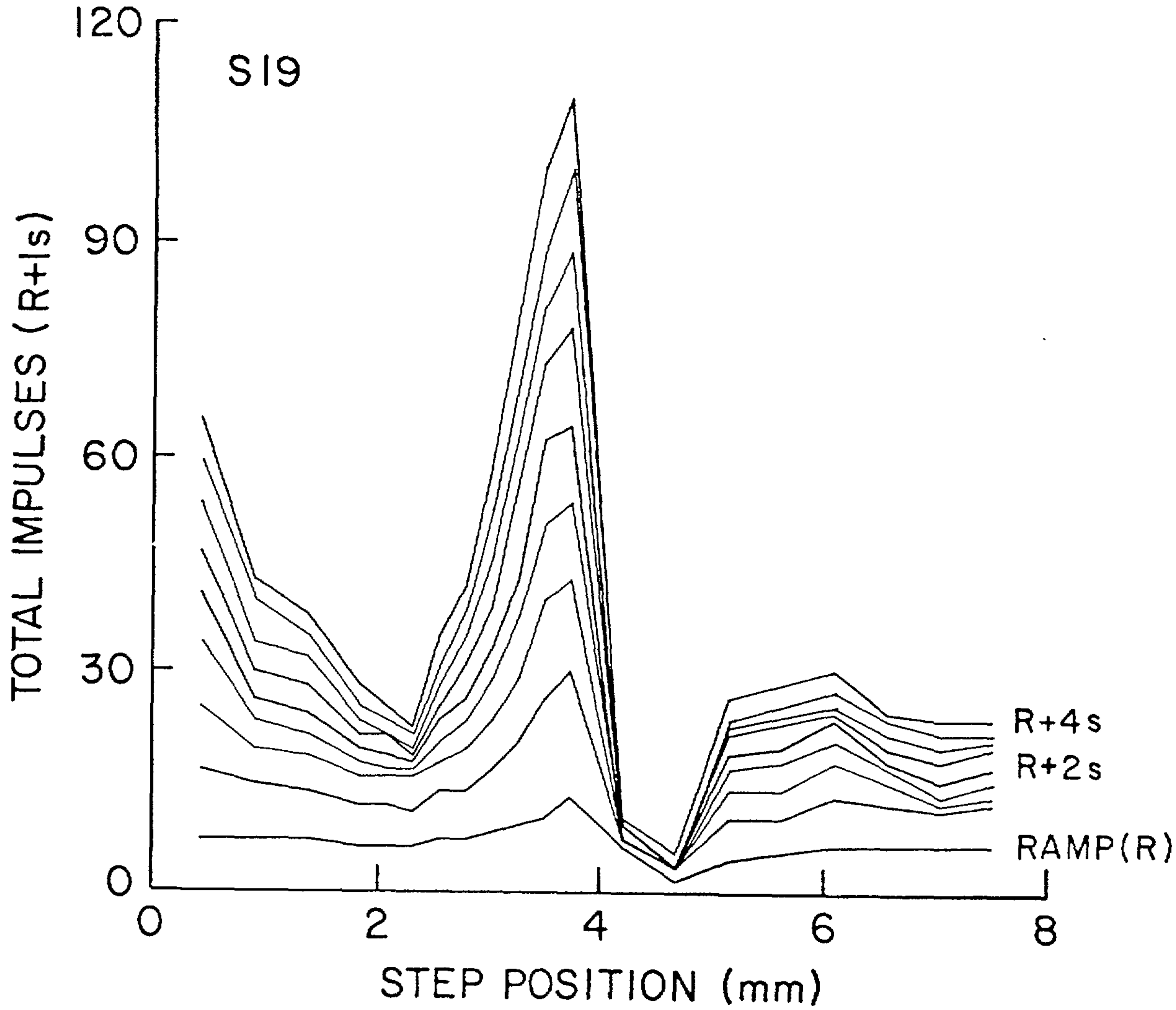
aperiodic grating and considering an SA whose curvature sensitivity is dominant in governing its response. Shown in Figure 11A is the assumed skin surface profile for an arbitrary gap of width 2ℓ. In order to specify the profile by a smooth curve, we demand the following conditions: The curve should have continuous second derivatives with (i) its first and third derivatives equal to zero at $x = o$, (ii) second derivative equal to zero at $x = b$, (iii) first and second derivatives equal to zero at $x = b+2a$. Such a curve can most simply be expressed as two separate fourth degree polynomials in regions $o < x < b$ and $b < x < b+2a$. If Δ is defined as the depth of indentation caused by the bar, it can be shown that the curvature of the skin after deformation is given by:

$$\frac{d^2w}{dx^2} = \frac{12\Delta}{b(5b+8a)}\left\{1 - \frac{x^2}{b^2}\right\} \quad \text{for} \quad 0 \le x \le b \qquad (10a)$$

$$= \frac{12\Delta}{5b+8a}\left\{-\frac{(x-b)}{a^2} + \frac{(x-b)^2}{2a^3}\right\} \quad \text{for} \quad b \le x \le b+2a \qquad (10b)$$

where = vertical skin displacement.

The resulting skin surface profile under the grating with 0.5mm bars used by Phillips and Johnson (1981a) is as shown in Figure 11B. The corresponding spatial profile of skin surface curvature is plotted in Figure 11C (by taking $a = 0.35$ for $\ell < 0.75$ and 0.5ℓ for $\ell > 0.75$; $\Delta = 15\ell^2$). It is clear that with an addition of base response due to the displacement of the most sensitivespot, the profile matches very well with the SA response observed by Phillips and Johnson (1981a,b).



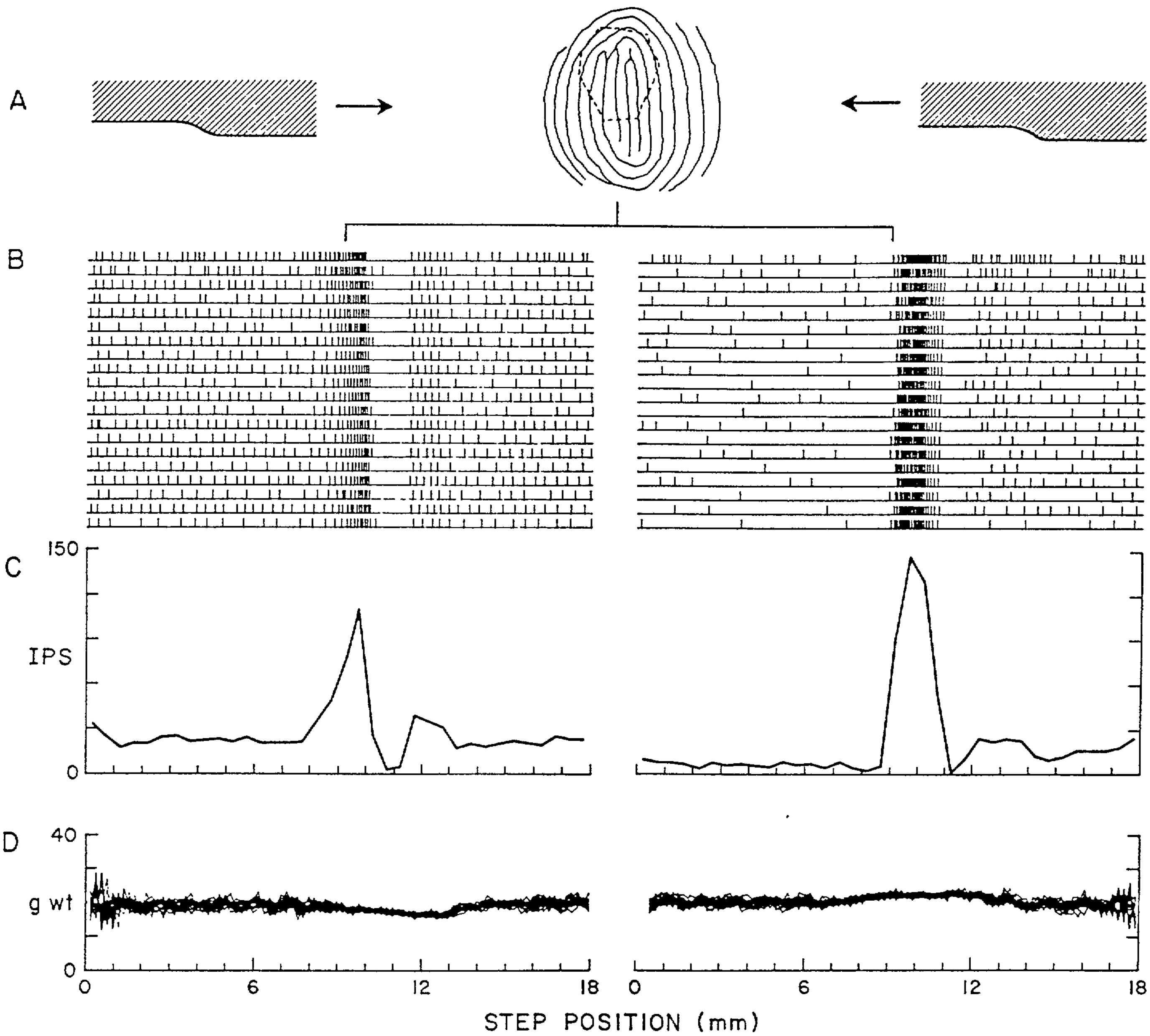
Spatial response profiles of a typical SA (S19) constructed from responses to successive indentations across the receptive field by step 1. The lowest curve indicates the total number of impulses during the ramp (R). Subsequent response profiles were obtained at 0.5s time intervals after the end of the ramp, and represent the cumulative number of impulses at the respective times.

Fig. 12

Shown in Figure 12 is the response of a typical SA when a step shaped as a half-cycle sinusoid was used to vertically indent the skin at successive positions across the receptive field. The spatial response profiles of impulses during the ramp and at 0.5 second intervals thereafter (Srinivasan and LaMotte, 1985) are displayed. The major features of this profile are the basal response to the flat plate (with some inter-trial adaptation effects on the left side), peak response when the sharpest part of the step is on the most sensitive spot, and a very low response when the most sensitive spot is not in contact with the stimulus surface due to a gap that develops right next to the sharpest portion of the step. These results demonstrate the fact that when displacement and velocity are approximately the same, SAs are very sensitive to changes in the curvature of the skin at the most sensitive spot. Sensitivity is maximum under the sharpest part of the step, medium under the flat part and minimal at the gap. This conclusion is further supported by the finding that the peak response diminished when the maximum curvature of the step was reduced by increasing the half-cycle wavelength (step width) and keeping the height of the step constant.

The response pattern of impulses of an SA to a sinusoid step stroked back and forth over its receptive field under constant overall compressional force (LaMotte and Srinivasan, 1985), is shown in Figure 13:

Consider now the step-off stroke. During the initial part of the stroke, the flat part on the high side of the step will be on the most sensitive spot. Thus, there is a positive change in curvature (c) with respect to the resting state, which remains constant as long as that flat part of the step is one the most sensitive spot. Next, there is a sharp increase in c when the



Responses of an SA (S26) to a step stroked across its receptive field. A. Schematic showing the cross-sectional profile of step #3 used to elicit the responses below. The sinusoidal portion of the step is drawn to scale but the total length of the step is less than actual. In the middle is a drawing of the papillary grooves on the monkey's fingerpad. The dashed, oval line indicates the boundary of the SA's receptive field, determined with a von Frey filament delivering a force of 1.70 mN. The scale is the same as that for the step positions during stroking, indicated below. On each trial, the step is stroked with a force of 20g wt at 10mm/s, first from left to right, i.e. from high to low side of the step, and then back again, going from low to high. B. Spatial plots of nerve impulses evoked in S26 during each stroke from left to right (left panel) and right to left (right panel). Each vertical tic mark indicates the spatial location of the reference mark (at the beginning of the convex curvature on the high side of the step) when an action potential occurred. On each horizontal line are the responses to a single stroke. The branched line connecting the papillary groove drawing to the spatial impulse plots indicates that point when the reference mark, and therefore the sharpest portion of the step, reached the center of the von Frey receptive field. C. Histograms of the mean discharge rate (impulses/s or ips) per consecutive bins of 0.5mm, were obtained from the data in B. D. The force applied by the step against the skin during each stroke in each direction. The force traces obtained from each of the 20 strokes in a given direction are superimposed.

sharpest part of the step is on the most sensitive spot, followed by a gap (refer to Figure 12) that develops between the skin and the step surface. This causes the skin curvature at the most sensitive spot to be close to its value at the resting state, implying a sharp decrease in c. The lower flat part of the step then comes into contact with the most sensitive spot, causing c to increase up to its value during the initial part of the stroke and remain constant till the end of the stroke. This sequence of events can be represented as the dotted path on the S-plane in Figure 14.

Neglecting the effects of skin stretch and any asymmetry between ON and OFF strokes that may be present in the skin deformation, the changes in curvature of the skin as a function of time during the on stroke would be the mirror image of that of the off stroke and is as shown in Figure 14.

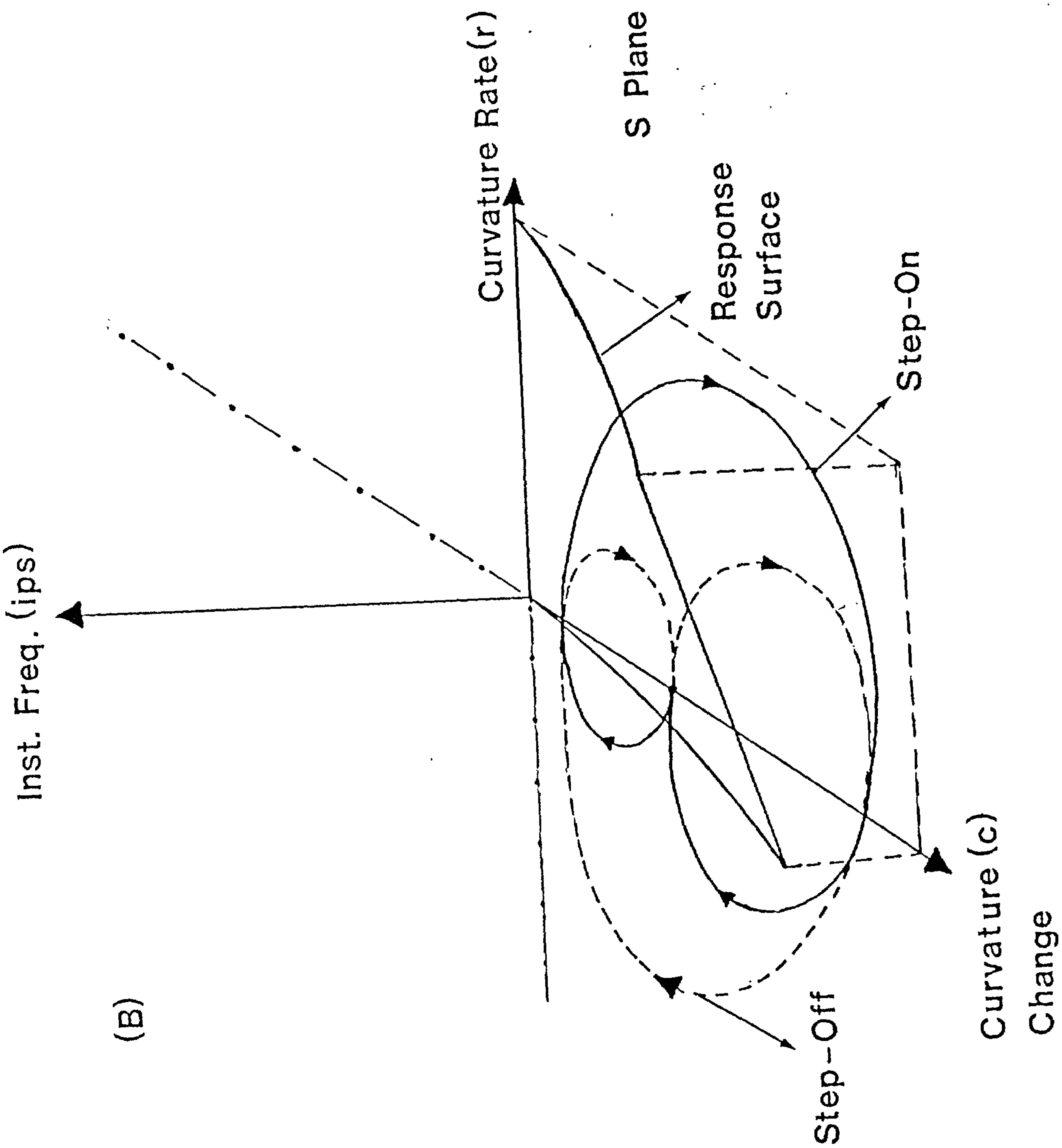
It is seen that the SA responds when the change in curvature is either constant or increasing, and becomes quiet when the change in curvature is decreasing. Therefore, the relevant S-space (Figure 14) is defined by areas representing change in skin curvature (c) and its rate (r). The traces corresponding to the ON and OFF stroke of the step are as shown and the chosen response surface are seen to predict the response shown in Figure (13).

In the next section, we shall describe the means by which the proposed representation can be tested.

5.2 Identification, prediction, verification

(a) Experiments using an object of single curvature

When an object such as a cylindrical bar of single curvature is used to indent or vibrate the most sensitive spot, the curvature of the skin at that spot is almost always the same as that of the object, and hence, constant.



(B)
Inst. Freq. (ips)
Curvature Rate (r)
S Plane
Response Surface
Step-On
Step-Off
Curvature (c) Change

Fig. 14

Therefore, it is enough to define the S-plane with axes representing displacement and velocity of the most sensitive spot (Figure 10B). In such a case a response surface can be constructed using vertical indentation experiments as explained in section 4.5 with one change: the maximum depth of indentation in each experiment should also be varied, since SA response in the steady phase varies with it. As before, the response surface can be used to predict the responses to, say, sinusoidal vibration of the most sensitive spot with the same cylindrical bar. These predictions can be checked against results obtained from actually performing the vibration experiment on the same unit with the same bar.

b) Experiments with irregular surfaces

Consider the cross-section of the corrugated surface shown in Figure 15:

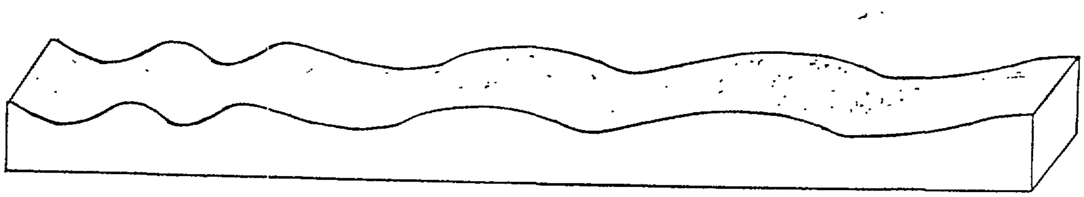


Figure 15

In investigating how shapes of surfaces are encoded in the periphery, we would like to predict the responses of SAs when this surface is stroked across the receptive field under constant overall force and horizontal velocity. If the corrugated surface is such that the skin surface is almost always in full contact, the displacement of the most sensitive spot can, for simplicity, be assumed to be constant. Thus, we only need a two-dimensional S-plane defined by axes representing the change in skin curvature (c)and its rate (r).

To construct the response surface on this S-plane, as before, we need to perform simple experiments to determine the responses on certain points in the S-plane which can then be used in interpolation. The steady frequency of response in the plateau phase of vertical indentation with cylindrical bars of different curvatures provide us with several response ordinates on the curvature axis. When each of these cylindrical bars is stroked across the receptive field, an appropriate constant force is chosen such that the displacement of the skin under the bar is the same as it would be when the corrugated surface vertically applied at the desired force and not stroked*; when the horizontal velocity is varied from one stroke to the next, we obtain the responses under varying curvature rates. Each of these strokes represents a line in the S-plane over which the response is known. Suitable interpolation then enables the determination of the response surface.

Since the corrugated object was so chosen that the skin was almost always in full contact, the time sequence of skin curvatures at the most sensitive spot for a given horizontal velocity is known. The associated path can then be traced on the S-plane.

Integration of the ordinates on this path over time provides us with the predicted sequence of impulses which can be checked against the experimental results.

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*To a first approximation, this means that pressure under the bar and the corrugated surface should be the same.

5.3 Modification of the representation

Two features of SA response have not been represented adequately in the present scheme. One is the transient behavior of adaptation during the plateau phase of vertical indentation experiment (Figure 9D) and the other is the effect of horizontal skin stretch due to friction when an object is stroked (Figure 16, where responses are shown of an SAI fiber that had a base discharge to a flat plate stroked in one direction, but not to it stroked in the opposite direction). The adaptation effects can be taken care of by considering the response surface as time dependent (i.e., the impulse frequency decreases with time as we stay at a point on the displacement axis in Figure 10), which makes the prediction calculations more difficult. The stretch effect probably is simpler to take care of. Perhaps simple stroking experiments at varying horizontal velocities, with a flat surface of about the same roughness as the corrugated surface would provide the responses to stretch at different velocities, which can then be superimposed on the earlier predictions.

6. Conclusion

In this paper, the general problem of modeling a mechanoreceptor was posed and the first successful step taken by Phillips and Johnson was discussed. Because of the unverifiability of the various aspects of their model, we proposed an alternative gross input-output approach, wherein the receptor and the skin structure around it are taken together as a system. This system is first "identified" by performing simple experiments on it. Then, an appropriate theoretical framework is used to predict the responses of the system under more complex experiments. These predictions can be verified by actually performing the latter experiments on the same system. In the

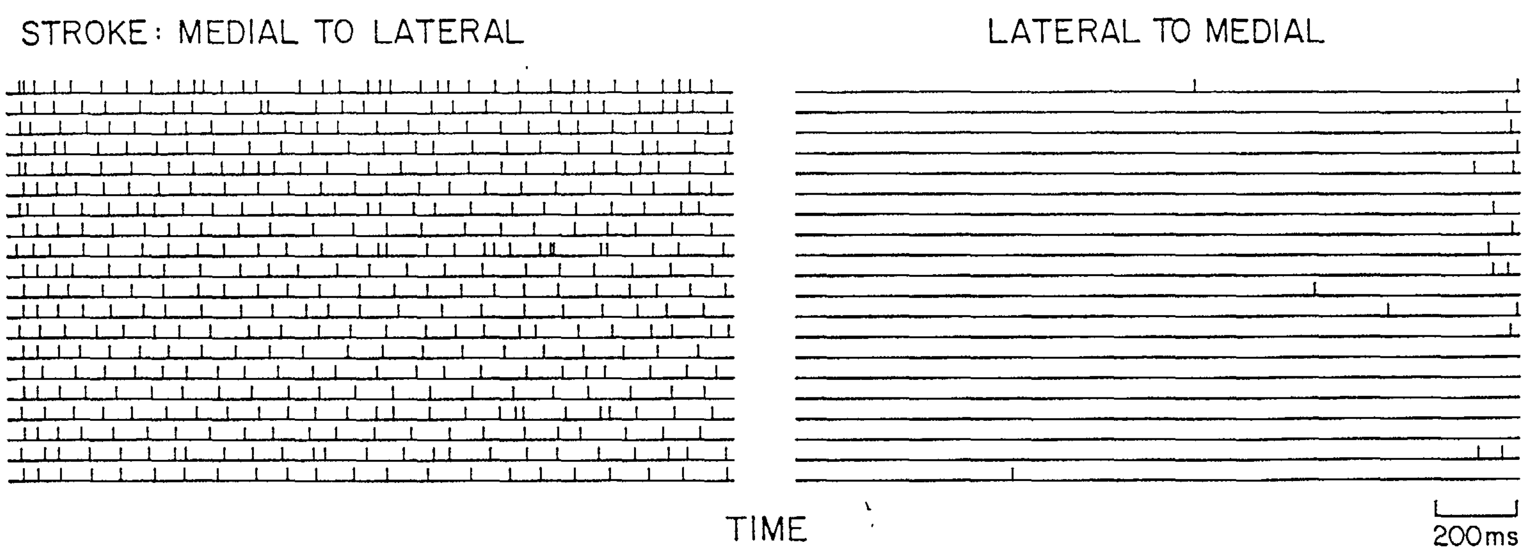

Fig. 16

Phillips and Johnson model, the pressure distribution under the indenting object is of prime importance. However, this is not measurable at present. Alternatively, it is possible that an entirely equivalent specification of the input exists in terms of kinematic variables such as skin surface displacement, curvature, etc. Insisting on the choice of variables that are measurable, we proposed a theoretical framework with the kinematic variables at the most sensitive spot of a receptor as the relevant input variables. We demonstrated that this approach leads to testable hypotheses and that the representation is flexible enough to accept modification if necessary. Once the appropriate representation of the stimulus with minimum number of variables to describe the phenomenon of interest has been attained, and the input-output behavior of the system has been adequately modeled at the gross level, finer investigations which might shed light on the transducer mechanism can be conducted. The confidence achieved by having a unified understanding of the gross behavior of the receptor under diverse circumstances and the existence of a theoretical framework enables posing of specific questions and hypotheses at the fine level.

The view proposed here that an impulse is emitted wherever the time integral of impulse frequency reaches unity suggests an accumulation process similar to that of the generator potential. If the proposed approach grows successfully, we might have a theory of mechanoreceptors which can be linked to molecular mechanisms at the receptor level. However, in the meantime, the proposed framework has practical predictive value and the approach can also be used in the study of the central nervous system as well as peripheral. Since the powerful technique of phase plane representation used in the study of differential equation is employed here, it may be possible to systematically infer laws of input-output behavior in terms of differential equations by representing the experimental results appropriately.

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