Published in final edited form as:

J Neurophysiol. 2006 March ; 95(3): 1771–1782.

SA1 and RA Afferent Responses to Static and Vibrating Gratings

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Abstract

SA1 and RA afferent fibers differ both in their ability to convey information about the fine spatial structure of tactile stimuli and in their frequency sensitivity profiles. In the present study, we investigated the extent to which the spatial resolution of the signal conveyed by SA1 and RA fibers depends on the temporal properties of the stimulus. To that end, we recorded the responses evoked in SA1 and RA fibers of macaques by static and vibrating gratings that varied in spatial period, vibratory frequency, and amplitude. Gratings were oriented either parallel to the long axis of the finger (vertical) or perpendicular to it (horizontal). We examined the degree to which afferent responses were dependent on the spatial period, vibratory frequency, amplitude, and orientation of the gratings. We found that the spatial modulation of the afferent responses increased as the spatial period of the gratings increased; the spatial modulation was the same for static and vibrating gratings, despite large differences in evoked spike rates; the spatial modulation in SA1 responses was independent of stimulus amplitude over the range of amplitudes tested, whereas RA modulation decreased slightly as the stimulus amplitude increased; vertical gratings evoked stronger and more highly modulated responses than horizontal gratings; the modulation in SA1 responses was higher than that in RA responses at all frequencies and amplitudes. The behavioral consequences of these neurophysiological findings are examined in a companion paper.

INTRODUCTION

Two types of mechanoreceptive afferent fibers in human glabrous skin have been shown to convey information about the spatial structure of tactile stimuli: rapidly adapting (RA) and slowly adapting type 1 (SA1) fibers (see Johnson and Hsiao 1992 for a review). Both fiber types are well suited to convey fine spatial information as they have small receptive fields (RFs) and densely innervate the distal fingerpads where tactile acuity is high. The evidence suggests that, although RA fibers convey information about the coarse spatial features of the stimulus (e.g., gaps >3–4 mm), the finest discriminations of which humans are capable rely on SA1 fibers. In examining the spatial sensitivity of these fibers, stimuli typically have consisted of gratings or letters, either indented into or scanned across the fingerpad (Darian-Smith and Oke 1980; Goodwin and Morley 1987a,b; Goodwin et al. 1989; Morley and Goodwin 1987; Phillips and Johnson 1981a,b; Yoshioka et al. 2001), embossed dots scanned across the fingerpad (Blake et al. 1997; Connor and Johnson 1992; Connor et al. 1990; Darian-Smith and Oke 1980; Darian-Smith et al. 1980; Johnson and Lamb 1981; Lamb 1983; LaMotte and Whitehouse 1986), or arrays of patterned vibrating pins presented by means of the Optacon, a reading aid for the blind (Gardner and Palmer 1989, 1990).

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GRANTS

This work was supported by National Institutes of Health Grants NS-18787, NS-38034, and DC-00095.

It has been shown in a number of psychophysical studies that subjects can make fine discriminations of the spatial structure of stimuli indented statically into the skin (Craig and Kisner 1998; Johnson and Phillips 1981). Indented stimuli have been found to produce a strong sustained response in SA1 afferent fibers but only a weaker transient one in their RA counterparts. Spatial event plots indicate that information about the fine spatial structure of these stimuli is likely conveyed by SA1 fibers. At the other extreme, the tactile display of the Optacon consists of an array of pins vibrating at 230 Hz, which has been found to excite PC and RA fibers while evoking little to no activity in SA1 fibers (Gardner and Palmer 1989). Spatial information about patterns presented with the Optacon must therefore be conveyed by RA fibers as PC responses are largely insensitive to the spatial features of the stimulus (Johnson and Lamb 1981; Palmer and Gardner 1990). The reduced spatial acuity for high-frequency vibrating patterns has been interpreted as further evidence that RA fibers carry a less spatially defined signal than their SA1 counterparts.

Indented gratings excite one population of spatially sensitive mechanoreceptive fibers and vibratory stimuli generated with the Optacon preferentially excite the other population. However, typical contact with objects involves lateral movement between skin and surface, a property that neither indented nor Optacon-generated stimuli possess. Studies have shown that patterned stimuli evoke a robust response in both SA1 and RA fibers when scanned across the skin. SA2 afferent fibers, which innervate Ruffini end organs, also respond to scanned stimuli, but the resolution of the signal they carry is too low to mediate human performance in spatial acuity tasks (Phillips et al. 1992). The improvement in spatial acuity in scanned relative to static touch (see Johnson and Hsiao 1992 for a review) has been attributed to the increment in (primarily SA1) afferent activity in the scanning relative to the indented condition (Johnson and Lamb 1981). SA1 fibers are thought to convey the bulk of the spatial information as the spatial image conveyed by these fibers is sufficiently isomorphic with the tactile stimulus to account for psychophysical performance on spatial acuity tasks using scanned stimuli. The difference in spatial sensitivity between SA1 and RA afferent fibers suggests that, although RA fibers carry a spatially modulated signal, this signal does not contribute to the tactile perception of fine spatial detail. Even the spatial patterns perceived by means of the Optacon must be considerably larger than analogous raised patterns to be perceived with the same accuracy (Johnson 2002).

Another well-documented way in which SA1 and RA fibers differ is in their responses to vibratory stimuli. First, SA1 fibers tend to have higher absolute and entrainment thresholds than their RA counterparts (Freeman and Johnson 1982a; Johansson et al. 1982). Furthermore, SA1 sensitivity decreases with frequency over much of the frequency spectrum ($f > \sim 5$ Hz) (Freeman and Johnson 1982a), while the RA threshold-frequency function is U-shaped, with maximum sensitivity at $\sim 30 - 40$ Hz (Talbot et al. 1968). Differences in the spectral sensitivities of these populations of mechanoreceptive afferent fibers have been exploited in psychophysical studies, the aim of which was to assess the ability of one or the other mechanoreceptive population to convey information required to perform various perceptual tasks. Using such an approach, for instance, researchers were able to establish that different populations of mechanoreceptors mediate human detection thresholds in different portions of the frequency spectrum (see Bolanowski et al. 1988 for a review).

SA1 and RA fibers can thus be distinguished on the basis of their response to spatial stimuli, on the one hand, and to vibratory stimuli, on the other. Bridging these two threads in somatosensory research, we assess in the present study the ability of SA1 and RA fibers to convey information about the fine spatial features of a stimulus and determine the extent to which the spatial resolution of the peripheral signal changes when the stimulus vibrates at various frequencies. Because tactile grating orientation discrimination has become the standard measure of tactile spatial acuity on glabrous skin, we use tactile gratings as stimuli (see Craig

and Johnson 2000 for a review). We present gratings vibrating at various frequencies and spatial periods and characterize the effect of vibratory frequency on the spatial resolution of the signals conveyed by SA1 and RA fibers. We also investigate the effect of a grating's spatial period, amplitude and orientation on the spatial modulation of the neural signal it elicits, i.e., on the degree to which the afferent fiber's response changes as the location of its receptive field moves relative to the stimulus. Generally, an afferent fiber will produce a stronger response when its receptive field is located under a ridge than when it is located under a groove. Based on previous findings, we expected the spatial modulation of the neural response to increase with the spatial period of the gratings (cf. Phillips and Johnson 1981a) and SA1 modulation to be greater than its RA counterpart. Furthermore because grating orientation discrimination has been found to be relatively insensitive to the depth at which gratings are indented into the skin (Gibson and Craig 2005a; Johnson and Phillips 1981), we also expected stimulus intensity to have little effect on spatial modulation. In a set of psychophysical experiments discussed in a companion paper, we explore the perceptual consequences of the neural phenomena reported here, and draw conclusions as to the respective roles of SA1 and RA fibers in the tactile perception of fine spatial features in naturalistic settings.

METHODS

Stimuli

The stimuli were square-wave gratings analogous to the gratings that have been used extensively in psychophysical tasks. These stimuli are also used in the companion psychophysical study. Stimuli were generated and delivered by means of a dense tactile array, consisting of 400 independently controlled probes arrayed in a 20×20 matrix (see Fig. 1) (Pawluk et al. 1998). The probes, spaced at 0.5 mm, center to center, cover a 1×1 cm area.

Gratings consisted of alternating ridges and grooves of equal widths. The spatial periods of the gratings (1 ridge + 1 groove) were 1, 2, 4, 6, 8, and 10 mm. The bars were oriented either parallel or perpendicular to the axis of the finger so that we could assess the degree of spatial anisotropy in the neural responses. Gratings were either static or vibrated at 5, 10, 20, 40, or 80 Hz, frequencies that span the range to which the two classes of afferent fibers are maximally responsive. For the static gratings, ridges were indented into the skin beyond a baseline indentation (an indentation of 1 mm, see neurophysiological procedure below); the duration of the on and off ramps was 35 ms. The ridges of the vibrating gratings oscillated sinusoidally about the baseline indentation (of ~1 mm). Stimulus amplitudes were set such that the subjective intensity of the gratings was equal at all frequencies as determined in a companion psychophysical study (Bensmaïa et al. 2005). The stimulus amplitudes, shown in Fig. 7 and reported as zero-to-peak, were 325 μm for static gratings and 232, 169, 124, 45, and 47 μm for gratings vibrating at 5, 10, 20, 40, and 80 Hz, respectively.

Most of the measurements were made at a single intensity. In a separate set of recordings, we examined the effect of stimulus intensity by testing two additional intensities, 5 and 10 dB below the values matched for equal subjective magnitude (We used lower rather than higher intensities because the subjectively matched intensities approached the upper limits of the stimulator's capacity). For these measurements, the gratings were oriented parallel to the long axis of the finger with a spatial period of 6 mm.

Each grating was presented three times at each nonredundant spatial offset in 0.5-mm increments (the lower limit of the probe's spatial resolution). The presentation of a grating at multiple spatial offsets is analogous to stepping the grating laterally across the fiber's RF in steps of 0.5 mm (cf. Phillips and Johnson 1981a). The grating with a 1-mm spatial period was presented six times, three repetitions at each of two spatial offsets (0 and 180° corresponding to 0 and 0.5 mm), whereas the 10-mm grating was presented sixty times, three times at each

of twenty offsets (0, 18, 36, . . . , 342° corresponding to 0, 0.5, 1, 1.5, . . . , 9.5 mm). Gratings with spatial periods of 2 and 6 mm are illustrated at every nonredundant spatial offset at the bottom of Fig. 1. The stimulus duration was 100 ms for all but the 5-Hz vibrating grating, for which 200 ms was used so that each stimulus interval consisted of a full sinusoidal cycle. The inter-stimulus interval was 50 ms. In a subset of measurements, the stimulus duration was 1 s for the 5-Hz gratings and 500 ms for all the other gratings, with inter-stimulus intervals lasting 100 ms.

Neurophysiology

All experimental protocols complied with the guidelines of the Johns Hopkins University Animal Care and Use Committee and the National Institutes of Health Guide for the Care and Use of Laboratory Animals. Single unit recordings were made from the ulnar and median nerves of 4 Macaque monkeys (*Macaca mulatta*) using standard methods (Talbot et al. 1968). Standard procedures were used to classify the mechanoreceptive afferents according to their responses to step indentations and vibratory stimulation (Freeman and Johnson 1982b; Talbot et al. 1968). Given the geometry of the experimental apparatus, only fibers the RFs of which were located on the distal fingerpads could be stimulated. The tactile array was centered on the point of maximum sensitivity of the fiber and indented 1 mm into the skin. A stimulus protocol was then initiated to map the fiber's RF and ensure that it was centered on the probe. The probe was repositioned if necessary before the beginning of the experimental run.

Analysis

The objective of the study was to examine the extent to which first-order afferent fibers convey spatial information. To that end, we wished to assess the degree to which the spatial profile of the neural response followed that of the grating patterns. To quantify the spatial modulation of the neural response, we adopted an index analogous to the Michelson contrast

$$m = \frac{f_{\max} - f_{\min}}{f_{\max} + f_{\min}} \quad (1)$$

where $f_{\max}$ and $f_{\min}$ are the maximum and minimum firing rates evoked by a grating across spatial offsets, respectively. The quantity m takes on its maximum value (1.0) if ridges evoke a response while grooves do not and a minimum value (0) when the responses evoked by the ridge and the groove are equal. The contrast was set to 0 if the maximum firing rate at any offset was <5 Hz as this index becomes unreliable for low response rates. Unless otherwise specified, results obtained from vertical and horizontal gratings were combined.

As noted, the modulation index is based on maximum and minimum firing rates. A potential difficulty with the index m is the fact that the number of data samples increases with spatial period. The number of data samples—each corresponding to a unique spatial offset—ranged from 2 for a spatial period of 1 mm to 20 for a spatial period of 10 mm. As the number of data samples increases, the probability of more extreme values increases, which may cause the degree of spatial modulation to be overestimated at the higher spatial periods. To correct for this possibility, a Monte Carlo simulation, described in the APPENDIX, was performed to obtain an estimate of the baseline modulation as a function of the number of spatial offsets, taking into account the magnitude of and variability in the neural response. The measure of baseline modulation constituted an estimate of the quantity m that would be observed if the neural response was variable but essentially flat, i.e., exhibited no spatial modulation. The measured corrections were small and increased to some extent with spatial period. For each spatial period and temporal frequency, the estimated baseline modulation was subtracted from the measured modulation m . The corrected measure, m_c , thus constituted an estimate of the

spatial modulation in the neural response independent of its inherent variability. It is this measure m_c that was used in subsequent data analyses.

To assess the generalizability of our findings, we also computed another index of spatial modulation, namely the difference between the mean spike rate when the RF center is under a groove and the mean rate when the RF center is under a ridge, normalized by the sum of the two means. The advantage of this alternative index of spatial modulation is that it is relatively insensitive to the inherent variability in the neural response. The drawback of this measure is that it tends to underestimate modulation. For instance, the edges of a stimulus ridge tend to produce a larger response than the middle of the ridge as they exert greater forces on the skin (Phillips and Johnson 1981b; Wheat and Goodwin 2000). This increased response can serve to enhance the peripheral representation and thus the perceptual salience of that edge. Also the drop-off in the neural response as the RF center moves from ridge to groove is not abrupt but rather somewhat graded (see Fig. 2). A modulation index based on mean firing rates tends to wash out edge effects and overestimate the neural response evoked by stimulus grooves, both independently leading to an underestimation of the modulation. In contrast, m_c is not prone to these effects. For this reason, we report m_c rather than its alternative. Nonetheless, results obtained using the alternative index of spatial modulation yielded conclusions identical to those obtained using m_c .

RESULTS

Results obtained from 17 SA1 and 12 RA fibers are reported here.

Figure 2, *top*, shows the responses evoked by vertically oriented gratings in a typical SA1 fiber. To compare responses across temporal frequencies, spike rates are normalized by the maximum at each frequency. For stimuli with high spatial periods (wide ridges and grooves), spike rates tended to be high when the fiber's hotspot (i.e., its point of maximum sensitivity) was under a stimulus ridge, in particular near the edge of a ridge (Phillips and Johnson 1981b; Wheat and Goodwin 2000), and low when it was under a groove. However, the dependence of the fiber's response on stimulus offset was greater for the coarse gratings than for the fine ones. In other words, spatial modulation systematically increased with spatial period. Furthermore, the afferent response exhibited comparable spatial modulation at all vibratory frequencies (contours in Fig. 2 are similar from one frequency to the next).

Figure 2, *bottom*, shows the (normalized) response of a typical RA fiber. Again the responses exhibited little spatial modulation at the low spatial periods, but modulation increased with spatial period. The spatial modulation of this fiber's response was lower than that of its SA1 counterpart shown in the top panel. Like the SA1 response, however, the RA response exhibited comparable spatial modulation at all vibratory frequencies.

Effect of spatial period on spatial modulation

Figure 3, *top*, shows the effect of spatial period on the spatial modulation of SA1 (*left*) and RA (*middle*) responses with vibratory frequency as the parameter. For both types of fibers, spatial modulation increased with spatial period. To test the reliability of the effect, we performed an ANOVA on the modulation with spatial period, vibratory frequency, stimulus orientation and neuron as factors. Controlling for vibratory frequency, stimulus orientation, and differences across fibers of a given type, the effect of spatial period on spatial modulation was highly significant for both SA1 and RA fibers [$F(5,770) = 186$ and $F(5,557) = 253$ for SA1 and RA fibers, respectively, $P < 0.001$]. The increase in modulation as a function of spatial period replicates findings obtained in other studies (Phillips and Johnson 1981a; Wheat and Goodwin 2000).

It is likely that the spatial modulation in the afferent response is somewhat underestimated at the low spatial periods due to the limited spatial resolution of the probe (0.5 mm). Indeed, at the lowest spatial period, there are only two observations per stimulus cycle, which may result in an underestimation of the spatial modulation of the neural response to these gratings. To correct for this aliasing effect, we performed a simulation, described in detail in the APPENDIX, to estimate the degree to which the actual amplitude of the stimulus is underestimated, on average, when n samples are obtained per stimulus cycle. Figure 4 shows the spatial modulation of the neural response as a function of the spatial period of the gratings before and after correcting for aliasing effects. The correction is negligible for spatial periods ≥ 4 mm.

Effect of vibratory frequency on spatial modulation

Figure 3, *bottom*, shows the effect of vibratory frequency on the spatial modulation of SA1 (*left*) and RA (*middle*) responses, with spatial period as the parameter. Spatial modulation was somewhat higher at the high frequencies than at the low frequencies for both SA1 and RA fibers. The effect of frequency was stronger in RA afferent fibers, particularly at higher spatial periods. Controlling for spatial period and differences across fibers, the slight dependence of modulation on vibratory frequency was significant for both SA1 and RA fibers [$F(5,771) = 5.1$ and $F(5,557) = 10.5$ for SA1 and RA fibers, respectively, $P < 0.001$]. However, the size of the effect of vibratory frequency on modulation ($\eta^2 = 0.032$ and 0.086 for SA1 and RA fibers, respectively) was very small relative to that of spatial period ($\eta^2 = 0.547$ and 0.70). Post hoc inference testing revealed that the observed peak in RA modulation at 40 Hz was statistically significant: the spatial modulation at 40 Hz was significantly greater than that at 20 or 80 Hz for these fibers [$F(1,168) = 8.4$ and 6.5 , respectively; $P < 0.05$]. The peak in modulation at 40 Hz may be mediated by a dip in effective intensity at that frequency (see following text). Note that the effect of frequency on spatial modulation remained significant when data obtained from 40-Hz gratings were not included in the analysis.

Effect of fiber type on spatial modulation

Examination of Fig. 3, *left* and *middle panels*, reveals that SA1 modulation was higher than its RA counterpart at all frequencies and amplitudes. SA1 and RA modulations are compared explicitly in Fig. 3, *right*. The *top right panel* of Fig. 3 shows SA1 modulation—averaged across frequencies—to be consistently higher than its RA counterpart at all spatial periods; the *bottom right panel* shows SA1 modulation—averaged across spatial periods—to be consistently higher than RA modulation at all vibratory frequencies. Controlling for vibratory frequency, spatial period and stimulus orientation, the main effect of fiber type was highly significant [$F(1,1355) = 177$, $P < 0.001$].

Effect of stimulus intensity on spatial modulation

As mentioned in the preceding text, stimulus amplitudes were set so that the subjective intensity of the gratings (measured in humans) was equated across frequencies (Bensmaïa et al. 2005). The choice of stimulus intensities did not ensure, however, that the stimuli were equally efficacious in stimulating both populations of fibers. The subjective intensity of a vibratory stimulus has been shown to be a complex function of the activity it evokes in the three principal vibrotactile channels (associated with SA1, RA and PC fibers in the periphery) (Hollins and Roy 1996). Figure 5 shows spike rates as a function of frequency. It is clear that firing rates do not remain constant across frequencies and, in fact, that the function is nonmonotonic. Specifically, both SA1 and RA spike rates are highest for the static gratings likely because their amplitudes were higher than those of the vibrating gratings (and the velocity of their on-ramps was higher than the peak velocity of the vibrating grating); furthermore, both SA1 and RA firing rates dip at 40 Hz.

Because the stimuli were not equated for their ability to stimulate either SA1 or RA fibers, the effect (or lack thereof) of vibratory frequency on spatial modulation may have been determined, at least in part, by the degree to which stimuli at different frequencies stimulated the fibers. We therefore investigated the effect of stimulus intensity on spatial modulation in a separate set of recordings. In this experiment, gratings at a single spatial period and orientation were presented at three stimulus intensities (see METHODS).

Figure 6 shows the effect of grating amplitude on spatial modulation at each vibratory frequency. The spatial period of the gratings, all oriented parallel to the axis of the finger, was 6 mm. Vibratory amplitude had no effect on SA1 spatial modulation [$F(2,180) = 0.62$, $P > 0.5$]. On the other hand, RA modulation decreased significantly with increasing amplitude [$F(2,95) = 13.2$, $P < 0.001$]. The RA modulation decreased with grating amplitude because the overall firing rate increased more than the difference in the firing rates evoked by ridges and grooves: although $f_{\max} - f_{\min}$ increased with grating amplitude, $f_{\max} + f_{\min}$ increased to a greater extent (see Eq. 1). In this set of measurements, the effect of vibratory frequency on spatial modulation was only significant for RA fibers [$F(5,95) = 8.6$, $P < 0.001$ for RA fibers; $F(5,180) = 0.98$, $P > 0.4$, for SA1 fibers].

To further assess the effect of stimulus intensity on spatial modulation, we presented gratings such that stimulus intensities were set according to the fiber's sensitivity. Specifically, stimulus intensities were set so that they fell within the center of each fiber's dynamic range. We hypothesized a priori that the spatial modulation of the neural response would be maximal in this condition. We tested two orientations and six temporal conditions but only five spatial periods. First, the rate-intensity function at each vibratory frequency was obtained over a wide range of amplitudes for each fiber using vibratory stimuli similar to the gratings except that all the probes moved in synchrony. The stimulus intensities were then derived by estimating, at each frequency, the half-entrainment point, i.e., the intensity at which the stimulus evokes a spike on every other stimulus cycle. In some cases, particularly for SA1 fibers, the stimulator could not generate vibratory stimuli of sufficient intensity to reach the half-entrainment point at the higher frequencies. In these cases, the highest attainable stimulus amplitude was used. For static stimuli, the steepest point of the rate-intensity function was used instead of the half-entrainment point.

Setting the stimulus intensities according to the fibers' spectral sensitivities yielded comparable results as when these were equated in subjective intensity: the main effect of spatial period on spatial modulation was highly significant for both SA1 and RA fibers [$F(4,344) = 64.5$ and $F(4,226) = 45.1$ for SA1 and RA fibers, respectively; $P < 0.001$]; the main effect of frequency was small but significant for SA1 and RA fibers [$F(5,344) = 5.3$ and $F(5,226) = 7.2$; $\eta^2 = 0.072$ and 0.14 , respectively; $P < 0.001$]; SA1 modulation was significantly greater than its RA counterpart [$F(1,588) = 6.3$, $P < 0.05$], though less so than when stimulus intensities were matched for subjective magnitude: The difference in the grand means of modulations for SA1 and RA fibers was 0.13 when intensities were matched subjectively and 0.055 when matched neurally. SA1 and RA modulations were more similar in the neural matching condition probably because stimulus intensities were lower when set according to RA sensitivity than when matched for subjective magnitude: RA modulation increases as stimulus intensity decreases while SA1 modulation is relatively insensitive to variations in stimulus amplitude (Fig. 6).

Response anisotropy

In the preceding analyses, we pooled the responses to horizontal and vertical gratings. However, psychophysical and neurophysiological evidence suggests that responses to horizontal gratings, i.e., to gratings oriented perpendicular to the finger ridges, may be weaker and less modulated than those to vertical gratings (oriented parallel to the ridges; note that skin

ridges of Rhesus macaques run parallel to the axis of the finger) (Craig 1999; Essock et al. 1992, 1997; Gibson and Craig 2005a; Wheat and Goodwin 2000). Figure 8 shows the spatial modulation of the responses to horizontal gratings versus the spatial modulation in the responses to vertical gratings. The SA1 modulation showed no effect of grating orientation, while the spatial modulation of the RA responses evoked by vertical gratings was greater than that evoked by horizontal gratings. Paired t -tests confirmed that the modulation in SA1 responses was independent of grating orientation [$t(35) = 0.21$, $P > 0.8$], whereas modulation in RA responses was significantly anisotropic [$t(35) = 3.0$, $P < 0.005$]. Furthermore, the firing rates evoked by vertical gratings were significantly greater than those evoked by horizontal gratings for both SA1 [$t(35) = 3.3$, $P < 0.001$] and RA [$t(35) = 3.7$, $P < 0.001$] fibers: the points in Fig. 8 (*bottom*) fall slightly but consistently below the unity line.

Population analysis

Although individual SA1 and RA responses to static and vibrating gratings differ systematically, it is possible that signals from these two populations of afferent fibers combine in such a way as to eliminate these differences. To investigate this possibility, we combined the responses of all the fibers of each type and compared their spatial profiles. Although sample sizes were relatively small, any artifacts of the single fiber analyses would tend to be less prominent in the population analysis. Because the fibers' RFs occupied slightly different positions relative to the probe, it was necessary to spatially align their responses. In view of that, we computed the spatial offset of each fiber's hotspot relative to the center of the probe. We then shifted the spatial profile of that fiber's response to each grating by the computed offset. The resulting response profiles constituted estimates of the profiles that would have been obtained had the fiber's RF been centered on the probe.

Figure 9, *top*, shows the spatial profiles of SA1 (*left*) and RA (*right*) responses to the six vertically oriented gratings (results obtained from the horizontal gratings were comparable; however, see following text). Both populations of fibers produce highly modulated responses to the gratings with the highest spatial periods. One notable feature of the spatial profiles is the prominent edge enhancement in the neural response, particularly for SA1 fibers. Figure 9, *bottom*, shows the spatial modulation of the responses as a function of spatial period. As expected, because the peaks and troughs in the neural response of different fibers do not align perfectly, the spatial modulation of the population response is less than that of individual afferent responses. To the extent that the spatial profile of the response is similar from fiber to fiber, the spatial modulation in individual and population responses will be similar.

As was found in the single-fiber analysis, the modulation in the SA1 population response is higher than its RA counterpart. Furthermore, the various contours, each corresponding to a different vibratory frequency, overlap almost completely, suggesting that the small effect of vibratory frequency observed in the single fiber analyses disappears when looking at the population response and may have been an artifact. Figure 10 shows the population responses to gratings of different amplitudes. The *top panels* show that modulation in SA1 responses is unaffected by stimulus intensity within the range of amplitudes used while RA modulation decreases with increasing amplitude. The effect of amplitude on RA modulation is smaller in the population response than it is in the responses of individual fibers but is still statistically significant [$F(2,10) = 4.81$, $P < 0.05$; note that the effect of amplitude on RA modulation is significant even if data obtained at 40 Hz are not included in the analysis]. The population analysis thus yields conclusions similar to the single fiber analysis regarding the effects of vibratory frequency, amplitude, spatial period, and fiber type.

When we compare the spatial modulation of the response to horizontal gratings to that of vertical gratings, we find a strong and significant anisotropy in both SA1 and RA responses [see Fig. 11; $t(35) = 6.43$ and 5.66 for SA1 and RA fibers, respectively; $P < 0.001$]. The

anisotropy in the RA population response was much larger than that observed in the single fiber analysis (slopes of the functions relating horizontal modulation to vertical modulation were 0.86 in the single fiber analysis and 0.59 in the population analysis). Furthermore, the significant anisotropy observed in the SA1 population responses stands in contrast to its absence in the responses of single fibers (see DISCUSSION).

DISCUSSION

Spatial period

For both SA1 and RA fibers, spatial modulation increased monotonically with spatial period (see Figs. 3 and 9) for static gratings, as has been found to be the case in previous studies (Phillips and Johnson 1981a), as well as vibrating gratings. The degree of SA1 modulation is similar to that described by Phillips and Johnson (1981a), who presented stimuli analogous to the static gratings of the present study and used the same index of spatial modulation. The lack of spatial modulation in the neural response to gratings at low spatial periods stems from the mechanics of the skin (Phillips and Johnson 1981b). Indeed, the skin acts as a low-pass spatial filter, causing the high-frequency components of the spatial modulation in the stresses and strains at the location of the mechanoreceptor (produced by a stimulus at the surface) to decrease as the depth increases. At the location of SA1 and RA receptors, ~0.5 mm below the surface of the skin (Johnson 2002; Phillips and Johnson 1981b), the spatial modulation of stresses and strains produced by the fine gratings is virtually nil.

Vibratory frequency

One of the novel findings in the present study is that the spatial modulation of the neural response evoked by vibrating gratings is similar to that evoked by static ones. Indeed, vibratory frequency had a negligible effect on the spatial modulation of SA1 and RA responses. In fact, the effect of vibratory frequency on modulation disappeared completely when afferent responses were analyzed as a population. The fidelity of the peripheral spatial image thus seems to be independent of the temporal properties of the stimulus.

Natural tactile exploration of spatially modulated surfaces involves lateral movement between skin and surface. Scanning a textured surface elicits vibrations in the skin, the frequency of which is determined by the scanning velocity and the dimensions of the elements in the stimulus (Bensmaïa and Hollins 2003). Each instantaneous frame of a scanned stimulus thus contains a strong dynamic component. The frequency independence of spatial modulation suggests that stimulus dynamics do not alter the instantaneous spatial image the stimulus evokes in the population of afferent fibers. If spatial sensitivity was completely determined by the quality of the peripheral neural representation (i.e., by the spatial modulation in the afferent response), one would expect spatial sensitivity to be unaffected by vibratory frequency.

Grating amplitude

One motivation for investigating the effect of grating amplitude on spatial modulation was to ascertain whether the observed changes in modulation across vibratory frequencies (or lack thereof) were truly frequency-dependent. Because the sensitivity of SA1 and RA fibers changes with stimulus frequency, the effects of frequency are confounded with those of intensity. Any attempt to equate sinusoidal stimuli for intensity is predicated on assumptions about the relevant response metric (overall spike rate, spike rate relative to the dynamic range, etc.). For example, when the grating amplitude is set to the midpoint between the absolute and entrainment thresholds at each frequency, i.e., to the center of the fiber's dynamic range, the evoked spike rate increases in proportion to the vibratory frequency. That these stimuli are equated in effective intensity is thus arguable. Other strategies to equate effective amplitude across frequencies run into analogous problems. Thus, because stimuli cannot be meaningfully

equated in their ability to stimulate one or the other population of mechanoreceptive afferent fibers, both stimulus frequency and amplitude must be manipulated to draw conclusions about the effects of vibratory frequency on the response property of interest.

The spatial modulation of SA1 responses was found to be independent of amplitude over the range of amplitudes tested. In contrast, RA modulation exhibited a slight but statistically significant tendency to decrease as the amplitude of the gratings increased (Figs. 6 and 10, *right*). We conclude, then, that SA1 modulation is insensitive to both the temporal and intensive aspects of the stimulus over a wide range of frequencies and amplitudes. On the other hand, RA modulation is relatively insensitive to the temporal frequency of the stimulus and slightly sensitive to its amplitude.

As discussed in the preceding text, SA1 fibers are thought to mediate the perception of fine spatial features at the limits of human acuity. Furthermore, human spatial acuity has been found to be largely independent of the depth to which a grating is indented into the skin (Gibson and Craig 2005b; Johnson and Phillips 1981). It is no surprise, then, that the spatial signal conveyed by SA1 fibers is relatively independent of stimulus amplitude.

Grating orientation

There are two hypotheses as to the cause of the observed anisotropy in afferent responses to gratings, one mechanical and the other neural. The effect of grating orientation may be due to a structural anisotropy in the skin. Phillips and Johnson (1981b) propose that “the dermal ridges may act like parallel rods in a sheet, making it stiff in one direction and flexible in the other” (p. 1218). As a result, the skin conforms more readily to gratings oriented parallel to the finger ridges than gratings oriented perpendicular to them (Gibson and Craig 2005b; Vega-Bermudez and Johnson 2004). This greater conformance along the perpendicular axis may allow for a more spatially modulated pattern of stresses and strains along that axis, thereby leading to a more spatially modulated neural signal.

Another possibility is that the anisotropy in the response is due to afferent branching (Pare et al. 2002): mechanoreceptors aligned along the axis of the finger will convey matching information about a vertical grating (because they will be under the same ridge or groove) but will convey information about spatially offset portions of a horizontal grating (one may be under a ridge while the other under a groove). If these receptors all provide input to a given fiber, the spatial resolution of that fiber will be greater along the finger than across it. If afferent fibers tend to innervate receptors aligned along the finger ridges, then the modulation in the responses to vertical gratings will be greater than the modulation in the responses to horizontal gratings (at least in macaques, for which the ridges are oriented along the finger). The extent to which mechanical anisotropy and afferent branching play a role in producing the observed effects of grating orientation on spatial modulation is unclear.

The anisotropy in the population response was found to be appreciably larger than the anisotropy in the responses of individual fibers. One interpretation of this finding is that the spatial profiles of the responses to vertical gratings are more similar from fiber to fiber than the profiles of the responses to horizontal gratings: the peaks and troughs in the former tend to align better than the peaks and troughs in the latter. A possible explanation for this phenomenon is that the fine structure of afferent RFs varies more along the longitudinal axis than along the lateral axis, possibly due to anisotropies in afferent branching.

Fiber type

RA axons have been found to branch more widely than SA1 axons (Pare et al. 2002). The larger RF size of RA relative to SA1 fibers has been attributed to this difference in axonal branching

(Vega-Bermudez and Johnson 1999). The lower spatial sensitivity of RA relative to SA1 fibers may also stem from this structural difference between the two types of mechanoreceptive afferent fibers: if multiple receptors are innervated by a single fiber, these receptors convey information about spatially offset portions of the stimulus, thereby degrading the quality of the spatial signal conveyed by the afferent fiber.

An analogous explanation may apply to the small effect of grating amplitude on RA modulation. RA RFs grow more in size than do SA1 RFs as the stimulus amplitude increases (Vega-Bermudez and Johnson 1999): more intense stimuli recruit a greater number of Meissner than Merkel receptors (innervated by a given RA or SA1 fiber), thereby further reducing the spatial sensitivity of RA relative to SA1 fibers.

Finally, differences in afferent branching may also explain why RA responses exhibit greater anisotropy than SA1 responses. Indeed, if branches are preferentially longitudinal in orientation, then the wider branching will lead to increased anisotropy. The differential sensitivity of SA1 and RA responses to grating orientation may also result from differences in the locations of their respective mechanoreceptors within the skin and the coupling of these receptors with the surrounding tissues. Indeed, Meissner corpuscles (innervated by RA fibers) are located more superficially in the dermal papillary ridges than Merkel receptors (associated with SA1 fibers) (Cauna 1966; Pare et al. 2002; Quilliam 1978). Perhaps the close association of Meissner corpuscles with the finger ridges makes these receptors more susceptible to effects of the skin's mechanical anisotropy.

These hypotheses as to the causes of response anisotropy predict that afferent RFs should be elliptical with their long axis oriented parallel to the axis of the finger as has been found to be the case in some neurophysiological studies (e.g., Johansson and Vallbo 1980; Knibestöl and Vallbo 1970). Furthermore, the ellipticity should be more pronounced in RA than SA1 fibers (although see Vega-Bermudez and Johnson 1999). In our neural sample, both SA1 and RA RFs were often elliptical with their long axis oriented longitudinally (data not shown).

Behavioral predictions

Previous results from joint psychophysical/peripheral neurophysiological studies indicate that the limits of human spatial acuity on the fingerpad, as measured by grating orientation discrimination for example, are set at the sensory periphery (see Johnson and Yoshioka 2002 for a review). Our results suggest that the grating orientation threshold, i.e., the spatial period at which subjects can reliably discriminate the stimulus orientation, will be the same regardless of whether the gratings vibrate, at least for vibratory frequencies ≤ 80 Hz. Furthermore, if the threshold is mediated peripherally by SA1 fibers, thresholds will be independent of stimulus amplitude over the range of amplitudes tested in these neurophysiological experiments. On the other hand, to the extent that grating orientation discrimination relies on RA signals, thresholds will increase (and thus sensitivity will decrease) as stimulus amplitude increases. In a companion paper, we carry out psychophysical experiments investigating the effects of vibratory frequency and amplitude on grating orientation discrimination and draw conclusions as to the roles of SA1 and RA fibers in the perception of the fine spatial structure of tactile stimuli.

Acknowledgements

We thank F. Damann and J. Killebrew for invaluable technical assistance and J. Yau and M. Hollins for a careful reading of the manuscript.

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APPENDIX

Calculation of m_c

First, we computed, from the data obtained from each grating (at a given spatial period and frequency), the mean of the response across spatial offsets, R_{pf} , and the SD of the response across spatial offsets, S_{pf} . To compute the latter, the mean of the three measured responses at each spatial offset was first subtracted from each measured response at that spatial offset, then the SD of all the resulting values, centered around zero, was computed. S_{pf} is thus an estimate of the variability of the neural response across repeats. We then randomly generated values for the neural response from a uniform distribution such that the mean and SD were matched to measured values at a given spatial period and temporal frequency (i.e., to R_{pf} and S_{pf}). The mean of three such simulated spike rates— counterparts to the three repetitions used to obtain the actual mean spike rates—was computed for each of the n spatial offsets; samples of simulated mean spike rates were thus matched in size (n) with measured mean spike rates obtained at that spatial period (e.g., $n = 2$ samples for a spatial period of 1 mm; $n = 20$ samples for a spatial period of 10 mm). The minimum and maximum values of the simulated mean spike rates were then used to compute the baseline modulation from Eq. 1 at each spatial period and frequency. The mean of 100 such estimates was used as a measure of baseline modulation for each spatial period and temporal frequency to ensure that the estimate was robust. The measure of baseline modulation constituted an estimate of the quantity m that would be observed if the neural response was variable but essentially flat, i.e., exhibited no spatial modulation. To obtain m_c , the baseline modulation was subtracted from the measured modulation m .

Estimating the amplitude correction as a function of sampling frequency

Due to the limited resolution of the probe, the neural response could only be sampled every 0.5 mm. A smaller number of samples was thus obtained from gratings with low spatial periods than from those with high spatial periods: The sampling frequency, f_s , was 2 samples per stimulus cycle (spc) for the smallest grating and 20 spc for the largest grating. Because fewer spatial offsets were used to estimate the spatial modulation in the neural response to fine gratings, the modulation in the response to those gratings was likely underestimated. To estimate the degree to which the modulation was underestimated, we simulated the sampling process as follows. We assumed the modulation to be sinusoidal with a zero-to-peak amplitude of 0.5 and centered around 0.5, i.e., with values ranging from 0 to 1; the true modulation was then 1. Note that square waves with duty cycles >50% are much less susceptible to aliasing than are sinusoids. For each value of f_s (ranging from 2 to 20, each corresponding to the number of samples obtained from a grating at a given spatial period), we drew f_s regularly spaced samples from a single cycle of the sinusoid at each possible spatial offset/phase (with a spatial resolution of 1/1000th of a cycle, or $\pi/500$ radians). We then computed the modulation m of the sample obtained at each phase. We then averaged these estimates across phases to obtain the mean estimated modulation at that sampling frequency

$$m(f_s) = \frac{1}{N_\phi} \sum_{n=1}^{N_\phi} \frac{[\max(x(\phi_n, f_s)) - \min(x(\phi_n, f_s))]}{[\max(x(\phi_n, f_s)) + \min(x(\phi_n, f_s))]} \quad (\text{A1})$$

where $m(f_s)$ is the mean modulation estimate obtained with sampling frequency f_s (the actual modulation was 1), $x(\phi_n, f_s)$ is the set of samples obtained at f_s with the first sample at phase ϕ_n ($0 \leq \phi_n < 2\pi$ in increments of $\pi/500$), and N_ϕ is the number of phases (N_ϕ was 1,000 to obtain a precise estimate). From $m(f_s)$ (Fig. 12), we computed the factor by which the estimated modulation should be multiplied to correct for aliasing. This correction factor, $c(f_s)$, was simply

$$c(f_s) = \frac{1}{m(f_s)} \quad (\text{A2})$$

FIG. 1.

Top: bottom view of the 400-probe stimulator with every 4th probe included to show the internal structure. In the working stimulator, the pins, 0.3 mm in diameter and spaced 0.5 mm center-to-center, are driven by 400 motors, each independently controlled by computer. The range of motion of each probe is ~2 mm. The stimulator allows for the generation of arbitrary spatiotemporal stimuli. *Bottom:* illustrations of gratings at spatial periods 2 and 6 mm at every possible spatial offset. The 2-mm grating was offset by 0, 0.5, 1, and 1.5 mm; the 6-mm grating was offset by 0, 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, and 5.5 mm.

FIG. 2.

Spatial profile of the response of an SA1 (19_00) and an RA (11_03) fiber to gratings that vary in vibratory frequency and spatial period. Each colored trace corresponds to a different vibratory frequency (0 Hz refers to static gratings). Spike rates at each frequency are normalized by the mean spike rate at that frequency to show the similarity of the spatial profiles across vibratory frequencies. One cycle of each stimulus is shown in gray at the bottom of the figure. Afferent response are spatially modulated in a stimulus-dependent manner. The traces at different frequencies overlap to a large extent, suggesting that the degree of spatial modulation is independent of stimulus frequency. *Insets:* spatial modulation as a function of spatial period.

FIG. 3.

Top: effect of spatial period on spatial modulation. *Left:* each trace corresponds to a temporal frequency. Spatial modulation increased with spatial period at all frequencies for both types of fibers. *Right:* modulation, averaged across frequencies, as a function of spatial period for SA1 (blue) and RA (red) fibers. SA1 modulation was higher than its RA counterpart at all frequencies and spatial periods. *Bottom:* effect of vibratory frequency on spatial modulation. *Left:* each trace corresponds to a spatial period, indicated to its right. Spatial modulation increased slightly with vibratory frequency. *Right:* Modulation, averaged across spatial periods, as a function of frequency. Temporal frequency had little systematic effect on spatial modulation ($N_{SA} = 11$, $N_{RA} = 8$).

FIG. 4. Spatial modulation as a function of spatial period before (--- and ···) and after (—) the application of the anti-aliasing factor. The effects of aliasing are negligible for spatial periods ≥ 4 mm.

FIG. 5.

Firing rates as a function of vibratory frequency for SA1 (*left*) and RA fibers. Each trace corresponds to a spatial period. The amplitudes were chosen such that the stimuli were equated in subjective intensity, as measured in a companion psychophysical study (Bensmaïa et al. 2005). Firing rates evoked by gratings vibrating at 40 Hz were depressed for both SA1 and RA fibers. The specific reason for the drop in spike rate at 40 Hz is unclear. However, the decline is likely due to the way in which signals from the relevant populations of mechanoreceptive afferent fibers are combined to convey information about the subjective magnitude of the stimulus. When stimuli were set relative to the sensitivity of individual fibers, the neural response was no longer anomalous at 40 Hz.

FIG. 6.

Effect of vibratory amplitude on spatial modulation. Each trace corresponds to a vibratory frequency. The orientation of the gratings was parallel to the axis of the finger and their spatial period was 6 mm. The intensity levels are expressed in decibels relative to the amplitudes matched for subjective intensity (0dB re: max corresponds to the amplitudes denoted by . . . in Fig. 7). Increasing the stimulus amplitude had no effect on the spatial modulation of SA1 responses. On the other hand, RA modulation decreased with amplitude ($N_{SA} = 9$, $N_{RA} = 5$).

FIG. 7.

Stimulus intensities used in the 2 sets of recordings. . . . the stimulus intensities that were matched for subjective magnitude (Bensmaïa et al. 2005). - - - and —, show the mean stimulus intensities when these were set according to SA1 and RA sensitivity, respectively ($N_{SA} = 6$, $N_{RA} = 4$). *Inset:* the mean spike rates for neurons of each type as a function of vibratory frequency.

FIG. 8.

Top: Mean spatial modulation of responses evoked by horizontal gratings (oriented perpendicular to the axis of the finger) vs. the mean modulation of responses evoked by vertical gratings (oriented parallel to the axis of the finger). RA modulation exhibited a strong anisotropy, whereas SA1 modulation did not. *Bottom:* mean firing rates evoked by vertical gratings vs. mean firing rates evoked by horizontal gratings at each vibratory frequency for all the fibers. For both types of fibers, firing rates exhibit a slight but significant tendency to lie below the diagonal, indicating an effect of grating orientation on the strength of the response ($N_{SA} = 11$, $N_{RA} = 8$).

FIG. 9.

Population analysis. *Top*: the spatial profile of the summed responses of 11 SA1 and 8 RA fibers. Each trace corresponds to a vibratory frequency (see *bottom* for legend); different symbols denote different spatial periods. Spike rates at each frequency are normalized by the mean spike rate at that frequency to show the similarity of the spatial profiles across vibratory frequencies. The gray outline at the bottom of each plot shows the stimulus profile. *Bottom*: the spatial modulation as a function of spatial period, with vibratory frequency as a parameter. Spatial modulation increases monotonically with spatial period. Furthermore, vibratory frequency has no effect on spatial modulation, as is suggested by the spatial profiles shown (*top*).

FIG. 10.

Population analysis of the effect of amplitude on spatial modulation. Gratings with a spatial period of 6 mm are presented at 3 intensities and 6 vibratory frequencies. The spatial profiles of the responses evoked by each stimulus are aligned and summed across fibers. To facilitate comparison of the spatial profiles across conditions, we divide the spike rates elicited by gratings at a given amplitude and frequency by the mean firing rate across offsets at that amplitude and frequency. Grating amplitude has no effect on SA1 modulation whereas RA modulation decreases slightly but significantly as amplitude increases. The reason for the high RA modulation at 40 Hz and -10 dB is unclear. This data point is likely a statistical anomaly in the data as no single fiber is responsible for this large, seemingly stimulus-dependent modulation ($N_{SA} = 9$, $N_{RA} = 5$).

FIG. 11.

Anisotropy in SA1 (*left*) and RA (*right*) population responses. There is a strong and significant anisotropy in SA1 and RA responses to static and vibrating gratings (compare regression line with unity slope). Specifically, the spatial modulation of the responses to vertical gratings is greater than the spatial modulation of the responses to horizontal gratings for both SA1 and RA fibers. The effect of grating orientation is much stronger at the population level than it is at the level of individual fibers for SA1 fibers ($N_{SA} = 11$, $N_{RA} = 8$)).

FIG. 12.

Estimated amplitude of a sinusoid of amplitude 1 as a function of the sampling frequency f_s (expressed in samples per cycle). The modulation depth of afferent responses to the smallest gratings would be underestimated by an average of 35% given that only 2 samples are obtained per stimulus cycle.