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Single tactile afferents outperform human subjects in a vibrotactile intensity discrimination task

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Arabzadeh E, Clifford CW, Harris JA, Mahns DA, Macefield VG, Birznieks I. Single tactile afferents outperform human subjects in a vibrotactile intensity discrimination task. *J Neurophysiol* 112: 2382–2387, 2014. First published August 20, 2014; doi:10.1152/jn.00482.2014.—We simultaneously compared the sensitivity of single primary afferent neurons supplying the glabrous skin of the hand and the psychophysical amplitude discrimination thresholds in human subjects for a set of vibrotactile stimuli delivered to the receptive field. All recorded afferents had a dynamic range narrower than the range of amplitudes across which the subjects could discriminate. However, when the vibration amplitude was chosen to be within the steepest part of the afferent's stimulus-response function the response of single afferents, defined as the spike count over the vibration duration (500 ms), was often more sensitive in discriminating vibration amplitude than the perceptual judgment of the participants. We quantified how the neuronal performance depended on the integration window: for short windows the neuronal performance was inferior to the performance of the subject. The neuronal performance progressively improved with increasing spike count duration and reached a level significantly above that of the subjects when the integration window was 250 ms or longer. The superiority in performance of individual neurons over observers could reflect a nonoptimal integration window or be due to the presence of noise between the sensory periphery and the cortical decision stage. Additionally, it could indicate that the range of perceptual sensitivity comes at the cost of discrimination through pooling across neurons with different response functions.

microneurography; neural coding; neurometrics; psychometrics

THE SOMATOSENSORY SYSTEM offers unique opportunities for making direct recordings of peripheral neurons while concurrently obtaining perceptual judgments from awake, neurologically normal human participants; this microneurography technique allows recording of single impulses with percutaneously inserted tungsten microelectrodes (Vallbo and Hagbarth 1968).

Classic experiments on tactile sensitivity have identified a clear relationship between the psychophysical performance of humans and the physiological properties of sensory afferents (Harrington and Merzenich 1970; Johansson and Vallbo 1979a; Talbot et al. 1968; Werner and Mountcastle 1965; but see Knibestöl and Vallbo 1980). A high correlation was found between the absolute detection threshold of the participant and that of the most sensitive tactile afferents (Johansson and Vallbo 1979a). Similar findings in other sensory systems (Hawken and Parker 1990; Vogels and Orban 1990) suggest a "lower envelope principle," whereby the perceptual detection threshold is set by the most sensitive neurons available (Parker and Newsome 1998).

When responding to stimuli near the lowest end of detectable intensities, pooling the activity of multiple neurons effectively results in the "readout" of the most sensitive neurons. While this pooling strategy may be optimal for stimulus detection, it may not be as effective for discriminating between two stimuli at higher intensities. Figure 1 schematically illustrates the difference that would arise from pooling across two neurons. In this example, one neuron with a low threshold responds differentially to two low-intensity stimuli (L_1 and L_2) but responds equally strongly to two high-intensity stimuli (H_1 and H_2). The other neuron with a higher threshold does not respond to L_1 and L_2 but does respond differentially to H_1 and H_2. Participants attempting to discriminate between these stimuli would be most efficient if they could identify the most appropriate neuron for a given intensity and base the perceptual judgment on the activity of that neuron. Pooling across both neurons would achieve equivalent performance when discriminating between the low-intensity stimuli because only the more sensitive neuron responds to those stimuli, but pooling would reduce discrimination sensitivity between the higher-intensity stimuli because it would add uninformative input from the nondiscriminating neuron.

The foregoing discussion indicates that pooling across peripheral inputs can reduce perceptual sensitivity. However, other evidence indicates that pooling can lead to perceptual sensitivity that is superior to that of any single peripheral unit. In a Vernier judgment, human observers are able to discriminate the spatial offset between two line segments when the offset is 5 arcsec, which is 5–10 times smaller than the maximum spatial resolution of individual photoreceptors (Westheimer 1981). This "hyperacuity" can only be achieved by advantageous pooling across peripheral inputs. In summary, it is difficult to provide any a priori estimation of perceptual sensitivity to a stimulus from the sensitivity of individual peripheral neurons. Here we compared the accuracy of perceptual judgments by human subjects with the performance of their simultaneously recorded single tactile afferents in a vi-

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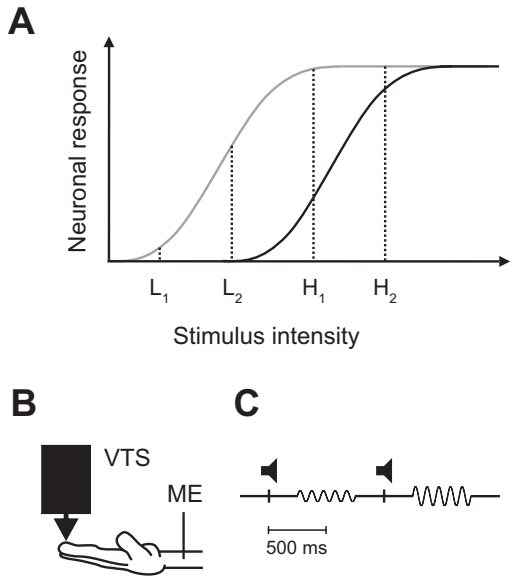

Fig. 1. *A*: schematic representation of the response functions of 2 neurons. The functions have a sigmoid shape where each neuron is sensitive to a limited range of stimuli. The neuron that is more sensitive to the low-intensity range (gray curve) responds differentially to *stimuli* L_1 and L_2, but its response does not differentiate between *stimuli* H_1 and H_2. By contrast, the neuron that is insensitive to low intensities (black curve) is able to discriminate between H_1 and H_2. *B*: a tungsten needle microelectrode (ME) was inserted into the median nerve, and impulses were recorded from single tactile afferents supplying the glabrous skin of the hand. A vibrotactile stimulator (VTS) was positioned at the center of the receptive field of the recorded afferent. *C*: schematic representation of the 2-alternative forced-choice paradigm: each trial contained 2 intervals, the beginnings of which were marked by an auditory cue. At the end of the second interval, subjects indicated the interval containing the stronger stimulus.

bration amplitude discrimination task across a range of stimulus amplitudes.

METHODS

Subjects and recording procedure. In eight experiments, six healthy human subjects (5 men and 1 woman) participated after providing written informed consent. All procedures were performed under the approval of the Human Research Ethics Committee of the University of New South Wales and conducted in accordance with the Declaration of Helsinki. Three of the subjects were authors; the other three were naive to the purpose of the experiment. Subjects sat comfortably in a dentist's chair with their right upper arm abducted at ~30°, while their elbow rested on a horizontal extension of the chair. The arm was immobilized by straps around the wrist. To stabilize the distal phalanges, the dorsal aspect of the index, middle, and ring fingers was fixed into a plasticine mold. A tungsten microelectrode was inserted into a cutaneous fascicle of the median nerve at the wrist, and neural activity was amplified (2×10^4, 0.3–5 kHz; ISO-80, World Precision Instruments); an uninsulated subdermal microelectrode served as the reference. Impulses were recorded from single afferents that terminated in the palm, index, middle, or ring finger. For each isolated fiber, calibrated nylon monofilaments (Semmes-Weinstein Esthesiometers, Stoelting) were used to determine the afferent's threshold force and to define the receptive field. Neuronal activity was sampled continuously at 12.8 kHz, and spikes were sorted off-line with a template matching protocol written in MATLAB (MathWorks, Natick, MA). Microelectrode recordings from the median nerve have revealed four classes of myelinated low-threshold mechanoreceptor (Johansson and Vallbo 1983; Macefield and Birznieks 2008).

Single fibers were classified as slowly adapting type I or II (SA-I or SA-II) and fast-adapting type I or II (FA-I or FA-II) by the established criteria of responses to static stimuli, responses to rapidly changing stimuli, and receptive field size (Johansson and Vallbo 1979b, 1983; Vallbo and Johansson 1984). Impulses were recorded from a total of 40 single tactile afferents during 8 recording sessions. These included 21 SA-I, 5 SA-II, 11 FA-I, and 3 FA-II neurons. Of these, 32 single afferents were successfully maintained throughout all phases of the experiment (see below).

Characterizing neuronal response function. After the afferent was classified and its receptive field determined, the tip of a rod (1 mm in diameter), attached to a custom-made mechanical stimulator, was placed in the center of the receptive field. The rod was used to present sinusoidal vibrations spanning a range of amplitudes while we measured the afferent's response. Each set of vibratory stimuli lasted for 500 ms, with a 500-ms interval between vibrations. Figure 1*B* illustrates the experimental setup. Stimuli were generated in MATLAB and played via a National Instruments (Austin, TX) interface board. To estimate the amplitude response function, a frequency was selected to drive the afferent effectively (between 10 and 60 Hz). The amplitude of the sinusoidal stimulus systematically increased from 0 to 60 μm with steps of 0.6 μm. We observed the afferent response as the vibration amplitude progressively increased. This allowed us to estimate the minimum amplitude that generated spiking in the neuron and the maximum amplitude for which spiking seemed to plateau. We selected one or more base amplitudes (always multiples of 6 μm) that fell within the estimated minimum and maximum amplitudes and used these for the simultaneous psychophysical and neuronal discrimination task. If the neuron responded to the smallest vibration, then base amplitude was set to 0. The amplitude response function was then saved for off-line analysis to verify the choice of the base amplitude relative to the dynamic range of the neuronal response. The afferent response was characterized off-line by fitting a piecewise linear function to each amplitude response function (Fig. 2). With the exception of one afferent, all recordings were fitted well by the piecewise linear function, revealing the three distinct response regions: the subthreshold, the saturated, and the dynamic range. The off-line analyses showed that of the 64 selected base amplitudes 52 were in the dynamic range of the neuron. These sessions are analyzed to provide a direct comparison of psychophysical and neuronal discrimination performances.

Simultaneous psychophysical and neuronal discrimination task. We used an adaptive staircase procedure (Kontsevich and Tyler 1999), within a two-interval, two-alternative forced choice (2AFC) paradigm to measure each subject's just-noticeable difference (JND) for 500-ms sinusoidal vibrations presented to the center of the receptive field of the simultaneously recorded neuron. Each trial comprised two 1-s intervals, each marked by an auditory cue (Fig. 1*C*). Subjects made a forced-choice judgment to indicate which interval contained the stronger of two tactile stimuli. Using this 2AFC paradigm, we measured each subject's JNDs for vibrations of different base amplitudes. The amplitude of the stronger vibration varied from trial to trial according to a Bayesian adaptive-staircase method that optimized the information gain (in terms of measurement of the JND) on each trial (Kontsevich and Tyler 1999). The order of the base and higher-amplitude vibrations varied randomly from trial to trial, and the JND was estimated at the end of each 30-trial staircase. Subjects did not receive feedback on their responses.

RESULTS

Figure 2*A* shows typical examples of the amplitude response function for a fast-adapting (n_1) and a slowly adapting (n_2) neuron. Neurons showed a characteristic response profile consisting of *1*) a subthreshold range for which they did not fire any spikes, *2*) a range of amplitudes across which the response increased monotonically (we refer to this as the neuron's "dynamic range"), and *3*) a saturated range over which the

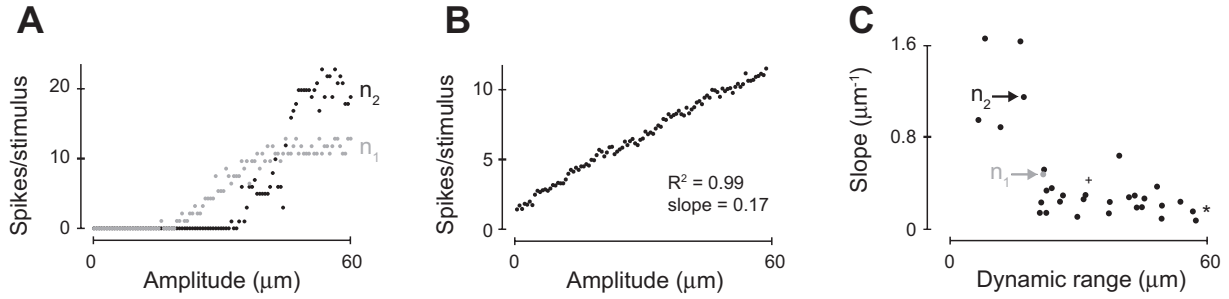

Fig. 2. Amplitude response function of 2 afferents. *A*: every stimulus amplitude is presented once, and the neuronal response is measured as the number of spikes generated over the whole stimulus duration (0.5 s). Stimulus frequency was 20 Hz for the neuron plotted in gray dots (n_1) and 40 Hz for the neuron plotted in black dots (n_2). *B*: the population response function is generated by averaging the spike counts across recorded afferents ($n = 32$) in response to each vibration amplitude. *Inset* indicates the slope and R^2 of regression. Similar to *A*, the function is based on 1 trial presentation per stimulus per afferent. *C* plots for each afferent the slope of the dynamic range as a function of the length of the dynamic range. The individual afferent's response function was fitted with a piecewise linear function. Plus sign indicates the average slope and dynamic range across afferents. Asterisk represents the range and slope for the average response in *B*. *Neurons* n_1 and n_2 from *A* are identified with arrows.

response was constant. In a few highly sensitive neurons the response threshold was low and no distinct subthreshold range was identified, while in a few other neurons the dynamic range extended beyond the maximum amplitude (60 μm) and the saturated range was not observed. To see how the full range of amplitudes was represented in the collective response of afferents, we averaged their activity ($n = 32$). The average activity (Fig. 2*B*) was a linear function of amplitude and covered the whole range of applied amplitudes (R^2 of the regression was 0.99). To quantify the response function of individual afferents, we fitted a piecewise linear function to each amplitude response function, revealing the three distinct response regions: the subthreshold, the saturated, and the dynamic range. Figure 2*C* plots for each afferent the length of the dynamic range versus its slope. All recorded afferents had a dynamic range narrower than that of the average response. Across afferents the average slope was 0.41, while the slope of the average response was 0.17.

Figure 3 illustrates the difference in the number of spikes fired by the recorded afferents in response to the two stimuli in each trial as a function of the amplitude difference between the two stimuli; dots in the upper right or lower left quadrant indicate trials in which the neuronal response covaried with vibration amplitude (i.e., a higher number of spikes for the higher-amplitude stimulus). For these trials, a hypothetical observer of the number of spikes fired by this neuron would discriminate correctly between the two stimuli. On the other hand, dots in the upper left or lower right quadrant in Fig. 3 indicate trials in which neuronal response was lower for the higher-amplitude stimulus. A decision based on the number of spikes fired by such a neuron would therefore lead to an incorrect discrimination. Dots falling on the *x*-axis in Fig. 3 indicate trials for which the neuronal response was identical for the higher- and lower-amplitude stimuli. A decision based on the neuronal response in these trials would lead to chance performance (50% correct). The subjects' performance can be assessed from the number of correct trials and incorrect trials (open circles and gray filled circles, respectively, in Fig. 3). Performance was then compared with that of a hypothetical observer making a decision on each trial based on the spike count of the simultaneously recorded neuron. For the two examples illustrated in Fig. 3, both subjects performed at 83.3% correct (accuracy was similar between subjects because the staircase titrated the task difficulty across trials so that each subject performed at about this level). The concurrent neuronal performance was at 96.7% and 83.3%, respectively.

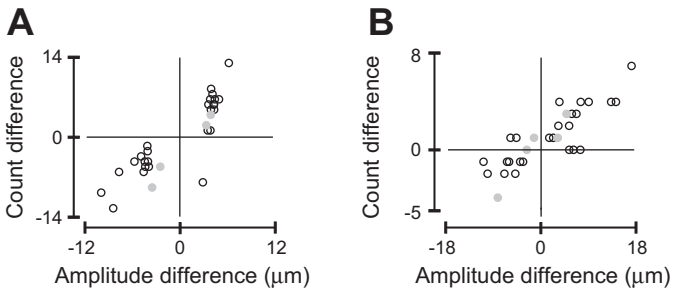

Fig. 3. Difference in number of spikes fired by 2 afferents (n_1 and n_2 from Fig. 2*A*) as a function of the amplitude difference between the vibrations for 2 subject-neuron pairs (*A* and *B*). Every circle represents 1 trial. Open circles indicate correct decisions by the subject, and gray filled circles indicate trials where the subject made an incorrect choice.

Figure 4*A* compares the performance of human subjects with those of single neurons across all 52 recorded staircases where the base amplitude was selected within the dynamic range of the neuron. This figure demonstrates that in the majority of cases the single neuron outperformed the subject. Figure 4*B* shows the distribution of performances for subjects and recorded neurons across the four afferent classes. The median performance was 93.3% for neurons and 83.3% for subjects. A Wilcoxon signed-rank test on the difference in performance between neuron and subject on each of the 52 staircases showed that the performance of the sample of individual neurons was significantly higher than the corresponding performance of the human subjects ($P < 0.001$).

Our analyses up to this point focused on the spike count measured across the whole vibration interval. This is based on the assumption that the ideal observer can access the spike count over the 500-ms vibration duration and decode a single spike difference between the counts generated for each of the two vibrations. Previous research has indicated that the spike count generated over a subsection of the vibration might be a more reliable predictor of perceptual discrimination (Luna et al. 2005). Figure 5 quantifies how in our data set the decoding performance depends on the integration time, and the precision with which the decoder detects differences in spike counts across the two vibrations. Figure 5*A* illustrates that for short integration windows the neuronal performance is inferior to the performance of the subject. The average neuronal performance

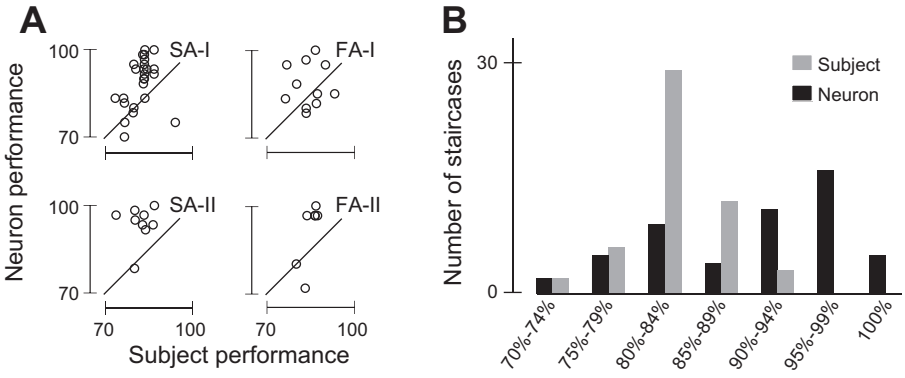

Fig. 4. Comparison of neuronal and psychophysical performance. *A*: every symbol represents data collected during 1 staircase procedure ($n = 52$). Different panels indicate the afferent type: slowly adapting type I and II (SA-I and SA-II) and fast-adapting type I and II (FA-I or FA-II). Diagonal lines mark equal performance between the subject and the neuron. *B*: distribution of subject and neuronal performances across all afferent classes.

progressively improves as the spike count duration increases and reaches a level significantly above that of the subjects (dashed horizontal line in Fig. 5*A*) when the duration is 250 ms or longer. Figure 5*B* illustrates that the superiority in neuronal performance over subjects critically depends on the precision with which spike counts can be compared. When the ideal observer of the neuronal response can detect a single spike difference across the two vibrations, it outperforms the subjects. As the decoding precision decreases, the average neuronal performance rapidly drops to below that of the subjects (dashed horizontal line in Fig. 5*B*).

DISCUSSION

We compared the sensitivity of single afferent fibers with the concurrently recorded psychophysical performance of human subjects in a vibrotactile amplitude discrimination task. The dynamic range for every afferent was narrower than the range across which subjects could discriminate vibration amplitudes. However, when the base amplitude was chosen to be within the afferent's dynamic range, the spike count in individual neurons could differentiate the amplitude significantly better than the human subjects could do perceptually. We quantified how the superiority of neuronal performance critically depends on the ability to integrate spikes over multiple cycles of the vibration (Fig. 5*A*).

The superiority in performance of individual neurons over observers could indicate that the range of perceptual sensitivity comes at the cost of discrimination through pooling across neurons with different response functions. Furthermore, noise could be introduced between the sensory periphery and the cortical decision stage. We quantified how a small amount of noise added during synaptic transmission to the cortical decision areas can reduce the single-neuron information to levels compatible with human performance (Fig. 5*B*). Consistent with this idea, previous simultaneous recordings of first-order and cortical neurons in rat somatosensory system (barrel cortex) revealed that first-order neurons carried more information about the kinetics of vibrotactile stimuli applied to whiskers than cortical neurons (Arabzadeh et al. 2005, 2006).

Previous experiments have described neuronal input-output functions with either a piecewise linear function or an S-shaped function, where input is the strength of the sensory event (e.g., vibration amplitude) and output is spiking probability (Johansson and Vallbo 1979a; Knibestöl and Vallbo 1980). The common finding that appears to generalize across species is that neuronal firing rate increases as the amplitude of a vibrotactile stimulus increases (for observations in primates, see Harvey et al. 2013; Hernández et al. 2000; Luna et al. 2005; for rats, see Adibi and Arabzadeh 2011; Arabzadeh et al. 2003). Neurons recorded in the present study showed a response profile that was well approximated by a piecewise linear function but with variable thresholds (Fig. 2). Nonetheless, single neurons recorded across different subjects consistently outperformed those same subjects in the discrimination task.

While previous neurophysiological experiments have indicated that the properties of the peripheral sense organs determine the psychophysical threshold (Hecht et al. 1942), others have argued that central mechanisms can limit detection sensitivity (Green and Swets 1966). Focusing on tactile detection thresholds, Johansson and Vallbo (1979a) found a good match

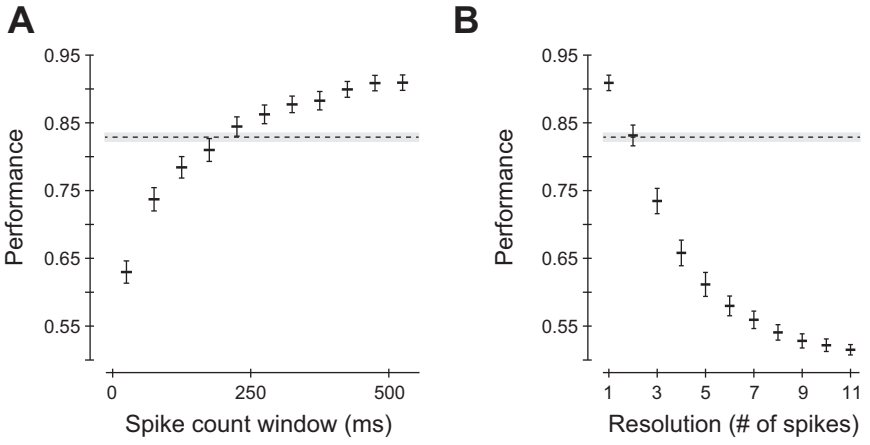

Fig. 5. Comparison of psychophysical and neuronal performance as a function of spike integration window and the "readout" precision. *A*: error bars indicate mean and SE of neuronal performance as a function of integration window (from 25 ms to 525 ms with 50-ms steps). *B*: neuronal performance is quantified as a function of the resolution with which the ideal observer can "read out" the number of spikes; 1 indicates maximum precision, whereby a single difference in spike count is detectable by the ideal observer. A resolution of n indicates that only spike count differences bigger than or equal to n can be decoded by the ideal observer. In *A* and *B*, horizontal dashed line represents average subject performance, with gray shading indicating SE across subjects.

between neuronal and psychophysical thresholds if the analyses were restricted to the FA-I afferents. Similar results were found in a few cases with Pacinian corpuscles but not with any slowly adapting unit. Based on the expected density of FA-I afferents, their average receptive field size, and the distribution of their thresholds, an argument is made that a single impulse in a single unit could be enough to produce the sensation of touch (Johansson and Vallbo 1979a, 1979b). The estimates also indicated that the number of units excited by stimuli at the minimal psychophysical thresholds is small. Indeed, using intraneural microstimulation of single afferents innervating the human hand, Vallbo et al. (1984) and Macefield et al. (1990) showed that activation of single SA-I, FA-I, and FA-II afferents evoked conscious experience (whereas activation of single SA-II and muscle spindle afferents did not). Overall, these findings indicate an efficient readout mechanism of afferent activity for stimuli close to detection threshold.

To determine how many sensory neurons are required to match the psychophysical sensitivity to thermal changes, Darian-Smith and colleagues compared the temperature sensitivity of afferents in anesthetized monkeys with that of human subjects (Darian-Smith et al. 1973). The results indicated that the sensitivity of a single temperature-sensitive afferent is on average less than the psychophysical sensitivity of human subjects, and 16 afferents were required to achieve the perceptual temperature sensitivity. Similar findings have been reported in higher sensory areas. In the visual system, Hawken and Parker (1990) compared the psychophysical detection threshold of spatial contrast patterns in humans with the neuronal detection function of monkey V1 neurons. The slope of the neuronal detection function correlated closely with that of the psychophysical detection function. Single neurons in macaque somatosensory cortex exhibited orientation tuning with a degree of sensitivity comparable to that measured in humans (Bensmaia et al. 2008). Similarly, in the primary visual cortex neuronal discrimination thresholds for orientation are comparable with monkeys' psychophysical performance (Vogels and Orban 1990). Recording from single direction-selective neurons in the middle temporal (MT) and medial superior temporal (MST) areas found trial-to-trial correlation between fluctuations in neural responses and the perceptual judgment, suggesting that performance was based on signals pooled across a population of neurons (Britten et al. 1996; Newsome et al. 1990; Shadlen et al. 1996). In the tactile domain, motion discrimination experiments involving moving gratings and plaids presented to monkey fingertips revealed populations of somatosensory cortical neurons that exhibited motion integration properties similar to neurons in visual area MT, with performances that matched those obtained in human psychophysics (Pei et al. 2010, 2011). Finally, recordings from primary and secondary somatosensory cortices have shown correlation between neuronal activity and monkeys' vibrotactile discrimination performance (Romo et al. 2003; Romo and Salinas 2003).

The present experiment explored the relationship between neuronal and psychophysical performance for stimuli that are well above detection threshold. There is substantial evidence that stimulus intensity is represented in a neuronal population code where different afferent types contribute with different weights (Bensmaia 2008; Muniak et al. 2007). The fact that our subjects performed worse than their peripheral neurons is consistent with the notion of an intensity code based on weighted pooling of the afferent inputs. This type of intensity code ensures a continuum of amplitude perception for a wide range of stimuli, but it reduces relative sensitivity (discrimination capacity) by including "noise" pooled from sensory units that do not discriminate between the stimuli being compared (see Fig. 1*A*). However, this conclusion is undermined by the observation that the peripheral sensory neurons we and others have recorded show little variation in their response to stimuli outside their dynamic range.

Another way that discrimination sensitivity could be reduced because of pooling across afferent inputs is if the total input were subjected to a logarithmic compression at the central level. This is in keeping with the Weber-Fechner law, which states that perceptual discrimination is based on the relative difference in neuronal responses, as a fraction of the mean response to the stimuli. From classic psychophysical experiments with humans, various forms of nonlinearity have been inferred in the amplitude response function (Knibestöl and Vallbo 1980). These nonlinearities shift from accelerating at low vibration amplitudes to decelerating at higher vibration amplitudes (Arabzadeh et al. 2008). Electrophysiological recordings in monkeys reveal that many neurons in somatosensory cortex show decelerating response rates with increasing stimulus amplitude (Mountcastle et al. 1969). A physiological rationale for this encoding principle is that it expands the psychophysical dynamic range and filters biologically insignificant stimulus details. However, a better understanding of this principle will depend upon identifying what the relevant intensity code is and which afferent input it is based on. We conclude that, while stimulus detection thresholds in human fingertip may be compatible with the lower envelope principle (Parker and Newsome 1998), amplitude discrimination displays characteristic features of pooled coding (Bensmaia 2008).

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: E.A., C.W.G.C., and J.A.H. conception and design of research; E.A. and I.B. performed experiments; E.A. analyzed data; E.A., C.W.G.C., J.A.H., D.A.M., V.G.M., and I.B. interpreted results of experiments; E.A. prepared figures; E.A. drafted manuscript; E.A., C.W.G.C., J.A.H., D.A.M., V.G.M., and I.B. edited and revised manuscript; E.A., C.W.G.C., J.A.H., D.A.M., V.G.M., and I.B. approved final version of manuscript.

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