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Research Report

Contribution of within- and cross-channel information to vibrotactile frequency discrimination

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ABSTRACT

Vibrotactile stimuli normally activate multiple information-processing channels starting from different types of mechanoreceptors, and the most sensitive channel alternates depending on the range of vibration frequency. How the tactile system encodes vibration frequency using within-channel information (e.g., the temporal pattern of neural activity of each channel) and/or cross-channel information (the relationship between activities of channels) has been examined, and the usefulness of the former has been evidently shown, while that of the latter remains controversial. To see the contribution of within- and cross-channel information to vibrotactile frequency encoding, we investigated frequency discrimination for near-threshold vibration, which can activate the channels more selectively than conventional supra-threshold vibration. At near-threshold intensity, the contribution of cross-channel information, if it exists, would be observed only when two vibrations activate different channels. In the first experiment, we examined the frequency discrimination thresholds for a wide range of frequencies. The results did not show a clear contribution of the cross-channel information, though that of the within-channel information was evident. In the second experiment, we compared the signal detection threshold and the frequency identification threshold between frequency pairs. We found that for certain pairs of stimuli whose frequencies were far enough apart from each other to activate different channels, each stimulus was identified as soon as it was detected. This suggests that each channel is a labeled line as expected from cross-channel encoding of vibration frequency, but not all data were consistent with this idea. We conclude that though a labeled-line structure might exist as a basis of cross-channel encoding, the cross-channel information does not play a dominant role in frequency discrimination.

1. Introduction

The vibration frequency on the finger pad while touching an object is the primary information the tactile system uses to analyze some fundamental object properties, such as roughness, texture, and hardness. There are two neural pathways for responding to vibrotactile frequency, each starting from a specific type of mechanoreceptor under the skin and sending sensory information to the brain. One channel (RA channel) consists of rapidly adapting afferent

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fibers associated with Meissner corpuscles, and is sensitive to lower vibration frequencies (mainly tens of hertz). The other channel (PC channel) consists of Pacinian afferent fibers associated with Pacinian corpuscles, and is sensitive to higher frequencies (mainly hundreds of hertz) (Bolanowski et al., 1988; Mountcastle et al., 1972; Talbot et al., 1968). The information that can be used for encoding vibrotactile frequency is classified into two categories: within-channel information that lies in the neural activities in each channel [e.g., inter-spike interval of neural responses (Ferrington and Rowe, 1980; Ghosh et al., 1994; Johansson et al., 1982; Johansson and Vallbo, 1983; Mountcastle et al., 1969, 1990; Talbot et al., 1968) and spike-count rate (Luna et al., 2005; Romo et al., 1998; Salinas et al. 2000)] and cross-channel information that lies in the relationship between the channels' activities [i.e., which channel is dominantly activated and how strong the activation of the dominant channel is relative to those of other channels (Morley and Rowe, 1990; Roy and Hollins, 1998)]. How vibration frequency is encoded using within- and cross-channel information is a fundamental question in vibrotactile frequency perception.

The roles of within- and cross-channel information in frequency encoding can differ depending on the frequency range. For high frequency vibrations, within-channel information is essential, since neural activations are confined to the PC channel, whose detection threshold is less than one-tenth of the RA channel in this range. This leaves no doubt that the within-channel information from the PC channel includes the code of vibrotactile frequency in some way or another, given that the discrimination performance at high frequencies does not change under RA-channel anesthesia (Talbot et al., 1968; Mahns et al., 2006), that the perception of fine texture, which was mainly mediated by PC channel, is not changed under adaptation to low frequency (Hollins et al., 2001), and that the discrimination performance for the high frequencies of supra-threshold vibration is constant regardless of stimulus amplitude (Horch, 1991). For low frequency vibrations, within-channel information from the RA channel is a dominant source of vibrotactile frequency perception, though the SA channel may also play some roles for very low frequencies (Roy and Hollins, 1998). It has been demonstrated that changes in within-channel information of RA channel are correlated with psychophysical performance regarding frequency discrimination (LaMotte and Mountcastle, 1975; Mountcastle et al., 1990; Romo et al., 1998), and the discrimination performance at low frequencies is not changed under adaptation to high frequencies (Bensmaïa and Hollins, 2000; Gescheider et al, 2004) or by changes in stimulus amplitude (LaMotte and Mountcastle, 1975; Romo et al., 1998).

For the vibration of middle frequencies, both the within- and cross-channel information can be used for encoding the frequency since a single frequency can activate the two channels, with the activity ratio between them changing according to the stimulus frequency. While the contribution of within-channel information to encoding frequencies is evident, that of cross-channel information remains a controversial issue. As in the case of, say, color vision (Wyszecki and Stiles, 1982), a channel ratio model has been considered as a potential coding mechanism of vibrotactile frequency, and previous studies have examined whether a change in vibration amplitude shifts the perceived frequency in a particular direction, as predicted by the proposed ratio model. However the observed trends were not consistent (Bekesy, 1959, 1960, 1962; Morley and Rowe, 1990; Roy and Hollins, 1998). It is unclear whether the failure to find evidence for the cross-channel encoding should be ascribed to the lack of a contribution of cross-channel information or to methodological limitations of the previous studies.

In this study, to gain insights into the contribution of within- and cross-channel information to vibrotactile frequency encoding, we investigated frequency discrimination for near-threshold stimuli. Most previous studies on vibrotactile frequency perception used vibration stimuli with strong supra-threshold amplitudes. Such stimuli likely stimulate multiple channels at the same time for a wide frequency range and therefore the contribution of within- and cross-channel information cannot be easily separated. Meanwhile, the near-threshold stimuli we used can activate channels more selectively than strong supra-threshold stimuli, and we can therefore consider the contribution of within- and cross-channel information to frequency encoding on the basis of frequency discrimination performance.

We conducted two experiments. In experiment 1, we evaluated vibration frequency discrimination performance in terms of the ratio of the just noticeable frequency difference (JND) relative to the standard frequency [Weber fraction (WF)]. We used five standards spanning a wide range of frequencies (15, 30, 60, 120, and 240 Hz), while fixing their intensities at 16 or 6 dB above the detection threshold. It is known that strong supra-threshold stimuli provide small and nearly constant WFs for a wide range of standard frequency (Franzén and Nordmark, 1975; Israr et al., 2006; LaMotte and Mountcastle, 1975; Mahns et al., 2006; Mowbray and Gebhard, 1957; Rothenberg et al., 1977; but see also Goff, 1967; Rothenberg et al., 1977). We expected to find the same trend in the results for our 16-dB condition. On the other hand, the results in our 6-dB condition do not have to provide constant WFs, and the pattern of deviation from the constant WFs will provide insight into the underlying encoding mechanisms. It is likely that high–high and low–low frequency pairs are discriminated only by using within-channel information of the PC and RA channels, respectively. The results for these pairs will therefore suggest how the intensity reduction affects the within-channel information of each channel. On the other hand, for pairs of low- and high-frequency stimuli that are expectedly detected by different channels, the activity ratio between two channels (cross-channel information) can provide an additional clue for frequency discrimination of the stimuli, and the frequency discrimination for near-threshold stimuli may be better at middle frequencies than at the other frequencies.

The results of experiment 1 showed that the WF elevated for near-threshold conditions relative to supra-threshold conditions, and that the magnitude of elevation was the smallest for low frequencies and gradually increased with frequency. The results are consistent with the idea that, for both the RA and PC channels, within-channel information mainly supports frequency discrimination, with the within-channel information in the PC channel being more degraded by intensity reductions. The data was not consistent with expected behavior of the use of the cross-channel information in frequency discrimination, such as a selective reduction of the WF for the middle