Research report

Somatotopic representation of tactile duration: evidence from tactile duration aftereffect

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ABSTRACT

Accurate perception of sub-second tactile duration is critical for successful human-machine interaction and human daily life. However, it remains debated where the cortical processing of tactile duration takes place. Previous studies have shown that prolonged adaptation to a relatively long or short auditory or visual stimulus leads to a repulsive duration aftereffect such that the durations of subsequent test stimuli within a certain range appear to be contracted or expanded. Here, we demonstrated a robust repulsive tactile duration aftereffect with the method of single stimuli, where participants determined whether the duration of the test stimulus was shorter or longer than the internal mean formed before the adaptation (Experiment 1A). The tactile duration aftereffect was also observed when participants reproduced the duration of the test stimulus by holding down a button press (Experiment 1B). Importantly, the observed tactile duration aftereffect was tuned around the adapting duration (Experiment 1C). Moreover, the effect was confined in the adapted sensory modality (Experiment 2) and the enacted fingers within a somatotopic framework (Experiment 3). These findings suggest the early somatosensory areas with the topographic organization of hands play an essential role in sub-second tactile duration perception.

1. Introduction

When a vibration is delivered to us, we perceive not only its frequency and intensity, but also its duration. The perception of tactile duration is fundamental to a wide range of human activities, such as playing the piano and video games. However, in past decades, although some somesthetic senses, such as tactile texture and location perceptions, have been well studied [1], we still know little about where tactile duration is encoded in the brain.

It is generally accepted that there is no specific organ dedicated to time discrimination. Time is one of the amodal and emergent properties of events. To account for this amodal nature, some models used a metaphor of a central clock for time measurement [2–4]. This clock typically includes a pacemaker and an accumulator, which extract durations from different modalities, indicating a supramodal mechanism for duration processing. According to these models, tactile duration should be encoded in cortical areas beyond the primary somatosensory cortex (S1). This view is supported by evidence that the superior temporal gyrus (STG) in the auditory cortex is involved in

processing the duration of tactile events, suggesting a supramodal role of the STG in tactile duration perception [5,6]. However, modality-specific view is supported by the mismatch negativity (MMN) components which were locked to unimodal auditory and tactile duration deviants and were generated in individual sensory cortical regions [7]. Furthermore, recent studies suggest that S1 is involved in tactile temporal processing [8,9]. Therefore, the processing level at which tactile duration is encoded remains incompletely understood.

We have investigated this issue by using the adaptation aftereffect paradigm. Adaptation aftereffects, as the "psychophysicist's micro-electrode" [10], have been widely used to uncover the sensory processing mechanisms in the brain. Previous adaptation research has shown that sensory stimuli were represented at various cortical processing levels, according to their complexity. For example, in vision, tilt aftereffect has been attributed to low-level orientation processing, with high specificity to retinal location [11,12]. In contrast, face aftereffect generalized to different retinal locations [13], orientations [14], and stimulus sizes [15], suggesting a high-level representation of faces. Adaptation aftereffects were also observed in other sensory modalities,

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including the tactile modality [16]. Perceptions of tactile properties, including size [17], distance[18], curvature [19,20], shape [21], motion [22,23], and roughness [24] are susceptible to adaptation, manifested as repulsive perceptual aftereffects. For example, in the well-known curvature aftereffect, participants judged a flat surface to be concave after being exposed to a convex surface, and vice-versa [19].

Similar to the aftereffects in the spatial domain, repetitive exposure to a duration results in the duration-selective repulsive aftereffect [25–27]. For example, prolonged adaptation to short visual durations (e.g.,160 ms) leads to the overestimation of the intermediate visual durations (e.g., 320 ms) presented subsequently, while prolonged adaptation to long durations (e.g., 640 ms) results in the underestimation of the same intermediate durations [25]. The duration aftereffect has also been used extensively to deduce the neural bases of duration perception in recent years. Studies have found that the duration aftereffects in vision and audition were modality specific [25,28]. Studies also showed that the duration aftereffect was contingent on the auditory frequency [28,29], but not on visual orientation and space [28,30,31]. Although the duration aftereffects in vision and audition have received much attention, surprisingly, there has been little work on the duration aftereffect in touch.

An empirical question about the tactile duration adaptation is whether and how a repulsive tactile duration aftereffect could be observed. With the presumed repulsive duration aftereffect in the tactile domain, the level of cortical mechanisms underlying the aftereffect is an important question. This question could be firstly addressed by examining the sensory transferability of the adaptation aftereffect. If the adaptation aftereffect could transfer between different sensory modalities, the supramodel processing view would gain support. Otherwise, a modality-specific adaptation mechanism would play a pivotal role in the aftereffect. For example, a cross-modal adaptation aftereffect on facial emotion suggests a high-level, supramodal representation of emotion [32]. Secondly, experimental results from topographic generalization could help to address this question. The cortical representations of body parts (i.e., somatotopic organization) have been established in mammals and humans [33–35]. In the tactile domain, the cortical representation of hand in S1 contains a detailed finger topography [36]. In the finger topography, studies have explored the cortical processing of many tactile properties, including orientation, pressure, and roughness. Benefits from discrimination learning on those properties could only transfer to adjacent and homologous fingers, indicating early cortical processing mechanisms [37,38]. The noticeable transfer of the curvature aftereffect between fingers regardless of the hands also indicates that the neural processing of curvature information involves the somatosensory cortex shared by fingers of both hands [39,40]. To our best knowledge, the potential topographic generalization of the tactile duration aftereffect has not been studied.

In the present study, we investigated whether the duration aftereffect could be observed in the tactile modality as in the visual and auditory modalities, to uncover the timing mechanisms for sub-second tactile duration processing. In Experiment 1, we observed the repulsive tactile duration aftereffect with both the methods of single stimuli (Experiment 1A) and duration reproduction (Experiment 1B). Moreover, we showed that the aftereffect was tuned around the adapting duration (Experiment 1C). In Experiment 2, we investigated its processing level by looking into the transferability of the tactile duration aftereffect between the auditory and tactile modalities. Experiment 2 implemented two paradigms: consecutive adaptation to either auditory or tactile duration (Experiment 2A) and simultaneous adaptation to both auditory and tactile durations (Experiment 2B). In Experiment 3, we further examined the topographic generalization of the tactile duration aftereffect. The results from Experiments 2 and 3 showed that the tactile duration aftereffect was modality specific, and was organized within a somatotopic framework, suggesting the somatotopic representation of tactile duration.

2. Experiments 1A, B and C : Adaptation to tactile duration induces the tactile duration aftereffect

We used the methods of single stimuli (Experiment 1A) and duration reproduction (Experiment 1B) to investigate whether adaptation to a tactile duration could affect subsequent tactile duration perception. In the method of single stimuli, participants classified a test duration as shorter or longer, compared with the mean of a group of test durations (i.e., the internal mean). This method is simple yet reliable, but the internal mean is initially formed before adaptation and could be contaminated by adapting durations in memory [41]. On the other hand, the duration reproduction method (Experiment 1B) allows participants to reproduce test durations by holding down a button press, which is not based on the internal mean or a comparative judgment which may itself have been distorted by adaptation as in Experiment 1A. Furthermore, we investigated whether the adaptation effect was tuned around the adapting duration with the duration reproduction method (Experiment 1C). We hypothesize that if duration-selective channels are involved in the tactile temporal processing, the tactile duration aftereffect would be tuned around the adapting duration.

2.1. Methods

2.1.1. Participants

Twenty-six participants attended Experiment 1. Details about the participant groups are listed as below: Experiment 1A (n = 8, 6 females, mean age: 24.75 ± 2.31 years), Experiment 1B (n = 8, 7 females, mean age: 21.63 ± 0.92 years), Experiment 1C (n = 10, 7 females, mean age: 22.20 ± 2.15 years). All participants reported normal tactile sensation and had no history of neurological diseases. They also self-reported right-handed, and were naïve to the purpose of the experiments. They were paid or given course credits for their time, and gave written informed consent before the experiments. The study was conducted in accordance with the principles of Declaration of Helsinki and was approved by the human subject review committee of Peking University.

2.1.2. Stimuli and procedures

Fingertip was stimulated by a round aluminium probe (6.0 mm in diameter). Sine-waveform vibration (150 Hz) characterized by 10-ms cosine on- and off-ramps was delivered to the probe by a MRI-compatible piezo-tactile stimulator system (Dancer Design, St Helens, Merseyside, England), which was connected to a digital-to-analog conversion sound card. The sample rate of the vibration signal was set at 48 kHz. The vibration was well perceived by participants. The probe was located in a hole (8.0 mm in diameter) in one end of the rectangular machined ceramic case. Participants placed their finger against the case and touched the flat surface of the probe with their fingertip. The probe vibrated generating a touch sensation. To fix the contact position between the finger and the probe, a finger rest was used during the experiments (Fig. 1A).

Participants sat in front of two table tops with one under the other in a dimly lit room. During the experiment, they put one hand (either left or right hand, counterbalanced across participants) with palm downward on the supporting desk (lower one). The vibrotactile stimuli were presented on the middle fingertip of this hand, which was located at the body midline. Participants used the other hand placed on the upper desk for issuing responses (Fig. 1B). Meanwhile, participants kept their eyes on the fixation on the screen placed on the upper desk. So they could not see the stimulated hand. To mask sound from vibration stimulation, they wore earplugs and head phones from which pink noise (˜60 Hz) was presented continuously throughout the experiment. Stimulus presentation and data collection were implemented by computer programs designed with Matlab and Psychophysics Toolbox extensions [42,43].

In Experiment 1A, participants made an unspeeded, two-alternative
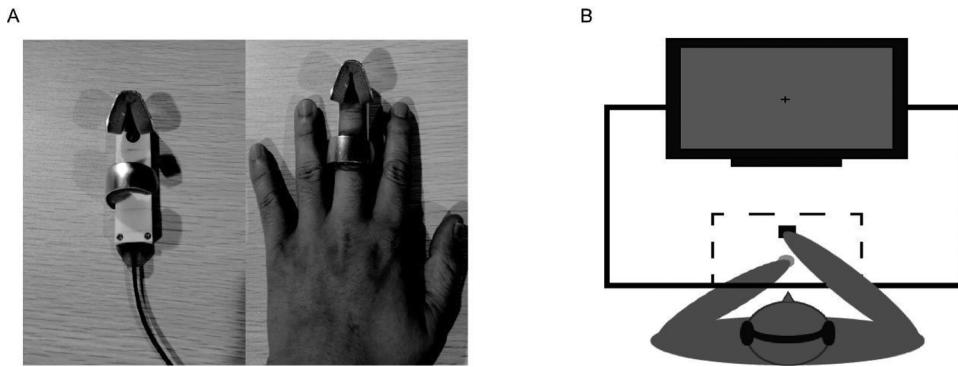
Fig. 1. Experimental setup of Experiment 1. (A) The probe was located in a hole in one end of the rectangular machined ceramic case. Participants placed their middle finger against the case and touched the flat surface of the probe with their fingertip, which was fixed by the finger rest. (B) Participants sat in front of two table tops with one under the other during the experiment. The stimulated hand was supported by the lower desk (indicated by the dash line) and participants used the other hand placed on the upper desk for issuing responses. During the experiment, participants kept their eyes on the fixation on the screen placed on the upper desk.

forced-choice (2AFC) response to determine whether the test duration was shorter or longer relative to the mean of the test durations (i.e., the internal mean, 322 ms). Using their stimulation-free hand, participants pressed one of the two keyboard buttons (counterbalanced across participants) to issue their responses. With the method of single stimuli, we did not provide an explicit reference standard; instead, participants completed a training session to establish the internal mean. During the training session, participants classified each test duration (see the adaptation block) as shorter or longer and then received feedback (the word "correct" or "incorrect" presented on the screen and lasting 500 ms). For example, when the test duration was shorter (longer) than the internal mean and participants classified it as shorter (longer), the feedback was "correct", otherwise the feedback was "incorrect". After 35 training trials, they received a formal test with 140 pre-adaptation test trials with feedback. The baseline (BA) performance was established in the pre-adaptation test.

Participants then performed the adaptation test. There were four adaptation blocks in Experiment 1A. In each adaptation block, participants were exposed to an adaptation phase and a test phase (Fig. 2). During the adaptation phase, an adapting tactile stimulus with a brief duration (160 or 640 ms) was repeatedly presented 100 times, with an inter-stimulus interval (ISI) of 500–1000 ms. After this initial adaptation phase and a 2000-ms pause, a test phase followed. In the test phase, the same adapting stimulus was repeated 4 times firstly ("top-up"). Then, a test stimulus was presented after an ISI of 500–1000 ms. The test tactile stimulus had one of the durations which varied in seven logarithmic steps from 237–421 ms [25]. Those durations were presented randomly but counterbalanced. Once the test stimulus had disappeared, participants classified the test duration as shorter or longer than the internal mean established before the adaptation test. Throughout the block, there was a fixation on the screen. The color of the fixation was black, except that the fixation turned red during the 2000-ms pause between the adaptation phase and the test phase, to

signal the transition between the two phases. Four adaptation blocks were implemented with two adaptation conditions: "adapt to short duration" (AS, 160 ms) and "adapt to long duration" (AL, 640 ms). Thus, for each adaptation condition, participants completed two blocks of 70 test trials with 10 trials for each of the test durations. Both the order of trials in a given block and the order of blocks were randomized. Participants took a break for at least two minutes between blocks.

The procedure of Experiment 1B was similar to that of Experiment 1A, except for the test durations and the method of response. Specifically, participants had to reproduce test duration of either 320 ms (80 %), 160 ms (10%) or 640 ms (10 %) after adaptation to either a short or long adapting duration (at 160 or 640 ms). The 160- and 640-ms test durations served as catch trials to prevent repetitive pressings. Participants held one key to reproduce the test durations, using the index finger of the stimulation-free hand. Before the adaptation blocks, participants were familiarized with the duration reproduction task, by practicing 30 trials without adaptation. They were given immediate feedback on the direction and magnitude of the reproduction error. And then participants completed 70 pre-adaptation test trials (without feedback) as BA condition. There were two adaptation blocks in Experiment 1B, corresponding to two adaptation conditions: AS (160 ms) and AL (640 ms). Thus, for each adaptation condition, participants completed one block of 70 trials with 56 trials for the test duration of 320 ms.

Experiment 1C was similar to Experiment 1B except that there were seven adaptation blocks, each corresponding to one of the seven adapting durations: 40, 80, 160, 320, 640, 1280, 2560 ms. We defined the BA as the average of the mean reproduction durations in two no adaptation blocks (one before and the other after the adaptation blocks). There were 30 trials, with 24 trials for the test duration of 320 ms for each adaptation block and each no adaptation block.
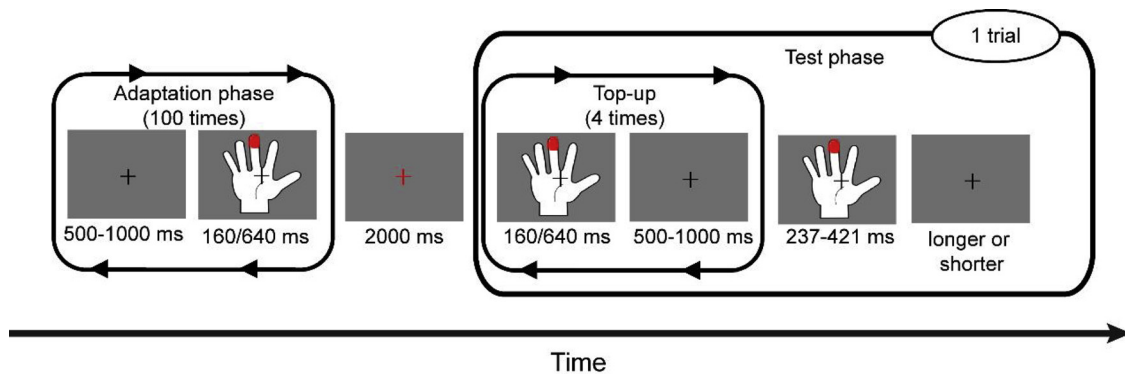
Fig. 2. Schematic description of an adaptation block in Experiment 1A. The adapting and test tactile stimuli were presented on the middle fingertip. Participants were instructed to keep eyes on the fixation of screen and pay attention to each tactile stimulus. Using the method of single stimuli, participants judged whether the test duration was shorter or longer than the internal mean.
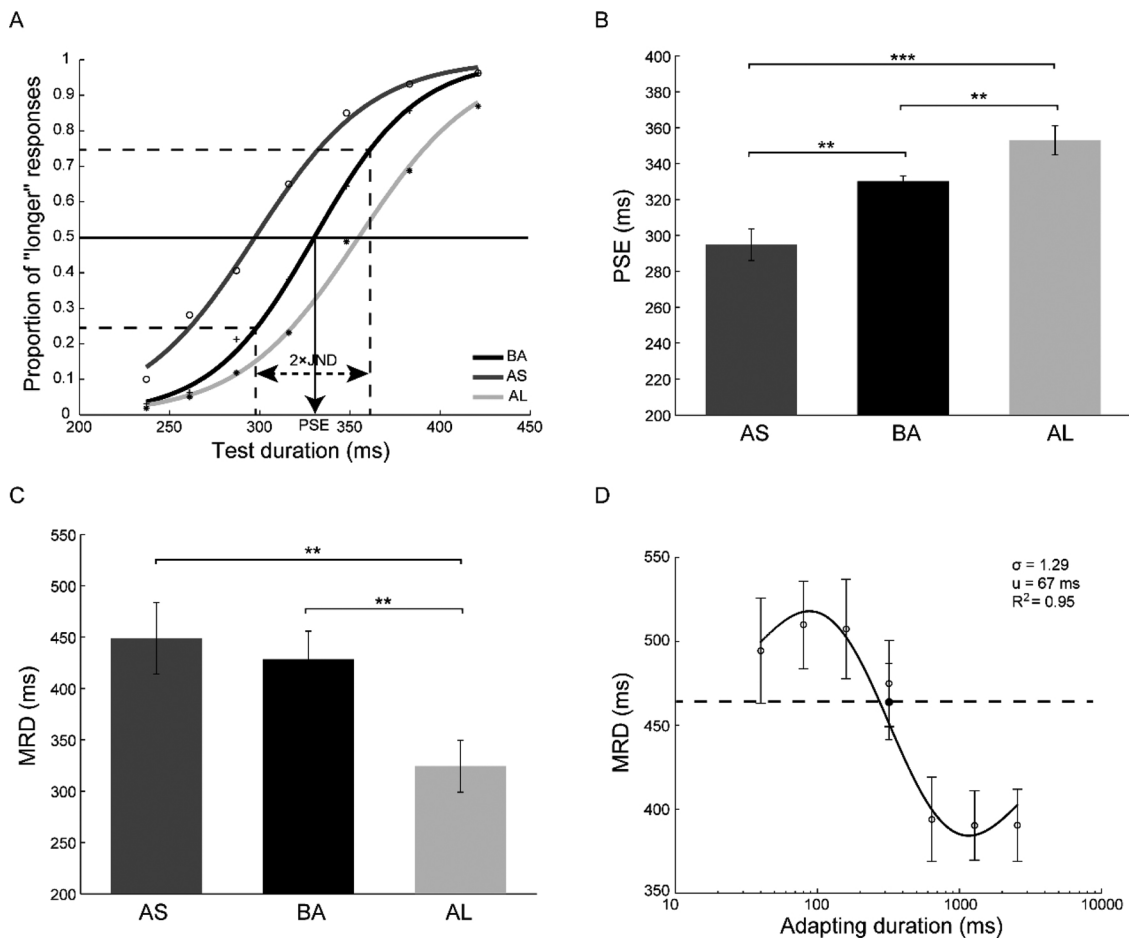
Fig. 3. Results of Experiment 1. (A) Psychometric functions for Experiment 1A. The proportion of "longer" responses to the test stimuli was plotted as a function of test duration in the three adaptation conditions (averaged across eight participants, BA: baseline without adaptation, AS: adapt to short duration, AL: adapt to long duration). Take the BA condition as an example, the PSE was corresponding to the 50% response level on the psychometric function (single-headed arrow) and the JND was corresponding to half the interquartile range of the psychometric function (double-headed arrow). (B) PSEs in the three conditions of Experiment 1A. (C) The MRDs in the three conditions of Experiment 1B. (D) The MRDs following adaptation to the tactile stimuli with durations of 40, 80, 160, 320, 640, 1280, 2560 ms (the circle symbols) and without adaptation (the disk symbol and the dash line). Data were fitted with the first derivative of a Gaussian: u, half amplitude of the function denoting the magnitude of the aftereffect, and σ (in log units), standard deviation of the function denoting the temporal tuning of the aftereffect. Error bars show standard errors. *** $p < 0.001$, ** $p < 0.01$.

2.1.3. Data analysis

In Experiment 1A, data for each condition were analyzed by calculating the point of subjective equality (PSE) at which participants were equally likely to classify the test duration as shorter or longer. In order to calculate the PSE, the proportion of "longer" responses for each condition was plotted as a function of test duration and was fitted with the binomial logit function (Fig. 3A). In addition, the just noticeable difference (JND, half the interquartile range of the psychometric function) was used to measure the temporal discrimination sensitivity. In Experiments 1B and C, only the reproduction durations for the 320-ms test stimuli were analyzed. The reproduced durations for the 320-ms tests, which were shorter than 100 ms or longer than 1000 ms, were treated as outliers and removed. Then, those in the remaining reproduction durations that were beyond three standard deviations from each participant's mean reproduction duration (MRD) in a block were discarded. With this criteria, 0.1% of all the trials in Experiment 1B and 0.97% of all the trials in Experiment 1C were not included for further analysis.

2.2. Results and discussion

In Experiment 1A, we used a repeated-measures analysis of variance (ANOVA), with three levels of adaptation (BA, AS, AL) as the within-subject factor, to analyze the PSEs. The analysis revealed a significant main effect of adaptation ($F(2, 14) = 25.559$, $p < 0.001$, $\eta_p^2 = 0.785$). The PSE was larger in the AL condition (M =353.0 ms, SEM =8.0 ms) than those in the BA (M =330.2 ms, SEM =3.0 ms, $p = 0.008$, Cohen's $d = 1.288$) and AS (M =294.8 ms, SEM =8.8 ms, $p < 0.001$, Cohen's $d = 2.241$) conditions. The PSE in the AS condition was smaller than that in the BA condition ($p = 0.005$, Cohen's $d = -1.413$) (Fig. 3B). The results demonstrated a clear repulsive tactile duration aftereffect. Moreover, a repeated-measures ANOVA showed that the main effect of adaptation on the JND was not significant ($F(1.199, 8.390) = 0.539$, $p = 0.514$, $\eta_p^2 = 0.071$). It suggests tactile duration adaptation doesn't modulate participants' temporal discrimination sensitivities.

Results of Experiment 1B are shown in Fig. 3C. A repeated-measures ANOVA showed that the main effect of adaptation was significant ($F(2,14) = 14.203$, $p < 0.001$, $\eta_p^2 = 0.670$). That is, the MRD was significantly shorter in the AL condition (M =324.3 ms, SEM =25.4 ms) than that in the BA condition (M =428.5 ms, SEM =27.3 ms, $p = 0.001$, Cohen's $d = -1.815$) as well as than that in the AS condition (M =449.1 ms, SEM =34.8 ms, $p = 0.001$, Cohen's $d = -2.011$). However, there was no significant MRD difference between the AS and BA conditions ($p = 0.536$, Cohen's $d = 0.230$). Nonetheless, the MRDs differed between the AS and AL conditions, providing further evidence for the duration aftereffect in the tactile modality.

In Experiment 1C, we found that the adaptation effect was modulated by the discrepancy between the adapting and test durations (Fig. 3D). This was particularly obvious for the shorter adapting durations. Specifically, compared to the BA condition, participants didn't significantly overestimate the test duration following a much shorter adapting duration ($t(9) = 1.231$, $p = 0.250$, Cohen's $d = 0.389$); but they significantly overestimated the test duration following a moderately shorter adapting duration ($t(9) = 3.326$, $p = 0.009$, Cohen's $d = 1.052$). They slightly overestimated the test duration after a slightly shorter adapting duration ($t(9) = 1.895$, $p = 0.091$, Cohen's $d = 0.599$). In contrast, relative to the BA condition, the MRDs after adaptation to all the longer durations were significantly shorter (all $t(9) < -3.311$, $p < 0.01$, Cohen's $d < -1.047$). Moreover, there was no significant MRD difference between the 320-ms adaptation condition and the BA condition ($t(9) = 0.796$, $p = 0.447$, Cohen's $d = 0.252$). Therefore, when the durations of the adapting and test stimuli were the same, the duration aftereffect vanished. Finally, the MRDs in the seven adaptation conditions were well fitted with the first derivative of a Gaussian ($R^2 = 0.95$) [25]. This result pattern suggests the tactile duration aftereffect is duration-tuned.

In Experiments 1B and C, we found that participants tended to overestimate the test durations irrespective of adaptation conditions. These results were consistent with previoius studies, which showed the overestimation of shorter duration with duration reproduction method [44–46]. It suggests that the duration reproduction method, in which participants reproduce the test durations by holding down a button press, is sensitive to motor noise that could result in greater overestimation and larger variance especially for short durations [47]. This could explain why we observed the grossly overestimation and large individual difference in the reproduction durations in Experiments 1B and C. Furthermore, unlike the visual and auditory duraiton aftereffects [25], both Experiments 1B and C showed an asymmetrical adaptation effect (Fig. 3C, D and S1). For example, significant tactile duration aftereffect was observed after adaptation to a slightly longer duration (640 ms), but not to a slightly shorter duration (160 ms). Given that the asymmetrical effect was not observed in Experiment 1A, it might be explained by the method adopted. Our data showed that the variance (SD) of the reproduced durations was significant larger in the BA condition than that in the adaptation condition (Experiemnt 1B: 93.8 ms vs. 69.8 ms, $t(7) = 3.094$, $p = 0.017$, Cohen's $d = 1.094$; Experiemnt 1C: 79.8 ms vs. 65.2 ms, $t(9) = 3.407$, $p = 0.008$, Cohen's $d = 1.077$). This suggests that duration adaptation affected the precision of duration reproduction. It is possible that the adapting duration repeatedly presented in the adaptation conditions would be helpful to establish stable duration representation. This would contribute to the precise duration reproduction. In contrast, in the BA without adaptation, reproduced duration would be more variable due to no stable duration representation to reference. Given that the greater overestimation and larger variance for short duration are usually concomitant when using the duration reproduction method, we speculated that duration adaptation might also reduce the overestimation induced by the reproduction method itself. That is, the overestimation from the reproduction method was greater in the BA condition than that in the adaptation condition. Thus, when comparing the MRDs between BA and AS conditions, we would found the MRD difference became smaller. This could have reduced the aftereffect magnitudes after adaptation to shorter durations.

We compared the values of σ and μ in the present study with those in the study of Heron et al. [25]. We found in the tactile duration aftereffect the σ (1.29) is larger than that (1.26) in the auditory duration aftereffect and smaller than that (1.44) in the visual duration aftereffect. However, we also found the μ (67 ms) in the tactile duration aftereffect is obvious larger than those in auditory (27 ms) and visual (32 ms) duration aftereffects. It seems to suggest that the magnitude of tactile duration aftereffect is larger than those of auditory and visual duration aftereffects. However, note that the duration discrimination

task was used in the study of Heron et al. [25], while the duration reproduction task was used in the present study. It is possible that the differences are due to the different tasks. Therefore, future studies systematically studying the duration aftereffects in different modalities with same task are needed.

The results of Experiment 1 showed that the tactile duration aftereffect was robust, bidirectional, and tuned around the adapting duration, suggesting a similar duration adaptation mechanism in the somatosensory system as those in the visual and auditory domains [25,27].

3. Experiments 2A and B: Tactile duration aftereffect is modality specific

Although Experiment 1 has established the existence of the tactile duration aftereffect, the processing level for this tactile aftereffect is still unclear. According to previous studies, auditory and tactile perceptions can interplay in a variety of behavioral contexts [48–51]. It has been shown that processing of auditory and tactile signals shares some common neural substrates [52,53]. For example, studies have found a supramodal role of the STG in tactile duration perception [5,6], indicating that duration adaptations in audition and touch may arise from an amodal timing mechanism. In Experiment 2, we tested the transferability of the tactile duration aftereffect between touch and audition. If a common mechanism underlies both the tactile and auditory duration aftereffects, we expect that the aftereffect could not only transfer between the two modalities, but also would vanish following simultaneous adaptation to two opposite durations in the two modalities.

3.1. Methods

3.1.1. Participants
Ten and eight new volunteers participated in Experiments 2A (6 females, mean age: 21.90 ± 2.18 years) and B (3 females, mean age: 22.50 ± 3.38 years), respectively.

3.1.2. Stimuli and procedures
In Experiment 2, both tactile and auditory stimuli were used as adapting and test stimuli. The tactile stimulus was the same as that used in Experiment 1, which was presented on the middle fingertip of the left or right hand (counterbalanced across participants). The auditory stimulus was a 150 Hz sine-waveform pure tone, with a 10-ms cosine ramp both at its onset and offset, which was presented via headphone. The rectangular case with the probe was placed into a foam groove to attenuate the sound produced by the tactile vibration. A finger rest was also used to fix the contact position between the finger and the probe. The intensities of tactile and auditory stimuli were matched based on participants' subjective report.

The procedure of Experiment 2A was similar to that of Experiment 1B (Fig. 4, left). There was only one adapting stimulus (tactile or auditory stimulus) and two test stimuli (tactile and auditory stimuli) in each adaptation block. The fixation also turned red after the last top-up stimulus to alert participants about the upcoming tactile or auditory test stimulus. Then, it turned black after the test stimulus disappeared, to prompt the participants to reproduce the duration of the test stimulus. There were four adaptation blocks in Experiment 2A, corresponding to four adaptation conditions: "adapt to short tactile stimulus" (AST, 160 ms), "adapt to short auditory stimulus (ASA, 160 ms)", "adapt to long tactile stimulus (ALT, 640 ms)" and "adapt to long auditory stimulus (ALA, 640 ms)". Thus, for each adaptation condition, participants completed one block of 60 trials with 24 trials for each of the 320-ms tactile and auditory test stimuli.

Similar to Experiment 2A, in Experiment 2B (Fig. 4, right) both tactile and auditory stimuli were included in the adapting and test stimuli. However, we adopted a simultaneous adaptation paradigm. That is, in the adaptation phase and top-up period, the tactile and
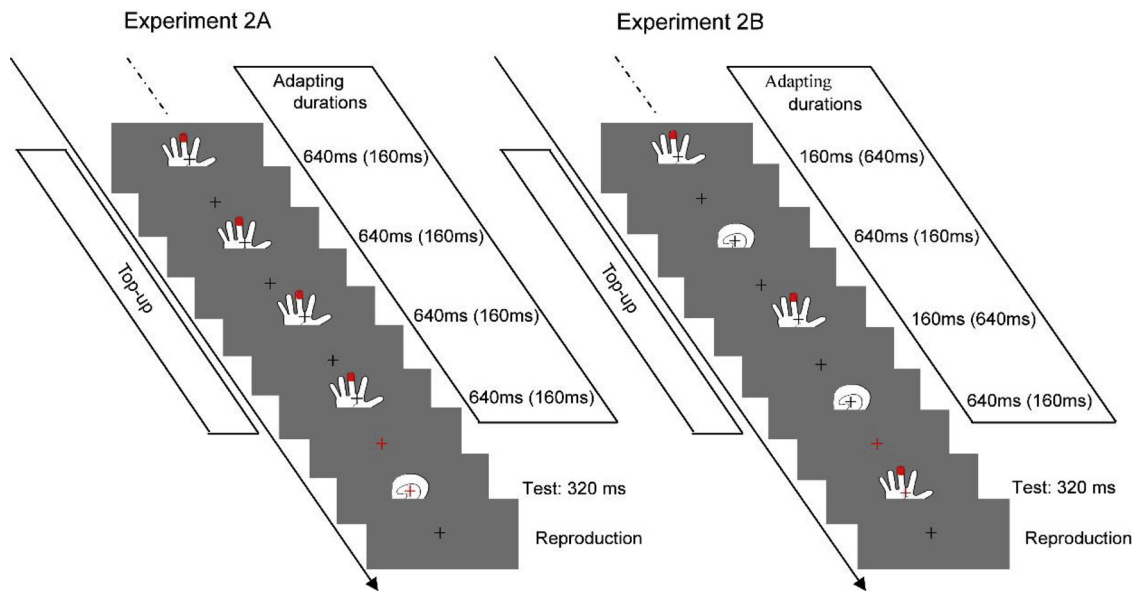
Fig. 4. Schematic descriptions of a top-up-test trial sequence in Experiments 2A (left) and B (right). Adapting and test stimuli included both tactile and auditory stimuli. After adaptation phase, each top-up-test trial began with a top-up period, in which four top-up stimuli from the preceding adaptation phase were presented. After the top-up period, a test stimulus was presented, and participants were asked to reproduce the duration of the test.

auditory adapting stimuli were presented alternately with 160/640 ms or 640/160 ms. There were 50 paired tactile-auditory stimuli in the adaption phase and two paired stimuli in each top-up period. Thus, the two adaptation conditions in Experiment 2B were "adapt to short (160 ms) tactile stimulus and long (640 ms) auditory stimulus" (STLA) and "adapt to long (640 ms) tactile stimulus and short (160 ms) auditory stimulus" (LTSA). For each adaptation condition, participants completed two blocks. And each block had 60 trials with 24 trials for each of the 320-ms tactile and auditory test stimuli. The starting stimulus (tactile stimulus first or auditory stimulus first) in the adaptation phase was counterbalanced across the four blocks.

3.1.3. Data analysis

Adopting the same criteria as those in Experiment 1B, 1.67% of all the trials in Experiment 2A and 0.92% of all the trials in Experiment 2B were discarded. To simplify the computation, the aftereffect magnitude (AM) was defined as the arithmetic difference between MRDs after short and long adaptations for each test modality: AM = (MRD$_{adapt\ S}$) − (MRD$_{adapt\ L}$). That is, in Experiment 2A, when the adapted modality was tactile (auditory), the AM in the adapted modality was the arithmetic difference between the MRDs with the tactile (auditory) test stimulus in the AST (ASA) and ALT (ALA) conditions. The AM in the unadapted modality was the arithmetic difference between the MRDs with the auditory (tactile) test stimulus in the AST (ASA) and ALT (ALA) conditions. In Experiment 2B, the AM in the tactile modality was the arithmetic difference between the MRDs with the tactile test stimulus in the STLA and LTSA conditions. In the auditory modality, the AM was the arithmetic difference between the MRDs with the auditory test stimulus in the LTSA and STLA conditions.

3.2. Results and discussion

In Experiment 2A, one-sample two-tailed t-tests showed that the AMs were significantly larger than zero in the adapted modalities (touch: M = 105.2 ms, SEM = 21.8 ms, $t(9)$ = 4.833, p = 0.001, Cohen's d = 1.528; audition: M = 99.0 ms, SEM = 33.6 ms, t (9) = 2.942, p = 0.016, Cohen's d = 0.930), but not in the unadapted modalities (audition: M = 2.8 ms, SEM = 32.1 ms, $t(9)$ = 0.089, p = 0.931, Cohen's d = 0.028; touch: M = -0.2 ms, SEM = 21.8 ms, $t(9)$ = -0.008, p = 0.994, Cohen's d = -0.002) (Fig. 5A). These results showed

that the duration aftereffect did not transfer to the unadapted modality. This finding was further supported by a 2 (adaptation modality: touch, audition) × 2 (test modality: adapted, unadapted) repeated-measures ANOVA on the AMs. The main effect of test modality was significant (F (1, 9) = 30.064, p < 0.001, η_p^2 = 0.770) — the AM in the adapted modality was significantly larger than that in the unadapted modality. The main effect of adaptation modality ($F(1, 9)$ = 0.990, p = 0.346, η_p^2 = 0.099) and the interaction effect ($F(1, 9)$ = 0.001, p = 0.974, η_p^2 < 0.001) were not significant.

One sample two-tailed t-tests were also performed with the AMs in Experiment 2B. The results showed that the AMs in both touch (M = 71.8 ms, SEM = 17.7 ms, $t(7)$ = 4.059, p = 0.005, Cohen's d = 1.435) and audition (M = 86.5 ms, SEM = 15.8 ms, $t(7)$ = 5.486, p = 0.001, Cohen's d = 1.940) were significantly larger than zero (Fig. 5B), even when participants adapted to two modalities in opposite directions simultaneously. Furthermore, paired two-tailed t-tests showed that there was no significant difference in AM between touch and audition ($t(7)$ = -0.554, p = 0.597, Cohen's d = -0.196). The results suggest that independent duration adaptation mechanisms operate simultaneously in the tactile and auditory modalities, providing further evidence for the modality specificity of the duration aftereffect.

Experiment 2 revealed that the duration aftereffect did not transfer across touch and audition, and operated in the tactile and auditory modalities simultaneously. The results are consistent with previous studies showing the modality-specific visual and auditory duration aftereffects [25,27,28]. They suggest that the duration adaptation mechanisms in the tactile and auditory modalities are relatively independent. Fundamentally, it remains debated whether the brain uses a centralised and supramodal sensory timing mechanism, encoding time across sensory systems; or rather distributed timing mechanisms, with multiple "internal clocks" overlooking each individual sense [3,54–56]. The results showed the adaptation effects were limited to the adapted modality, supporting the distributed sensory timing hypothesis.

4. Experiment 3: Tactile duration aftereffect is organized within a somatotopic framework

Experiment 3 investigated the topographic generalization of the aftereffect. If the tactile duration aftereffect is specific to the adapted finger or could generalize to fingers dictated by the topographic
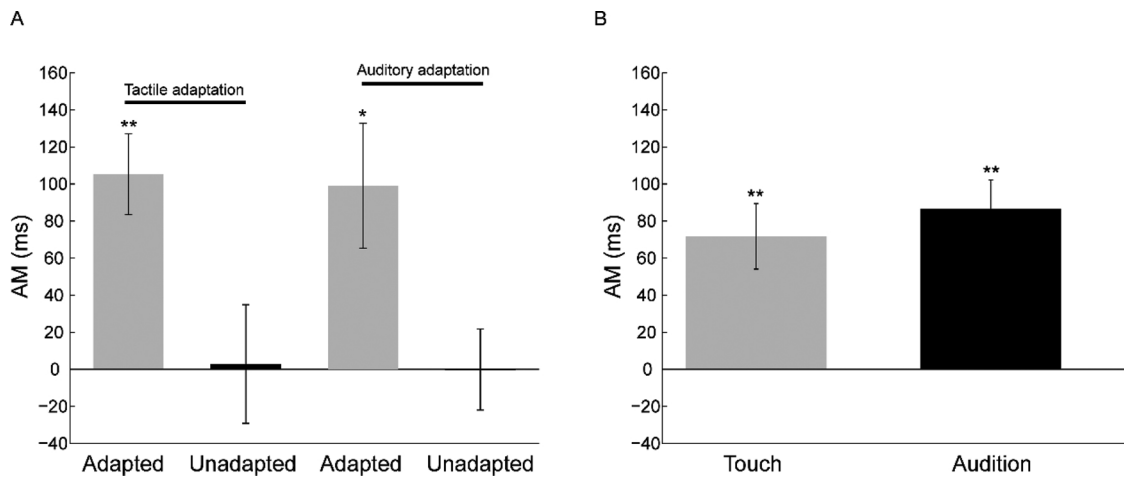
Fig. 5. Results of Experiment 2. (A) The AMs obtained from the four adaptation/test conditions in Experiment 2A. In the adapted conditions, the adapting and test stimuli were presented in the same modality, while in the unadapted conditions, the adapting and test stimuli were presented in different modalities. (B) The AMs of touch and audition in Experiment 2B. Error bars show standard errors. ** $p < 0.01$, * $p < 0.05$.

distance, this aftereffect might originate at the stage of somatotopic processing. However, a possible spread of the adaptation effect across all fingers regardless of the topographic distance, would indicate higher-level mechanisms in the somatosensory system. In Experiment 3, we investigated the topographic generalization by applying short and long duration adaptations to two fingers simultaneously. If adaptation is specific to the adapted finger, we would expect that the corresponding aftereffect is confined to the finger that had been adapted to a specific duration. In contrast, if adaptation could generalize across fingers, we would expect no difference in perceived duration between the two adapted fingers.

4.1. Methods

4.1.1. Participants

Thirty new volunteers participated in Experiment 3 (17 females, mean age: 21.63 ± 2.65 years).

4.1.2. Stimuli and procedure

Similar to Experiment 1, only vibrotactile stimuli were used in Experiment 3. We adopted the simultaneous adaptation paradigm similar to the study of Calzolari et al. [18]. During the adaptation phase, participants were touched in alternation on two different fingertips with different durations (160 or 640 ms) for 50 pairs. After a 2000-ms pause signaling the beginning of the test phase, two pairs of top-up stimuli identical to those presented in the preceding adaptation phase, were given. Subsequently, two tactile test stimuli were presented sequentially, one to each adapted fingertip. The durations of the two test stimuli were from one of the five duration pairs: 400/256, 320/256, 320/320, 256/320, 256/400 ms. Once the second test stimulus had disappeared, participants made an unspeeded, 2AFC judgment to indicate which stimulus (the first or second) lasted longer. We asked observers to report according to the order (first or second) rather than the location (left or right) of the stimuli, to avoid any potential response bias based on stimulus locations. Participants made their response by pressing one of the two switches (counterbalanced across participants) of a foot pedal. The foot pedal was located in the middle of participants' two feet.

According to which two fingertips were adapted, participants were evenly split into three groups: adjacent group, nonadjacent group and homologous group (Fig. 6). In the adjacent group, the tactile stimuli were presented on the index and middle fingertips of one hand (left or right, counterbalanced across participants). In the nonadjacent group, the tactile stimuli were presented on the index and ring

fingertips of one hand (left or right hand, counterbalanced across participants). In the homologous group, the tactile stimuli were presented on the homologous fingertips (middle or index fingertip, counterbalanced across participants) of the left and right hands. In each group, the physical distance between the two adapted fingertips was kept about 7 cm. For each group, there were four adaptation blocks, two blocks for each of two adaptation conditions: "adapt to short duration (160 ms) on the left fingertip and long duration (640 ms) on the right fingertip" (SLLR) and "adapt to long duration (640 ms) on the left fingertip and short duration (160 ms) on the right fingertip" (LLSR). A block consisted of 50 trials with 10 trials for each test pair. In addition, the starting stimulus (left stimulus first or right stimulus first) in the adaptation phase was counterbalanced across blocks.

4.1.3. Data analysis

The proportion of "right longer" responses to the test stimuli was fitted with a binomial logit function of the ratio between the test durations for the right and left fingertips (Fig. 7A). Then, the PSE and JND in each condition were calculated. Here, if the PSE is larger than 1, it means that participants were prone to underestimate the duration for the right fingertip. The AM was defined as the arithmetic difference in PSE between the SLLR and LLSR conditions.

4.2. Results and discussion

In Experiment 3, one sample two tailed t-tests showed that the AM in the adjacent group was not significantly different from zero (M = 0.06, SEM = 0.06, $t(9) = 1.063$, $p = 0.315$, Cohen's $d = 0.336$), but the AMs in the nonadjacent group (M = 0.08, SEM = 0.03, $t(9) = 2.964$, $p = 0.016$, Cohen's $d = 0.937$) and the homologous group (M = 0.18, SEM = 0.03, $t(9) = 6.964$, $p < 0.001$, Cohen's $d = 2.202$) were significantly larger than zero. These results suggest that the transfer of the tactile duration aftereffect depends on the topographic distance between fingers. Furthermore, one-way between-subjects ANOVA was performed on the AMs. The main effect of group was marginally significant ($F(2, 27) = 2.605$, $p = 0.092$, $\eta_p^2 = 0.162$). Specifically, the AM in the homologous group was significantly larger than that in the adjacent group ($p = 0.040$, Cohen's $d = 0.865$), and was marginally significantly larger than that in the nonadjacent group ($p = 0.096$, Cohen's $d = 1.122$). There was no significant AM difference between the nonadjacent group and the adjacent group ($p = 0.671$, Cohen's $d = 0.169$) (Fig. 7B). It suggests there may be partial transfer of the aftereffect between the nonadjacent fingers. We also performed a 3 (group: adjacent group, nonadjacent group, homologous
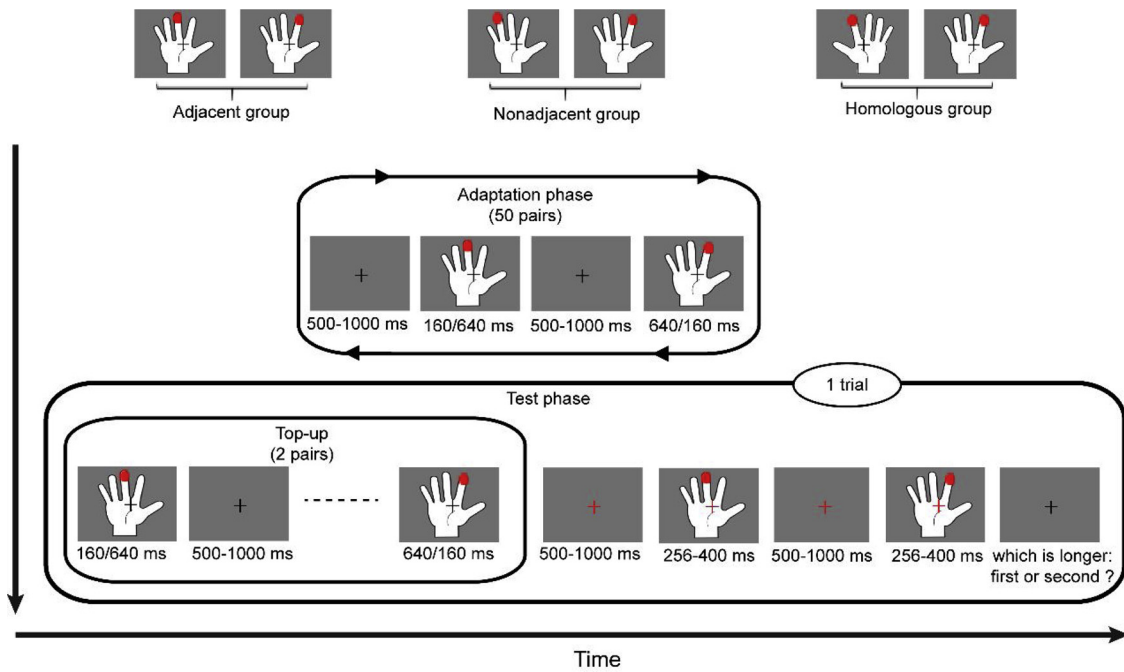
Fig. 6. Schematic description of the experimental procedure in Experiment 3. According to the adapted fingertips, participants were evenly split into three groups: adjacent group, nonadjacent group and homologous group. Take the adjacent group as an example, 50 pairs of the adapting tactile stimuli were presented alternately on the middle and index fingertips with different durations (160 or 640 ms) during the adaptation phase. In the test phase, after two pairs of top-up stimuli, a test pair were presented on the adapted fingertips successively. Participants were asked to judge which stimulus in the pair (the first or second) lasted longer.

group) × 2 (adaptation: SLLR, LLSR) repeated-measures ANOVA (mixed-subject design with group as the between-subjects factor) on the JNDs. The results showed that the main effect of group was not significant ($F(2, 27) = 1.805$, $p = 0.184$, $\eta_p^2 = 0.118$); the main effect of adaptation was not significant ($F(1, 27) = 2.577$, $p = 0.120$, $\eta_p^2 = 0.087$); their interaction was not significant ($F(2, 27) = 0.297$, $p = 0.745$, $\eta_p^2 = 0.022$). The results suggest the temporal discrimination sensitivity based on the finger location is not significantly affected by the topographic distance of the finger.

Given the somatotopic organization of hand representation in the somatosensory cortex, the topographic distance in the cortex is variable for different finger pairs. Typically, adjacent fingers are represented adjacently, while nonadjacent fingers are represented with a larger distance in S1. We found that the finger specificity effect, as indexed by

the AM, increased with the lengthened topographic distance of the adapted fingers. It suggests that the tactile duration aftereffect is organized within the somatotopic framework and at the somatotopic representation level. This inference is further supported by a control experiment (see *The supplement*). In the control experiment, participants simultaneously adapted to two homologous fingertips with different durations and with crossed hands. The tactile duration aftereffect was replicated. Notably, it was contingent on the finger location defined in the somatotopic frame, rather than in the spatiotopic frame. In sum, these results suggest that the tactile duration aftereffect is very robust and originates at the stage of somatotopic processing.
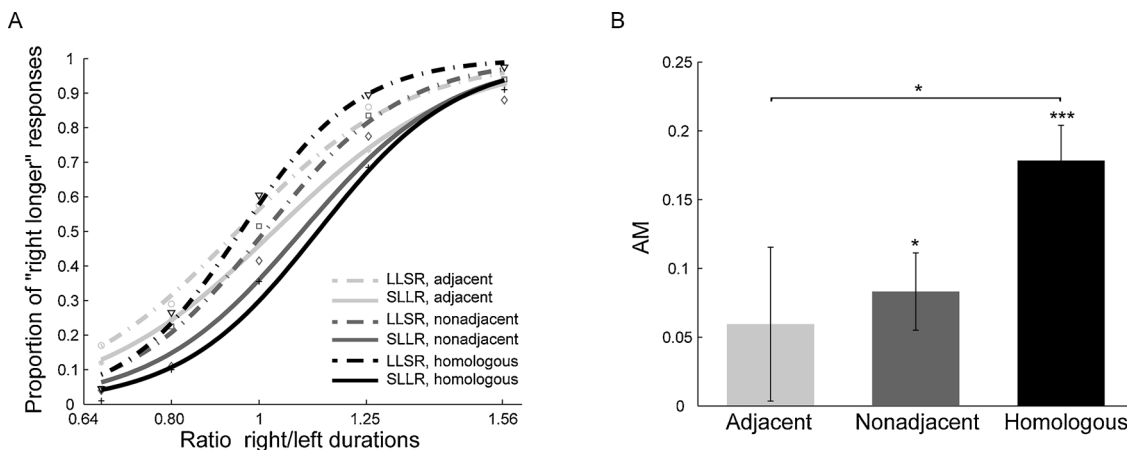
Fig. 7. Results of Experiment 3. (A) Psychometric functions showing the proportion of "right longer" responses to the test stimuli, which was plotted as a function of the ratio between the test durations for the right and left fingertips in each group (averaged across ten participants, light gray line: adjacent group, gray line: nonadjacent group, dark line: homologous group) and each adaptation condition (dash line: LLSR, adapt to long duration on the left fingertip and short duration on the right fingertip; solid line: SLLR, adapt to short duration on the left fingertip and long duration on the right fingertip). (B) The AMs each of which defined as the arithmetic difference in PSE between the SLLR and LLSR conditions. Error bars show standard errors. *** $p < 0.001$, * $p < 0.05$.

5. General discussion

In the present study, we explored whether and how duration adaptation in the tactile modality affects the perception of subsequent durations. Our results demonstrated the repulsive tactile duration aftereffect with passive touch. After prolonged adaptation to a shorter tactile duration, participants perceived subsequent medium tactile durations as being longer. When the adapting tactile duration was longer, the same subsequent medium tactile durations were perceived shorter. The tactile duration aftereffect was tuned around the adapting duration and was modality specific. More importantly, we also found that the tactile duration aftereffect was organized within a somatotopic framework. Our results thus provide clear evidence that the sub-second tactile duration is susceptible to sensory adaptation, and suggest the somatotopic areas play an essential role in sub-second tactile duration perception.

Aftereffects relevant to tactile temporal processing have been studied. For example, previous studies examined the temporal frequency adaptation, such as the temporal-compression aftereffect [57] and the bidirectional rate aftereffect [58]. In the present study, we investigated the temporal duration processing directly and verified the duration aftereffect in the tactile modality, which is analogous to the duration aftereffects in vision and audition [25,27,28]. Recently, the channel-based model has been used to explain the duration aftereffect [25]. According to this model, our brain is endowed with duration detectors, each of which responds selectively to a narrow range of durations centered on its preferred duration. Thus, adaptation could selectively diminish the responses of relevant detectors, thus altering the relative activation of these detectors and leading to the duration aftereffect. According to this model, the tactile duration aftereffect implies the existence of the duration-selective channels in the tactile modality. With that said, we should be cautious. Although the duration-tuned neurons for visual [59–62] or auditory [63–65] durations have been widely found, there is little neurophysiologic evidence supporting the duration-tuned neurons for tactile durations.

Previous studies found that the visual temporal-compression aftereffect induced by adaptation to 20 Hz oscillating motion is spatially selective in real-world (spatiotopic) coordinates [66,67]. At first glance it might be in contrast with the finger selectivity of tactile duration aftereffect, which was organized in the anatomical (somatotopic) coordinate system. Indeed, the temporal-compression aftereffect is different from the duration aftereffect. In temporal-compression aftereffect, we do not exploit any repeated presentation of duration as adaptors and underestimate the perceived duration. In the duration aftereffect, we use the recent experience (adaption to the duration itself) and either overestimate or underestimate the target duration in a bidirectional yet repulsive manner. Thus, these two aftereffects may originate from different neural mechanisms. However, our findings were also different to the studies on visual duration aftereffect in several aspects. For example, studies have shown that the visual duration aftereffect was position invariant [30,31], and spread into a region proportional to the size of the adapting stimulus [68]. These suggest the visual duration aftereffect might originate at later stages of visual processing. Given that both previous studies [25,28] and the results in Experiment 2 have suggested the modality-specific mechanism for duration aftereffect, we speculate that the duration adaptations in vision and touch may mobilize different stages of sensory processing.

The observed tactile duration aftereffect could result from adaptation in somatotopic areas. This inference is supported by the following evidence. *First*, we observed the modality-specific tactile and auditory duration aftereffects (Experiment 2). This result suggests that different neural mechanisms are involved in tactile and auditory duration adaptations. The modality-specific adaptation mechanism rules out the STG as the candidate cortical site responsible for the tactile duration aftereffect. *Second*, we further found that the tactile duration aftereffect was organized within a somatotopic framework (Experiment 3 and

supplement). Specifically, the transfer between adjacent fingers suggests a cortical adaptation mechanism for the tactile duration aftereffect. However, the finger-specific adaptation mechanism in the nonadjacent group, especially in the homologous group, suggests the early somatosensory cortex with the somatotopic organization of the hands representation contributes to the duration aftereffect.

The somatotopic organized tactile duration aftereffect is consistent with a previous study by Kuroki et al. [69]. In their study, they manipulated the somatotopic and spatiotopic distance of fingers to probe the level of tactile temporal processing. Their results showed that the temporal judgments for simultaneity, temporal order, apparent motion and inter-stimulus interval were significantly affected by the somatotopic distance, but only slightly affected by the spatiotopic distance, suggesting the somatotopic dominance in tactile temporal processing. In the present study, we found that the tactile duration aftereffect was contingent on the somatotopic, but not spatiotopic, representation of fingers. Our finding offers further evidence that temporal processing depends on the somatotopic processing. These characteristics are similar to the tactile distance aftereffect, which is defined in a skin-centered, rather than an external, reference frame [18].

Both S1 and the secondary somatosensory cortex (S2) show the somatotopic organization of body representation [70]. It has been showed that the receptive fields (RFs) of neurons in the S1 and S2 exhibit a hierarchical organization [71]. Neurons in S1 have relatively small RFs that are more restricted to the contralateral side of the body, while neurons in S2 receive inputs from S1 and have larger and more complex, even bilateral, RFs [70,72]. Since S2 integrates information from both hands (or hemispheres), the finger specificity of the aftereffect in the homologous group suggests that the neural locus of the duration adaptation may be in S1, rather than S2. Indeed, the majority of S1 neurons have RFs including more than one finger. For example, several functional magnetic resonance imaging (fMRI) studies have investigated human finger somatotopy in S1 and found the existence of cortical overlap between adjacent fingers [73–75]. Based on cytoarchitecture and connections, S1 is divided into four areas: Brodmann's area (BA) 3a, 3b, 1 and 2. In our experiments, we used high-frequency (150 Hz) vibrotactile stimuli, which mainly stimulate the fast-adaptive receptors. Neuronal signals from the fast-adaptive receptors are received by BA 3b through the spinal nerves and thalamus. BA 1 receives projections from BA 3b, and BA 2 receives projections from both BA 3b and 1 [70]. The RF size of S1 neurons increases from BA 3b, 1, to 2. It has been suggested the tactile RFs in BA 3b and 1 span adjacent fingers [76,77] and the RFs in BA 2 span adjacent and homologous fingers [78]. Thus, the transfer of the aftereffect between adjacent fingers but not homologous fingers implies that the tactile duration aftereffect is linked with the somatotopic representation in brain areas with smaller RFs, such as BA 1. This hypothesis should be further addressed in future studies with evidence from neuroimaging or cortical recording.

Transcranial magnetic stimulation (TMS) studies have shown that the continuous theta burst stimulation (cTBS) over S1 increased the somatosensory temporal discrimination threshold (STDT) [8,9,79]. STDT is defined as the shortest time interval that is necessary for a pair of tactile stimuli to be perceived as separate. These studies suggest that S1 is involved in the temporal processing of somatosensory information. In line with these studies, our results echoed the important role of S1 in tactile duration perception. However, the present study did not exclude the potential higher-order areas sensitive to tactile duration information. In fact, Nagarajan et al. [80] found that the learning effect on somatosensory interval discrimination generalized completely not only to untrained skin locations on the trained hand, but also to the corresponding skin location on the untrained hand. Furthermore, TMS over S1 impaired the tactile duration discrimination at 60 ms delay after tactile presentation, and TMS over STG also affected tactile temporal processing but at 180 ms delay [6]. Those findings indicate the hierarchy as well as the complexity of tactile duration processing.

6. Conclusion

The present findings demonstrate that duration adaptation bidirectionally modulates the tactile duration perception. The adaptation effect was tuned around the adapting duration, was modality specific and organized within a somatotopic framework. The present study thus provides new insights into the tactile timing mechanism: sub-second tactile duration perception mobilizes the somatotopic processing. In human-machine interaction, the choice of duration is importance for designing and rendering the vibrotactile messages, as it will be hard to perceive with too short vibrations (e.g., less than 100 ms), while the long vibrations (e.g., over 2000 ms) will slow down the rate of information transmission [81]. The current results would benefit the design of vibrotactile messages such as the tactile icons [82]. Understanding the adaptation effect on tactile duration perception gives us an opportunity to manipulate the perceived subjective durations to accommodate various needs.

Conflict of interest

The authors declare no competing financial interests.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.bbr.2019.111954.

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