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RESEARCH NOTE

Tactile motion aftereffects produced by appropriate presentation for mechanoreceptors

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Abstract Tactile motion perception is one of the most important functions for realizing a delicate appreciation of the tactile world. To explore the neural dynamics of motion processing in the brain, the motion adaptation phenomenon can be a useful probe. Tactile motion aftereffects (MAE), however, have not been reported in a reproducible fashion, and the indistinctive outcomes of the previous studies can be ascribed to the non-optimal choice of adapting and testing stimuli. Considering the features of the stimuli used in the studies, the stimuli activated the different mechanoreceptors in the adapting and testing phase. Consequently, we tested tactile MAE using appropriate combinations of adapting and testing stimuli. We used three pins to generate sensation of apparent motion on the finger cushion. They were sequentially vibrated with the frequency of 30 Hz both in adapting and testing phases. It is expected that this procedure ensured stimulation for the same mechanoreceptor (Rapid-Adapting mechanoreceptor) in both the adaptation

and test phases. Using this procedure, we found robust tactile MAEs in the various tactile motions such as the short-distance motion within the fingertip, the long-distance motion from the finger base to the fingertip, and the circular motion on the fingertip. Our development of a protocol that reliably produces tactile MAEs will provide a useful psychophysical probe into the neural mechanisms of tactile motion processing.

Keywords Tactile motion aftereffect · Tactile apparent movement · Vibro-tactile stimulation · Somatosensory coding

Introduction

One way humans explore the external world is through the sense of touch. The fingers are actively moved across the surface of the object, and various kinds of features, such as shape, roughness, and compliance, can be perceived. When the object is slipping out of the hand, its posture can immediately be adjusted thanks to the direction-sensitive mechanism for the tactile motion (e.g., Macefield et al. 1996). The information of the tactile motion between the fingertip and the object should play an important role in realizing the delicate appreciation of the tactile world.

The adaptation phenomenon has been useful to investigate the mechanism of information processing in the brain without imaging or neurophysiology. Especially, human visual perception of motion has been studied by the visual motion adaptation phenomenon. After prolonged observation of a waterfall, an illusory upward motion can be seen in a static environment. This phenomenon is referred to as Motion Aftereffect (MAE) (e.g., Wohlgenuth 1911; Mather et al. 1998). MAE in vision is a robust and rigid

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phenomenon. However, although previous physiological studies indicated the presence of the tactile motion detectors with directional selectivity (e.g., Hyvarinen and Poranen 1978; Constanzo and Gardner 1980), the tactile MAE has not been reported in a reproducible fashion (Thalman 1922; Hollins and Favorov 1994; Lerner and Craig 2002).

Thalman (1922) reported a number of conditions that might be expected to generate tactile MAEs. Since then, little research has been performed on this issue, and the conditions that produce reliable tactile MAE are even presently under discussion. Hollins and Favorov (1994) reported robust tactile MAEs with the use of a rotating metal cylinder, 9 cm in diameter and 10.7 cm in length. After 120 s of stimulation, the participants were instructed to lift their hands up, and the hand was then placed back on a stationary cylinder for 60 s. All five participants reported tactile MAEs in the most parts of the trials. However, in the study by Lerner and Craig (2002), 50 participants performed the replicated experiment, and no MAE was reported in about half of the trials. In addition, negative MAE was only about 10% of perceived MAEs, though one would expect the aftereffects to be in the negative direction, that is, opposite to the direction of adaptation. Lerner and Craig also performed experiments using OPTACON, a reading aid for the blind. Pin array consisted of 12 rows and six columns covered an area of $14.1 \times 11.4 \text{ mm}^2$. Each row of OPTACON was sequentially activated to create tactile motion. After adaptation for 120 s, the participants held their fingers in the air for 60 s. Also in this method, clear negative MAEs were not observed for seventeen participants. Apparently, these previous results indicated that the tactile MAEs were not robust or reproducible phenomenon. However, considering the mechanoreceptors stimulated in their adaptation and test phases, these indistinctive outcomes of the tactile MAEs can be ascribed to the non-optimal choice of adapting and testing stimuli.

Tactile mechanoreceptors can be classified into two categories, slow-adapting mechanoreceptor (SA) and rapid-adapting mechanoreceptor (RA). When a fast rotating cylinder was presented to the palm (Hollins and Favorov 1994; Lerner and Craig 2002), mainly RA would be stimulated, though SA could slightly be activated. A static cylinder, however, which was used as the test stimuli, would activate only SA. As a result, the adapted mechanoreceptor (RA) was not stimulated in the test phase. When the OPTACON was used as the stimulating device (Lerner and Craig 2002), the perceived motion was generated by the successive stimulation with rows of pins. It was reported that the OPTACON array would not activate SA, but RA in a barbiturate-anesthetized monkey study (Gardner and Palmer 1989). In Lerner's experiments, however, the participants held their fingers in midair in the test phase; thus no mechanoreceptor was activated after the adaptation phase. Considering these statuses of the mechanoreceptors in the adaptation and test phases, the diverging

reports in the cylinder experiments and the absence of MAE in the OPTACON experiment can be related to the non-optimal choice of adapting and testing stimuli. Consequently, here, we tested tactile MAEs using appropriate combinations of adapting and testing stimuli. We used successive stimulation of three pins to generate sensation of apparent motion on the finger cushion, and they were sequentially vibrated with the frequency of 30 Hz both in adapting and testing phases. It is expected that this procedure ensured stimulation for the same mechanoreceptor (RA mechanoreceptor) in both the adaptation and test phases. Using this procedure, we found robust tactile MAEs in the various tactile motions such as the short-distance motion within the fingertip, the long-distance motion from the finger base to the fingertip, and the circular motion on the fingertip.

Materials and methods

Apparatus

Three pins were arranged with 5 mm spatial intervals, and they were vertically vibrated through a hole in a metal board. The participant placed his/her right index finger on the board, as illustrated in Fig. 1A, and participant's finger was kept in contact with the pins. The pins were driven by a vibration generator (EMIC Inc., Kyoto, Japan, 511-A) with the frequency of vibration 30 Hz, maximum amplitude 0.06 mm, and duration 200 ms. The wave form was modulated with sinusoidal function. The pin material was piano wire of 1.0 mm diameter. When the pins were sequentially driven, the participant perceived apparent motion on the finger cushion. For example, pin "c" sticks out first, then "b" and finally "a", as in Fig. 1B; participants thus perceive the tactile motion to the fingertip. The magnitude of the perceived motion was controlled in the experiments by varying the Inter Stimulus Onset Interval (ISOI).

Participants

Six participants (one male author, three naive males, and two naive females), aged from 22 to 25 years, performed the first experiment, and the four participants from the six (one male author, and three naive males) participated in the other all experiments. Participants could not hear the sound of vibrations, and performed experiments with eyes open to maintain their arousal level.

Procedure

The experimental procedures are described in Fig. 1C. In the adaptation phase, the tactile motion was presented at 100 ms ISOI (that is, the duration of the motion was 400 ms). This

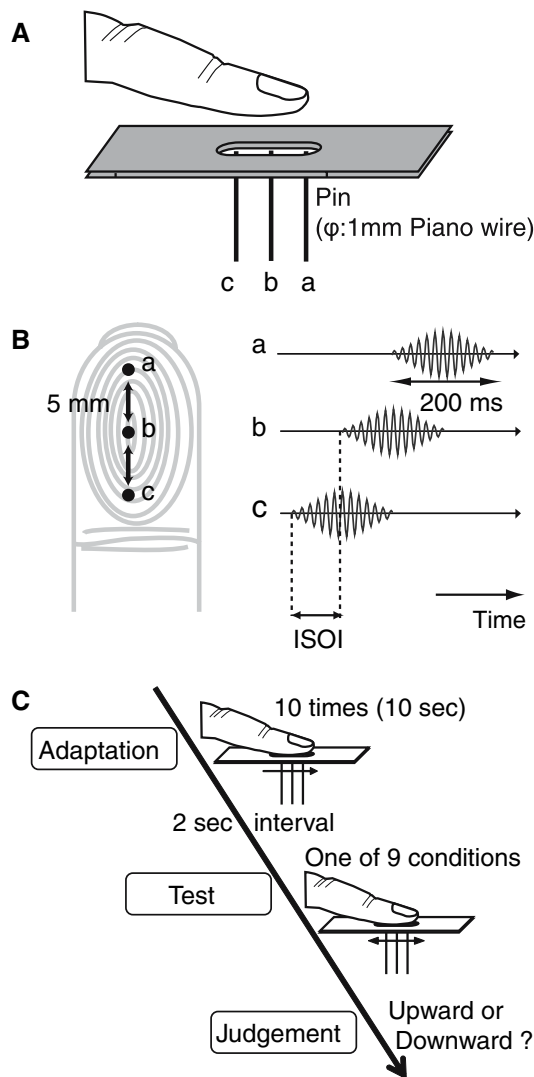


Fig. 1 **A** Stimulus arrangement. **B** Time chart. **C** Experimental procedure

ISOI was decided by the pilot experiments to generate clear sensation of apparent motion, and this value is consistent with the values obtained by the previous studies (Sherrick and Rogers 1966; Kirman 1974). The tactile motion was presented ten times at 600 ms intervals. After a 10 s adaptation, a 2 s interval was given, and test stimulus was then presented once with one of nine ISOIs (−120, −60, −30, −15, 0, 15, 30, 60, and 120 ms). Positive ISOI values mean motions to the fingertip (described as “Upward”), and negative values mean motions to the base of the finger (described as “Downward”). Participants answered “Upward” or “Downward” with two alternative forced choices. This experiment was performed under three experimental conditions (Upward adaptation, Downward adaptation, and No adaptation). In the No adaptation condition, the participant put his/her finger on the stationary contactors during the same period as the adaptation duration (10 s). The three conditions were carried out in separate blocks. One block of the

experiments consisted of 18 trials (each ISOI included two trials). Ten blocks were performed for each condition. Initial 30 s adaptation was made at the beginning of each block. Participants took enough rest more than 5 min between blocks. A total of 540 trials were performed for each participant (18 trials \times 10 blocks \times 3 conditions).

Results

Vertical motion

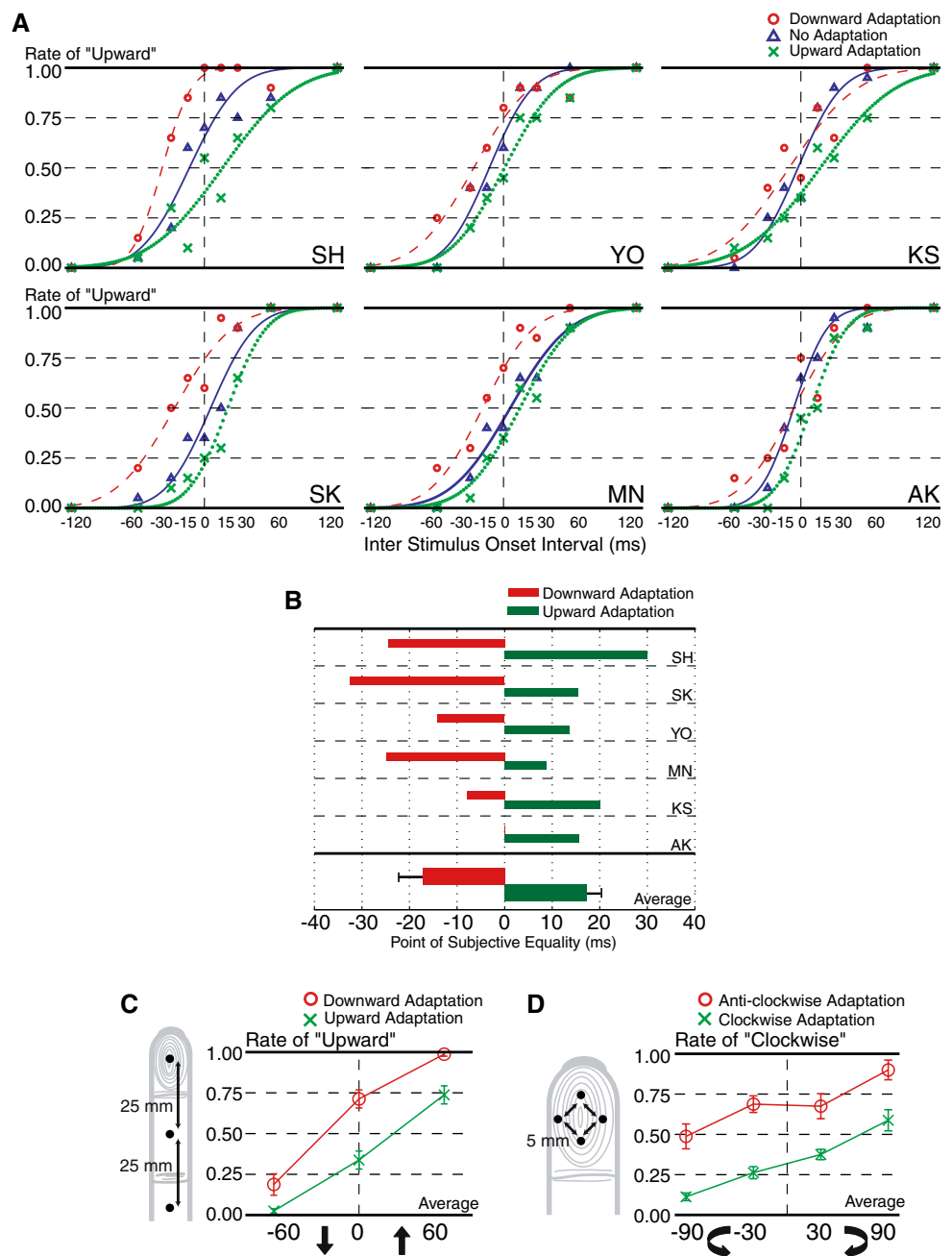
Figure 2A shows the individual data of “Upward” response rates. The horizontal and vertical axes represent the ISOIs of the pins, and the rate of a participant’s response of “Upward”, respectively. The blue triangles, green crosses and red circles represent the averages of each of 20 trials in No, Upward and Downward adaptation conditions, respectively. A thin blue line, a dotted green line and a broken red line indicate the fitted line with cumulative normal distribution. In the data of No adaptation (blue triangles), when the ISOI was 0, the rate of “Upward” answers was about 0.5, and when the ISOI of 120 or −120 ms was presented, all participants in all trials answered “Upward” or “Downward”. This means all participants surely perceived and judged the motion direction. If upward motion was presented in the adaptation phase (green crosses), less “Upward” responses were obtained in the wide range of ISOIs. On the other hand, in the downward condition (red circles), the rate of “Upward” responses increased. These tendencies were observed for all participants, except in the downward adaptation condition of the participant AK.

The values of Point of Subjective Equality are calculated for all adaptation conditions. The shifts of the PSEs in the downward (upward) adaptation condition from the no adaptation condition are shown in Fig. 2B. The red (green) bars represent PSEs of individual data and their average in the downward (upward) condition. The error bars represent standard errors. The averaged PSEs are −17.3 ms in the downward adaptation condition, and +17.3 ms in the upward adaptation condition. Considering relatively small standard errors (5.0 ms in the downward condition, and 2.9 ms in the upward condition), we can conclude that the tactile motion adaptation influenced the perceived direction of the motion presented in the test phase in such a way that the number of responses corresponding to the opposite direction to the adapted motion direction systematically increased. This implies that the tactile MAEs were reliably observed.

Long-distance motion and circular motion

Kirman (1974, 1975, 1983) had reported various kinds of tactile apparent motions including those produced by moving lines, rotating lines, and expanding boundaries. In

Fig. 2 Results of the experiment for vertical tactile motion. Horizontal and vertical axes represent ISOI (ms) and the rate of participant's "Upward" response. **A** Individual data. **B** Shift of PSE (error bars represent standard errors). **C** Result of the experiment for long-distance motion. **D** Result of the experiment for circular motion



order to investigate the generality of the tactile MAEs, our next investigation looked whether it could be induced by long-distance and circular motions.

The same experimental procedures as in the case of the vertical motion without ISOI variations were used. In the case of long-distance motion, the pins were vertically arranged with 25 mm spatial intervals, as illustrated on the left in Fig. 2C. Although the motion sensations were weaker than those in the first experiment with 5 mm spatial interval, the participants perceived the sequential stimuli more as motion than as spatially separated three stimuli. Indeed, Kirman (1974) reported that, if stimuli were arranged

within 2 in. distance, tactile apparent motion could be perceived and the temporal relationship played major role. The presented ISOIs were varied in -60, 0, and +60. The results are shown on the right in Fig. 2C. The vertical and horizontal axes represent the rate of the response "Upward" and the ISOIs, respectively. We carried out upward and downward adaptation conditions in separate blocks. In general, the participants gave more "Upward" answers after the downward adaptation, and vice versa. Clear divergence between the two adaptation conditions indicates the occurrence of the tactile MAE by long-distance motion.

In the case of circular motion, the pins were arranged in a square with 5 mm spatial intervals as illustrated on the left in Fig. 2D, and they were sequentially vibrated clockwise or anti-clockwise. All participants perceived circular motion with smooth direction changes, rather than square motion with sharp changes. This indicates that the tactile motion system was functioning here in such a way to interpolate the trajectory of the circular motion. The presented ISOIs were varied in -90 , -30 , $+30$, and $+90$. The results are shown on the right in Fig. 2D. Positive values in the horizontal axis mean clockwise motion, and vice versa. Basically, when the ISOI increased, more “Clockwise” responses were obtained. More “Clockwise” responses were obtained in the anti-clockwise adaptation condition than in the clockwise adaptation condition, suggesting that the tactile MAE can also be observed by circular motion.

These results indicate that the tactile MAEs can be robustly observed for the tactile motions of various types.

Discussion

We demonstrated that the tactile MAEs can be observed when the sequential pin stimulation was used for both adaptation and test stimuli. How can we explain this difference between earlier studies that did not report robust tactile MAEs, and our experiments? One reason may be that vibration generally makes our stimulus more effective in activating the relevant receptors and neurons (cf. Vierck Jr and Jones 1970), but we further consider it critical that we carefully chose stimulus parameters considering the selectivity of the mechanoreceptors to vibration frequency. Tactile mechanoreceptors, which would be stimulated in the rotating cylinder, the OPTACON and the pin stimuli (our) experiments, are shown in Table 1. The upper rows represent the statuses in the adaptation phase and the lower rows represent those in the test phase. This summary table suggests that, in the previous studies, the different mechanoreceptors might be activated in their adaptation and test phases. On the other hand, it is likely that the same mechanoreceptor (RA) was stimulated in both the adaptation and test phases in our experiment, and this may be why we could observe strong tactile MAEs. In addition, it was observed in our pilot study that when the participant lifted his/her finger off the stimulator

and held it in the air after the adaptation of the successive pin stimulation, as in the Lerner and Craig study, the tactile MAEs were not perceived. This observation also supports our claim that the activation of the same type of mechanoreceptors in both adapting and testing phases is essential in production of robust aftereffects. Examining the temporal frequency tuning of the tactile MAEs would be a promising future experiment for the purpose of estimating the quantitative characteristics of the underlying neural mechanism, and testing the validity of our hypothesis.

The neural mechanisms for tactile motion processing are not as well understood as those for visual motion. The primary somatosensory cortex S-1 contains four areas, Brodmann’s area 3a, 3b, 1, and 2. Area 3b and 1 are predominantly engaged in the analysis of cutaneous information from the mechanoreceptors in the skin (Dykes et al. 1980; Phillips et al. 1988). Most neurons in both areas respond to moving stimuli, and two types of neurons have been identified (Hyvarinen and Poranen 1978; Constanzo and Gardner 1980; Gardner and Constanzo 1980; Essick and Whitsel 1985; Warren et al. 1986; Ruiz et al. 1995): the motion sensitive, responding to motion in all directions, shown to a higher extent to be located in area 3b (Warren et al. 1986) and the direction sensitive, showing a clear preference for movement in one direction and to be located mostly in area 1. Considering the occurrence of the tactile MAEs for long-distance motion, which is beyond limited size of the receptive field in area 3b, it can be speculated that area 1 or/and higher areas can be involved with this phenomenon. Moreover, recent functional imaging studies showed that the human putative MT/V5, which has been considered to be responsible for the “visual” motion perception and MAE, is activated by the tactile motion stimuli (e.g., Hagen et al. 2002). An intriguing open question is how MT/V5 contributes to the tactile motion processing and its aftereffect.

Although the somatosensory information processing and their corresponding areas in the brain are intensively examined in non-human primates (e.g., Hyvarinen and Poranen 1978; Iwamura et al. 1994) and recent human (Bodegard et al. 2000) studies, few physiological studies have been performed on how the tactile motion can be processed in conjunction with kinesthetic information such as the finger positions and arm posture. Our development of a protocol that reliably produces the tactile MAEs will provide a useful psychophysical probe into the neural mechanisms of such tactile motion processing.

Table 1 Tactile mechanoreceptors that would be stimulated in rotating cylinder, OPTACON, and our experiments (Pins)

	Cylinder	OPTACON	Pins
SA in adapt	V		
RA in adapt	VVV	VVV	VVV
SA in test	VVV		
RA in test			VVV

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