Short Communication

Tactile interactions in the path of tactile apparent motion

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Abstract

Perceptual completion is a fundamental perceptual function serving to maintain robust perception against noise. For example, we can perceive a vivid experience of motion even for the discrete inputs across time and space (apparent motion: AM). In vision, stimuli irrelevant to AM perception are suppressed to maintain smooth AM perception along the AM trajectory where no physical inputs are applied. We investigated whether such perceptual masking induced by perceptual completion of dynamic inputs is general across sensory modalities by focusing on touch. Participants tried to detect a vibro-tactile target stimulus presented along the trajectory of AM induced by two other tactile stimuli on the forearm. In a control condition, the inducing stimuli were applied simultaneously, resulting in no motion percept. Tactile target detection was impaired with tactile AM. Our findings support the notion that the perceptual masking induced by perceptual completion mechanism of AM is a general function rather than a sensory specific effect.

1. Introduction

Our sensory systems are continuously exposed to internal and external noise from a range of sources. Our brain uses perceptual completion mechanisms to maintain consistent and robust perception against such noise. For example, we can perceive motion for two or more discrete stimuli alternately appearing and disappearing in different locations (apparent motion: AM) (Wertheimer, 1912). Under optimal spatiotemporal conditions, AM is subjectively indistinguishable from real motion (Korte, 1915), suggesting that perceptual completion occurs along the AM trajectory where no physical inputs are present.

Psychophysical studies have shown impairments in the visual processing of stimuli irrelevant to AM along the AM trajectory, providing strong evidence for the perceptual completion of AM (Hidaka, Nagai, Sekuler, Bennett, & Gyoba, 2011; Yantis & Nakama, 1998). Even simple detection performance is impaired on the AM trajectory (Hidaka et al., 2011), indicating that perceptual completion of AM affects early stages of visual processing. This automatic low-level perceptual masking induced by the perceptual completion mechanism for dynamic inputs can contribute to maintaining smooth, consistent motion perception in the face of noise. However, the perceptual masking induced by perceptual completion of AM has been demonstrated only in vision, although AM can be perceived in other sensory modalities such as touch, and there exists a shared spatiotemporal rule (Korte’s third law) for AM perception across sensory modalities (Lakatos & Shepard, 1997).

Whereas visual information is converted from a single sensory source (i.e., light) onto multiple light receptors on retina, tactile information is based on a variety of mechanical inputs (stretch, pressure, vibration, and so on) through four qualitatively different types of mechanoreceptor (Lederman & Klatzky, 2009; Saal & Bensmaia, 2014). Since each distal neuronal mechanism is unique for vision and touch, spatial and temporal properties are naturally different between these sensory modalities. The temporal resolution of the visual system is known to be relatively low (10–20 Hz) (Kelly, 1971) compared to touch (250–300 Hz; Gescheider, 1976), whereas the spatial resolution in vision (1′ in visual degree; Campbell & Gubisch, 1966) is superior to touch (less than 5 mm on finger pads; Mancini et al., 2014; Weinstein, 1968). The perceptual completion mechanism of AM is useful for the visual system to perceive smooth object motion because this mechanism allows us to compensate for the lack of information due to the innate low temporal resolution from perceptually-completed spatial information. It is thus possible that the perceptual masking induced by perceptual completion of AM is peculiar to the visual system for maintaining smooth motion perception.

On the other hand, the perceptual masking induced by the perceptual completion mechanism of AM might also exist for touch simply because...
touch is frequently exposed to internal (e.g., neural crosstalk) and external (e.g., temperature, which affects response characteristics of mechanoreceptors) noises (Lederman & Klatzky, 2009) interrupting the perception of smooth object motion. Intriguingly, visual and tactile motion processing appear to share perceptual and neural mechanisms: motion aftereffects transfer bidirectionally between visual and tactile stimuli (Konkle, Wang, Hayward, & Moore, 2009) and the motion-sensitive brain area MT+/V5 responds to both visual (Mather, Pavan, Campana, & Casco, 2008) and tactile motion (Hagen et al., 2002). These commonalities in the processing of visual and tactile motion suggest that analogous perceptual masking induced by the perceptual completion mechanism of AM may also exist in touch. As mentioned above, our sensory modalities have inherent differences in distal mechanisms and perceptual properties. Determining whether a common perceptual completion function for dynamic inputs exists can contribute to understanding whether and how our perceptual systems represent the outer world in coordination with these innate variabilities of sensory modalities.

Here, we investigated this question by testing whether tactile AM impairs processing of a transient input irrelevant to AM along the AM trajectory. Two vibro-tactile stimuli were alternatingly presented on the forearm to induce tactile AM. Participants tried to detect the presence of a tactile stimulus transiently presented at an intermediate position along the path of AM (Fig. 1). We compared detection performance in the presence of AM to a control condition in which the two inducing touches were presented simultaneously, so that no AM occurred. If the perceptual completion mechanism of tactile AM can induce low-level perceptual masking along its trajectory, then detection of the target should be impaired in the AM compared to the control condition. Our results support the notion that a low-level perceptual masking occurs in the path of tactile AM.

2. Methods

2.1. Participants and apparatus

Fifteen healthy participants took part in the study after giving informed consent (7 females; mean age: 30.9 years, SD: 8.5 years, mean handedness score according to the Edinburgh Inventory (Oldfield, 1971; 82.77, all right-handed, range: 41.2-100). The sample size was determined in reference to previous studies showing the perceptual interference effects of visual AM (Hidaka et al., 2011; Yantis & Nakama, 1998). In the study of Yantis and Nakama (1998), the effect of masking of visual stimuli along the path of AM had an effect size of Cohen’s $d = 0.867$ (estimated by the result of a paired sample t-test ($t(8) = 2.60$) in their forth experiment). A power analysis using G*Power 3.1 software (Faul, Erdfelder, Buchner, & Lang, 2009) with this effect size, alpha of 0.05, and power of 0.8 indicated that 13 participants were needed. Thus, our sample size is appropriately powered to detect a comparably sized effect in touch. All participants reported no abnormalities in sensory perception, and were naïve to the purpose of the study. They were paid or given course credits for their participation, and gave written informed consent. One participant was excluded from analyses because she/he was uncomfortable with the type of stimulation and aborted the experiment, and was replaced by a new participant. All procedures were approved by the Department of Psychological Sciences Research Ethics Committee at Birkbeck, University of London (Reference number: 171887; Title: Building body representations: an investigation of the formation and maintenance of body representations). The study was conducted in accordance with the principles of the Declaration of Helsinki.

Tactile stimuli were delivered to the forearm using three vibrators (Quaerosys, Schotten, Germany). The stimulator consisted of ten rods (1 mm in diameter), protruding from a flat surface of 4 x 8 mm. The rods protruded and retracted at 250 Hz for 50 ms (target) and 200 ms (inducers) with 0.5 ms accuracy, producing clearly perceivable skin indentations. Wave signal intensity for inducers was always set to 98% of the maximum intensity level available (1.48 mm in indented height). The intensity of the inducers was calibrated for each participant. Foot pedals (Yamaha FC5A Sustain Pedal) were used to record participants’ responses. Light emission diodes (LED) were used to present visual cues. The foot pedals and LEDs were connected with a digital analog converter (NI USB-6341, National Instruments). These apparatus were connected to a PC (DELL Precision T1700) through a USB port and controlled by a custom MATLAB (MathWorks, Natick, MA) script with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). We used headphones (Sennheiser HD 439 Audio Headphones) to present white noise bursts in order to prevent the participants from hearing noises generated by the tactile stimulator. Fabric athletic arm supporters were used to fix the tactile stimulators on the participants’ left forearm to ensure constant contact force between the skin and the stimulation devices throughout the experiment. Small cardboard boxes and a sheet of black cardboard were used to cover the tactile stimulators on the participants’ forearm. Participants were asked to keep their eyes open during the experiment and to fixate a pair of LEDs (i.e., threshold phase) or a black dot positioned on the wall in front of them.

2.2. Stimuli and procedures

Participants were asked to sit on a chair in front of a table, and to place their left hand and arm on the table with the palm side up in a comfortable position. Three vibrators were placed inline on the volar skin surface of the participant’s left forearm, which was covered by a black board. Black circles represent the inducers and purple (gray) circles the target. Two LEDs were placed in front of the participant. (B) Time course of stimulus presentations in the apparent motion and no-motion conditions. In the apparent motion condition, the inducers were alternatively turned on and off so that the participants felt apparent motion. On the contrary, in the no-motion condition, tactile vibrators were simultaneously presented from the inducers.
without, were sequentially presented with a 1000 ms interval. The target stimulus (i.e., the middle stimulator) was presented for 50 ms. The onset of the first and second tactile sequences was cued by the left- and right-side of the LEDs, respectively. For the target-present sequence, the target occurred 50 ms after the onset of one of the LEDs. After the observation of two sequences, the participant reported which sequence they felt with the target, by raising their left (the first sequence) or right (the second sequence) foot. The intensity of the target was initially set at the above threshold level (half-maximal intensity available, 0.73 mm in indented height), then gradually stepped down according to the participant’s responses. With this two interval forced choice task and QUEST method (Watson & Pelli, 1983), we estimated the 76% detection threshold level of each participant. We run the threshold estimation session twice, and averaged the last trial of the two thresholds (mean = 0.31 mm, SD = 0.07 mm in indented height).

The main experiment session had two conditions. In one condition, two tactile stimulators placed on the top- and bottom-most positions along proximodistal axis of the left arm alternatingly turned on for 200 ms with 100 ms of an inter-stimulus interval as inducers of AM. Each tactile stimulation was presented 20 times so that 10 times AM was perceived in each AM sequence in each trial. These temporal parameters were set by our preliminary observation in order to introduce the smoothest AM perception in our setup. The target stimulus (50 ms) was presented once at the middle stimulator 25 ms after the presentation of one of the inducers. The intensity level of the target stimulus was adjusted to the 76% detection threshold level for each participant based on the results of the threshold estimation session. We also presented the sequence without the target presentation. As a control condition, we presented the inducers simultaneously so that no motion was induced. After the experiment, we asked our participants whether the alternate and simultaneous presentations of the tactile stimulations were perceived as moving or not. All participants verbally confirmed that they felt AM or no AM in the AM and no-motion conditions, respectively. Another control condition could be that the target was presented out of the AM trajectory (“off-path” condition) (Hidaka et al., 2011; Yantis & Nakama, 1998). Our pilot observations revealed that the sensation of the tactile stimuli spread out at each stimulation site as covering the whole area along the mediolateral axis of the arm. Whereas we could introduce a spatial gap between the inducers and target in 1–3 cm in the medio-lateral axis, the above-mentioned sensory characteristics of tactile vibratory stimulation made it difficult to detect this spatial gap on the forearm. These observations seemed to be consistent with the findings that the 75% threshold of spatial gap detection in the mediolateral axis on forearm is 1 cm even for the single contractor (not vibratory) stimulus with 2 s duration (Gibson & Craig, 2005). We might be able to present the inducers and the target at different skin surfaces of the forearm (the hairy and glabrous skin surfaces). However, this idea was discarded that the 75% threshold of spatial gap detection in the mediolateral axis of the arm. Whereas we could introduce a spatial gap between the inducers and target in 1–3 cm in the medio-lateral axis, the above-mentioned sensory characteristics of tactile vibratory stimulation made it difficult to detect this spatial gap on the forearm. These observations seemed to be consistent with the findings that the 75% threshold of spatial gap detection in the mediolateral axis on forearm is 1 cm even for the single contractor (not vibratory) stimulus with 2 s duration (Gibson & Craig, 2005). We might be able to present the inducers and the target at different skin surfaces of the forearm (the hairy and glabrous skin surfaces). However, this idea was discarded that the 75% threshold of spatial gap detection in the mediolateral axis of the arm.

3. Results

We estimated 76% target detection threshold for each participant in the threshold estimation session and presented the target at that threshold level in the main session. In the main session, the d-prime for the AM condition (M = 0.31, SD = 0.69) was significantly smaller than in the no-motion condition (M = 0.63, SD = 0.64; t(14) = −2.52, p = .02, d = 0.65; Fig. 2B). D-prime was significantly higher than zero (t(14) = 3.82, p = .002, d = 0.97) in the no motion condition, but not in the AM condition (t(14) = 1.75, p = .10, d = 0.45). Finally, the beta values were not significantly different across conditions (AM: M = −0.17, SD = 0.98; no motion: M = −0.17, SD = 0.69; t(14) = −0.98, p = .36) as well as a significant effect of measurement (hit/false alarm). This found a significant interaction effect (BF10 = 2.71). As for the comparison between each d-prime and zero, the Bayesian one sample t-tests supported the alternative hypothesis (BF10 = 22.54) but the null hypothesis for the AM condition (BF01 = 1.12). The Bayesian paired sample t-tests supported the null hypothesis for the difference of the beta values between the conditions (BF01 = 3.80).

As shown in Fig. 2B, some data showed zero or negative d-prime values: 7 of 15 participants’ d primes were equal to or below zero (4 showed negative values) in the AM condition, whereas 2 of 15 participants’ d primes showed negative values in the no-motion condition. The zero and negative d-prime values indicate that the false alarm rates were equal to or higher than the hit rates, respectively. These results posed the question whether the observed difference in the d-prime between the AM and no-motion conditions was based on the degradation of detection performances (i.e., the reduction of the hit rates in the AM condition). To confirm this, we performed a two-way repeated measure analysis of variance (ANOVA) with conditions (AM/no-motion) and measurements (hit/false alarm). This found a significant interaction effect (F(1,14) = 7.86, p = .01, ηp² = 0.36) as well as a significant effect of measurement (F(1,14) = 9.42, p = .01, ηp² = 0.40), but a non-significant effect of condition (F(1,14) = 0.46, p = .51, ηp² = 0.03). A simple main effect showed
that the hit rate of the AM condition (M = 0.58, SD = 0.25) was significantly lower than that of the no-motion condition (M = 0.67, SD = 0.15) (p = .02) (Fig. 2A). In contrast, the false alarm rates were comparable between the conditions (AM: M = 0.48, SD = 0.33; no motion: M = 0.43, SD = 0.28; p = .19). These results demonstrated that the difference in the d-prime between the AM and no-motion conditions was mainly explained by the impairment of detection performances with tactile AM.

4. Discussion

This study demonstrated perceptual masking effects along the trajectory of tactile AM: sensitivity to the target (d-prime) reduced when targets were presented in the path of AM. The simultaneous presentation of two tactile stimuli at different skin locations produces a single illusory focal sensation at the center of the tactile stimulations when no physical input is presented (Bekesy, 1957; Chen, Friedman, et al., 2011; Yantis & Nakama, 1998), we would predict that the tactile AM trajectory can interfere with the perception of physical inputs irrelevant to AM perception. The perceptual completion mechanism of AM shared across sensory modalities enables us to maintain smooth motion perception against internal and external noise. We can assume that the perceptual masking induced by the perceptual completion mechanism of AM can be a general function rather than a sensory specific effect in motion perception.

Visual AM has been reported to induce the activation of the primary visual cortex (V1) whose receptive field covers the path of AM (Muckli, Kohler, Kriegeskorte, & Singer, 2005). It was also suggested that the perceptual completion along the visual AM trajectory is accomplished by feedback modulation from the higher-level motion processing area (MT+/V5) to V1 (Sterzer, Haynes, & Rees, 2006). Shared activations in the higher-level motion processing area are reported for tactile (Hagen et al., 2002) and visual (Mather et al., 2008) motion perception. A possible underlying mechanism for the perceptual masking of tactile AM may be feedback modulation from MT+/V5 to primary somatosensory areas (SI and SII), and the activation of the primary somatosensory areas or low-level ‘filling in’ would reduce tactile perceptual sensitivity along the path of AM. It should also be noted that a neuroimaging study (Alink, Schwierszik, Kohler, Singer, & Muckli, 2010) showed that predictive visual AM stimuli induced inhibition of neural responses in V1 along the path of AM. In line with this finding, it was reported that that the behavioral data of the visual AM perceptual masking effect can be explained by the inhibitory neural activations in V1 assumed by a computational predictive coding model (Van Humbeeck, Putzeys, & Wagemans, 2016).

Interestingly, involvements of the primary somatosensory areas including SI (e.g., Whitsel, Roppolo, & Werner, 1972) has been also reported in response to tactile motion, and the response characteristics of SI are found to be highly similar to those of MT+/V5 to visual motion (Pei, Hsiao, Craig, & Bensmaia, 2011). Also, sequential presentations of vibratory stimulations were reported to trigger the perceptual inhibitions between the stimulations on forearm (Bekesy, 1957). Future studies should investigate the underlying mechanisms of tactile AM masking effects with neuroimaging and computational techniques.

The current study provided the first demonstration of tactile masking along the AM trajectory. We demonstrated the tactile AM masking effect with the simple comparison between AM and no-AM situations, a single spatiotemporal parameter, and a single body site (i.e., the forearm). These limitations should be addressed in future research in order to give further understandings of phenomenological aspects and underlying mechanisms of the effect. Firstly, the relationships between AM perception and the masking effect should be examined. As in the visual AM masking effect (Yantis & Nakama, 1998), we would predict that the
perceptual quality or strength of tactile AM is positively correlated with the magnitude of the tactile AM masking effect. The comparison between the situations where the target presented along the AM trajectory and where the target appears in a spatial position off the trajectory of AM “off-path” situation (Hidaka et al., 2011; Yantis & Nakama, 1998) would also clarify the role of AM perception to the AM masking effect. The “off-path” condition may be introduced if we use a body site (e.g., the belly) whose size is larger than forearm (see also the methods section). Investigations of commonality and differences of the tactile AM masking effects across the body sites would also contribute to understanding whether common perceptual mechanisms exist and how motion perception is established in the somatosensory system across body parts. Investigations of spatiotemporal aspects of the tactile AM masking effect, for example testing the effects of presentation timing of the target relative to that of inducers along the path of AM (Schwiedrzik, Alink, Kohler, Singer, & Muckli, 2007), would facilitate our understandings of how AM representations are completed along the tactile AM trajectory. Examinations on how the tactile AM masking effect can interact with innate spatial (e.g., Longo & Haggard, 2011) and temporal (Hidaka, Tamé, Zafarana, & Longo, 2020) perceptual distortions of touch can also be of interest. These future studies can contribute to further understandings of the nature of perceptual completion mechanisms of tactile AM.

Data set

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