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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.

Keywords: apparent motion; perceptual completion; perceptual masking; touch

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 vibrotactile 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 (**Figure 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.

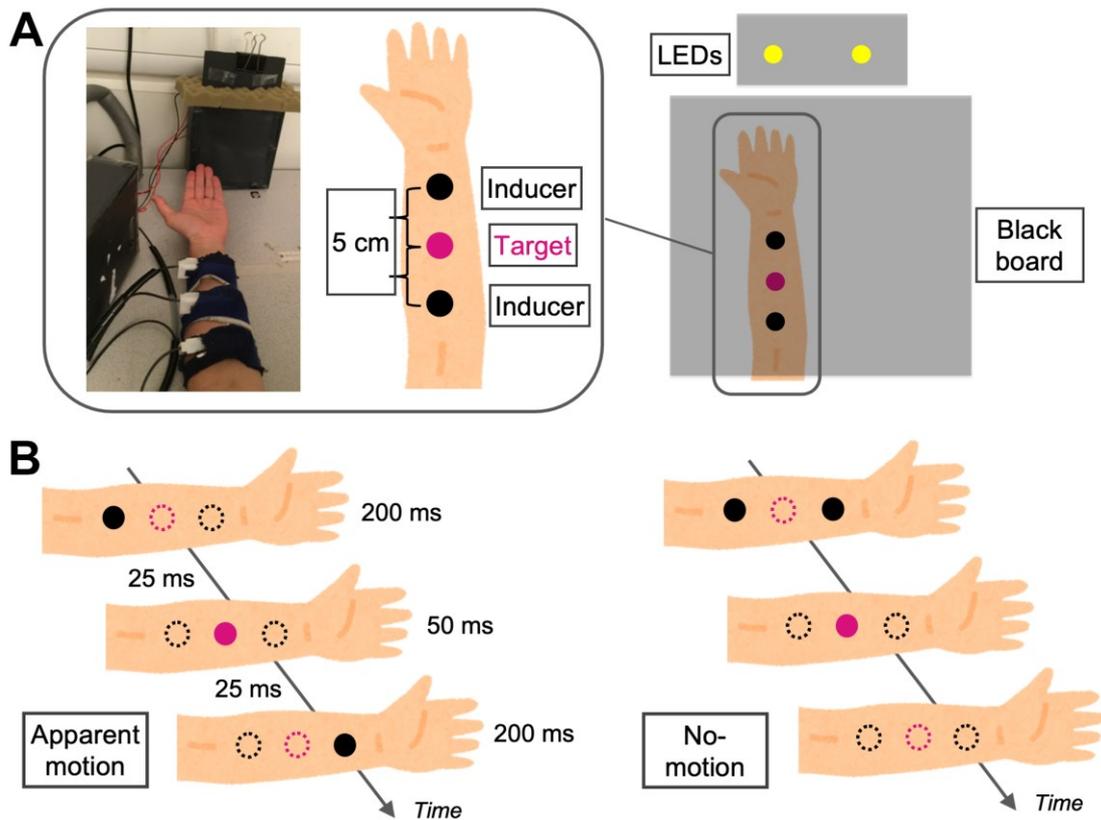


Figure 1. (A) A picture and schematic illustration of the experimental setup. Three tactile vibrators were put on the volar skin surface of the participant's left forearm, which was covered by a black board. Black circles represent the inducers and purple (gray) circles the target. Two LEDs were placed 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.

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 $d_z = 0.867$ (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 × 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 simulators 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 into line on the volar skin surface of the participant's left forearm. One was placed at a position nearby the left elbow (4 cm from the elbow joint). The other two were set along the proximodistal axis relative to the first one in 5 cm of distance (**Figure 1A**). Participant's left hand and arm were occluded by a black sheet of cardboard, which rested on four supports. Participants made responses using two foot pedals. They wore headphones with white noises to prevent audio cues from the tactile stimulators. No participant reported hearing sounds from the stimulators. Two LEDs were also placed in front of the participant. First, they completed a threshold estimation session using a two-interval forced-choice

procedure for determining the target intensity of the subsequent main session. Two tactile sequences, one with a target presentation and the other 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 alternately 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 simulator 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 mediolateral 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 seconds 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 because neural (Merzenich, Kaas, Sur, & Lin, 1978) and perceptual (Le Cornu Knight, Longo, & Bremner, 2014) characteristics are reported to be different between these skin surfaces. Due to these reasons, we did not include the “off-path” condition in the current study. The participants were asked to fixate the visual fixation dot during the stimulus presentations. We also asked participants to keep their tactile attention (and not visual gaze) on the forearm where the tactile target was going to be presented during the trial. After the presentation of these tactile stimulations, the participants reported whether they felt the target or not

during the trial. Half of the participants were asked to raise their left foot to report the target's present and their right foot to report its absence, and the other half used the reverse mapping. Our pilot experiment revealed that the detection task was highly difficult when the AM and no-motion conditions were intermixed in a single block. Thus, we separated these conditions into different blocks. The AM and control conditions were counterbalanced in an ABBA order, with the first condition counterbalanced across participants. Each block consisted of 40 trials, half with the target present and half with the target absent, making 160 trials in total. The presentation of the target present and absent trials was randomized across trials. The target presentation timing (between 2100 to 4200 ms after the initiation (the presentation of the first inducer(s)) of each trial for both the AM and control conditions) was also randomized across trials. The starting position of the AM sequence (from near to hand or to elbow) was also randomized across trials.

2.3 Analysis

We calculated hit and false alarm rate for each participant in the AM and no-motion conditions (**Figure 2A**). The target-present responses in the target-present trials were regarded as hits and those in the target-absent trials as false alarms. Then, we computed d-primes as an index of perceptual sensitivity on the basis of the signal detection theory (Macmillan & Creelman, 1991) by the following formula: $Z(\text{Hit}) - Z(\text{False alarm})$. For calculating Z scores from the proportions, we adopted a loglinear conversion method by adding 0.5 to the numbers of hits and false alarms, and adding 1 to the number of target-present and target-absent trials (Hautus, 1995). We also calculated beta values as an index of bias or criterion by the following formula: $-0.5 \times (Z(\text{Hit}) + Z(\text{False alarm}))$. The statistical tests were performed by JASP (JASP

Team, 2019). The data have been made publicly available via the Open Science Framework and can be accessed at <https://osf.io/jfg64/>.

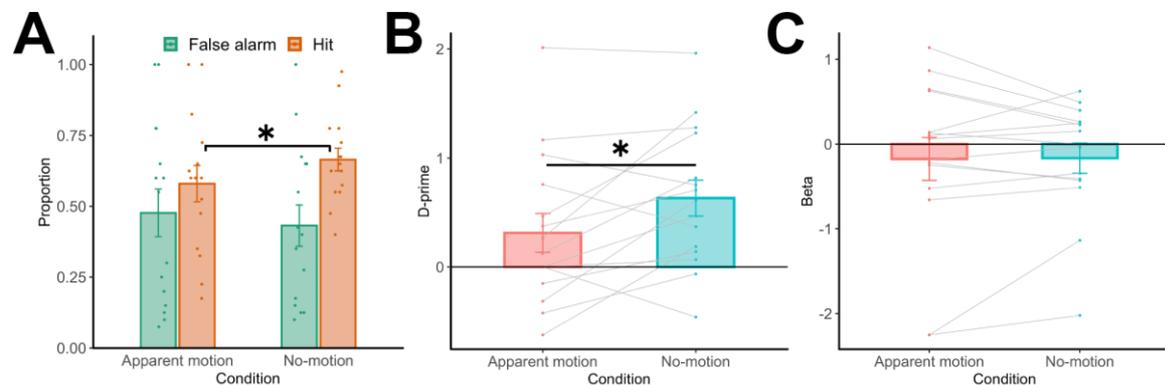


Figure 2. Results. (A) Proportions of false alarm and hit rates in the apparent motion and no-motion conditions. (B) D-prime and (C) beta values in the apparent motion and no-motion conditions. Dot indicates single participant's data ($N = 15$). Error bars denote standard errors of the means (\pm SEM). Asterisks indicate significant differences ($p < .05$).

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 ($M = 0.63$, $SD = 0.64$; $t(14) = -2.52$, $p = .02$, $d_z = 0.65$; **Figure 2B**). D-prime was significantly higher than zero ($t(14) = 3.82$, $p = .002$, $d_z = 0.97$) in the no motion condition, but not in the AM condition ($t(14) = 1.75$, $p = .10$, $d_z = 0.45$). Finally, the beta values were not significantly different across conditions (AM: $M = -0.17$, $SD = 0.98$; no motion: $M = -0.17$, $SD = 0.69$; $t(14) = -0.09$, $p = .93$, $d_z = -0.02$) (**Figure 2C**).

In order to evaluate the extent to which the obtained results provide positive support for alternative or null hypotheses, we also performed Bayes factor analyses. We calculated Bayes factors (default Cauchy prior width $r = 0.707$) and checked the estimated values were larger than 1. The Bayesian statistical analyses showed that the observed differences for the d-primes between the AM and no-motion conditions

were more likely to have occurred under the alternative hypothesis than the null hypothesis. The Bayesian paired sample t -tests supported the alternative hypothesis ($BF_{10} = 2.71$). As for the comparison between each d -prime and zero, the Bayesian one sample t -tests supported the alternative hypothesis for the no-motion condition ($BF_{10} = 22.54$) but the null hypothesis for the AM condition ($BF_{01} = 1.12$). The Bayesian paired sample t -tests supported the null hypothesis for the difference of the beta values between the conditions ($BF_{01} = 3.80$).

As shown in Figure 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 ($F(1,14) = 7.86, p = .01, \eta_p^2 = 0.36$) as well as a significant effect of measurement ($F(1,14) = 9.42, p = .01, \eta_p^2 = 0.40$), but a non-significant effect of condition ($F(1,14) = 0.46, p = .51, \eta_p^2 = 0.03$). 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 ($M = 0.67, SD = 0.15$) ($p = .02$) (Figure 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') 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 where no physical input is presented (Bekey, 1957; Chen, Friedman, & Roe, 2003; Sherrick, 1964). This tactile funneling effect can explain the relatively lower d' value observed in the no-motion condition: an illusory tactile sensation could occur at the intermediate, target position between the inducers and this sensation was hard to be distinguished from the actual target presentation. However, the perceptual masking effect observed along AM trajectory cannot be solely explained by the funneling effect, because the presentation of AM (AM condition) induced lower sensitivity to the target than the no-motion condition.

One possibility is that the reduction of the sensitivity to the target with tactile AM perception could result from attentional distraction from the target position induced by the alternately presented inducers. Attentional distraction from the target might simply induce an uncertainty for the status of the target, and this would result in poor performances both for the target's presence and absence (i.e., changes in both hit and false alarm rates) and/or changes in judgment criterion. However, we observed that only the hit rates were different between the AM and no-motion conditions and that the beta values were comparable across the conditions. We also asked our participants to keep their attention to the target position during

the presentations of the inducers in both conditions. Thus, we believe that attentional distraction cannot fully explain our findings.

Our data imply that the perceptual completion more frequently occurred for the AM condition (7 of 15 participants' d primes were equal to or below zero) relative to the no-motion condition (2 of 15 participants' d primes showed negative values). The goal of our perceptual systems is to construct optimal perception with limited information (Rock, 1983). The current study suggests that similar to vision (Hidaka et al., 2011; Yantis & Nakama, 1998), the perceptual completion along 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, Schwiedrzik, 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 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 Humber, 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 (Bekeasy, 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, Tamè, 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.

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Souta Hidaka: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Visualization. **Luigi Tamè:**

Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - Review & Editing. **Matthew R. Longo**: Conceptualization, Resources, Writing - Review & Editing, Funding acquisition.

Data set

Hidaka, S., Tamè, L., & Longo, M. R. Shared_data of “Tactile interactions in the path of tactile apparent motion”, Open Science Framework (<https://osf.io/jfg64/>), 2020. DOI: 10.17605/OSF.IO/DXVTP.

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