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THE TACTILE MOTION AFTEREFFECT

by

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ABSTRACT

The tactile motion aftereffect (tMAE) is a perceptual phenomenon in which illusory motion is reported following adaptation to a unidirectionally moving tactile stimulus. Unlike its visual counterpart, relatively little is known about the tMAE. For that reason, the purpose of this dissertation was to gain a better understanding of the tMAE using both psychophysical and neuroimaging techniques. In a series of five experiments the skin was adapted using a plastic cylinder with a square-wave patterned surface. Chapter 2 consists of two experiments, both of which adapted the glabrous surface of the right hand. Experiment 1 showed that the prevalence, duration, and vividness of the tMAE did not differ between the fingers (thumb excluded), palm and fingers (thumb included), and palm and fingers (thumb excluded). Thus, the divergent prevalence rates of two previous studies (Hollins & Favorov, 1994; Lerner & Craig, 1994) cannot be explained by the inclusion of the thumb in the latter study. Experiment 2 showed that as adapting speed increased from 15 to 75 rpm so did the prevalence, duration, and vividness of the tMAE. Previously it has been shown that the tMAE duration increases with adapting duration (Hollins & Favorov, 1994). Given that speed * duration = distance, increasing either adapting speed or duration also increases distance. As such, it was unclear which parameter(s) caused the observed increase in prevalence, duration, and vividness. Chapter 3 manipulated adapting duration (1, 2, and 4 min) and speed (30 and 60 rpm) in the same experiment, thereby allowing the effect of distance to be assessed in the interaction. The results showed that the prevalence, duration, and vividness of the tMAE increased with adapting speed. There was also a positive relationship between adapting duration and prevalence, but not duration or vividness, of the illusion. Distance

was only a factor when it came to the tMAE duration. To gain insight into the peripheral neural basis of the tMAE, Chapter 4 measured the prevalence, duration, and vividness of the tMAE on skin areas that differ in their composition of fast adapting (FA) mechanoreceptive units, namely the right cheek, volar surface of the forearm, and glabrous surface of the hand. While there was no difference in duration or vividness between the skin surfaces tested, the tMAE was reported twice as often on the hand than the cheek and forearm, which did not differ significantly from one another. This finding suggests that the tMAE can be induced by adapting FA type I (FA I) units in the glabrous skin (hand) and the hair follicle units (cheek and forearm) and/or the FA I (cheek) and field (forearm) units in the hairy skin. Chapter 5 investigated the central neural basis of the tMAE using functional magnetic resonance imaging (fMRI). Of the areas shown to be responsive to tactile motion on the glabrous surface of the right hand, namely the contralateral (left) thalamus, postcentral gyrus (PCG), and parietal operculum, only the PCG showed evidence of the tMAE; that is, there was a sustained fMRI response following the offset of the illusion trials (cylinder rotating at 60 rpm), but not the control trials (cylinder rotating at 15 rpm), presumably reflecting illusory motion perception. Taken together, the experiments described herein expand our knowledge of the tMAE. Using a cylinder adapting apparatus, it was shown that: prevalence is the best measure of tMAE strength; the tMAE is not as robust as its visual counterpart; adapting duration and speed positively affect the prevalence of the tMAE; the tMAE is twice as prevalent on the glabrous than the hairy skin; the FAI and hair follicle units likely underlie the tMAE; the tMAE is likely caused by adapting direction selective neurons in the contralateral PCG.

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CHAPTER 1

Our sense of touch provides us with pain, pressure, and thermal information about our immediate environment, enabling us to successfully and safely navigate and interact with the world around us. One aspect of touch that is particularly important is motion perception -- the ability to track potentially interesting stimuli on the surface of the skin and predict their future position.

Psychophysical research on the ability of humans to detect and discriminate between moving tactile stimuli dates back over a century (Hall & Donaldson, 1885). Within the primate somatosensory system, several areas have been shown to be responsive to moving tactile stimuli, including the primary somatosensory cortex (SI) (Costanzo & Gardner, 1980; Gardner, 1988; Hyvärinen & Poranen, 1978; Warren, Hamalainen, & Gardner, 1986; Whitsel, Roppolo, & Werner, 1972), secondary somatosensory cortex (SII) (Whitsel, Petrucelli, & Werner, 1969), and posterior parietal cortex (PPC) (Leinonen, Hyvärinen, Nyman, & Linnankoski, 1979; Sakata, Takaoka, Kawarasaki, & Shibutani, 1973). Neuroimaging research has shown that analogous areas underlie human tactile motion perception (Bremmer et al., 2001; Burton, MacLeod, Videen, & Raichle, 1997; Hagen, Franzén, McGlone, Essick, Dancer, & Pardo, 2002; Maihöfner, Schmelz, Forster, Neundörfer, & Handwerker, 2004; Nakashita, Saito, Kochiyama, Honda, Tanabe, & Sadato, 2008; Polonara, Fabri, Manzoni, & Salvolini, 1999; Summers, Francis, Bowtell, McGlone, & Clemence, 2009; Yoo, Freeman, McCarthy, & Jolesz, 2003). In addition to somatosensory cortical areas, there is ongoing debate about whether the middle temporal complex (MT+), typically regarded as a unimodal visual motion processing area, is in fact a multi-sensory motion processing

area. Several neuroimaging studies have reported MT+ activation in response to auditory motion (Berman and Colby, 2002; Poirier et al., 2005, 2006), while an equal number have either failed to observe MT+ activation (Smith, Okada, Saberi, & Hickok, 2004; Smith, Saberi, & Hickok, 2007) or have reported negative activation (Lewis, Beauchamp, & DeYoe, 2000). The results of tactile motion studies are equally inconsistent, with some groups reporting MT+ activation (Blake, Sobel, & James, 2004; Hagen et al., 2002; Ricciardi et al., 2007; Summers et al., 2009) and others reporting no activation (Bremmer et al., 2001) or negative activation (Bodegård, Geyer, Naito, Zilles, & Roland, 2000; Nakashita et al., 2008).

Historically, illusions have been used to gain insight into the normal perceptual system. One tool that has been used to study visual motion perception is the motion aftereffect (MAE) -- following prolonged viewing of a unidirectionally moving stimulus, stationary stimuli appear to move in the opposite direction. Several studies have shown that MT+ underlies the visual MAE (Antal et al., 2004; Berman and Colby, 2002; Culham et al., 1999; Hautzel et al., 2001; He, Cohen, & Hu, 1998; Taylor et al., 2000; Théoret, Kobayashi, Ganis, Di Capua, & Pascual-Leone, 2002; Tootell et al., 1995a; but see Huk, Ress, & Heeger, 2001). However, relatively little attention has been given to its tactile analogue, and the results of the few tactile MAE (tMAE) studies that have been conducted are far from conclusive. To date, three studies have reported reliable tMAEs (Hollins & Favorov, 1994; Thalman, 1922; Watanabe, Hayashi, Kajimoto, Tachi, & Nishida, 2007), while three others have been less successful (Hazlewood, 1971; Lerner & Craig, 2002; Wohlgemuth, 1911). Moreover, the central neural basis of the tMAE has yet to be investigated.

In a series of five experiments this dissertation studied the tMAE in humans using both psychophysics and functional magnetic resonance imaging (fMRI). Chapter 2 measured the tMAE prevalence, duration, and vividness on different regions of the glabrous right hand (Experiment 1) and at different adapting speeds (Experiment 2). Chapter 3 followed up Experiment 2 by manipulating adapting duration and speed in the same experiment, thereby allowing the interaction between the two variables to be assessed. In Chapter 4, the specificity peripheral neural basis of the tMAE was investigated by adapting skin regions that differ in their composition of fast adapting (FA) mechanoreceptive units. Finally, Chapter 5 studied the central neural basis of tactile motion processing and the tMAE using fMRI. The sections hereunder provide the reader with the necessary knowledge base for these experiments.

1.1 SOMATOSENSORY SYSTEM

1.1.1 Mechanoreceptors

The human body consists of three skin types: glabrous (or hairless), hairy, and mucocutaneous. Glabrous skin covers the lips, palms of the hands, and soles of the feet, while hairy skin covers the rest of the body. Mucocutaneous skin is located at the body orifices, or the transitional zones between the inside and outside of the body (e.g., mouth, anus), and is not critical for everyday tactile motion perception. Thus, I will focus on the former two skin types in this review.

Irrespective of skin type, the fast conducting, large-diameter A-beta (Aβ) class of sensory fibres is the primary mediator of mechanoreception (i.e., mechanical displacement of the skin). In the glabrous skin there are four types of low-threshold

mechanoreceptive units; FA types I and II and slowly adapting types I and II (Johansson & Vallbo, 1979; Knibestöl & Vallbo, 1970). Note that in the animal literature the FAI and FAII units are referred to as rapidly adapting (RA) and Pacinian corpuscle (PC) units, respectively (see Vallbo & Johansson, 1984). The four types of units are classified based on their adaptation rate to sustained skin indentation and receptive field (RF) characteristics (Knibestöl, 1973; Knibestöl, 1975; Knibestöl & Vallbo, 1970). The fast adapting units (FAI and FAII) are phasic, firing at the onset and offset of stimulation, whereas the slowly adapting units (SAI and SAII) are tonic, responding throughout the entire duration of stimulation (Knibestöl, 1973; Knibestöl, 1975; Knibestöl & Vallbo, 1970). The type I units (FAI and SAI) are located at the dermal-epidermal border, have relatively small RFs with several high sensitivity spots, and innervate the skin densely, whereas the type II units (FAII and SAII) are located in the dermis and subcutaneous tissue, have relatively large RFs with a single high sensitivity spot, and innervate the skin sparsely (Johansson, 1976, 1978; Johansson & Vallbo, 1979; Vallbo & Johansson, 1984; Vallbo, Olausson, Wessberg, & Kakuda, 1995).

Each type of mechanoreceptive unit signals a particular aspect of touch (Bolanowski, Gescheider, Verrillo, & Checkosky, 1988; Ochoa & Torebjörk, 1983; Torebjörk & Ochoa, 1980; Vallbo, 1981), and is associated with a unique end organ, or mechanoreceptor (Miller, Ralston, & Kasahara, 1958). Based on response similarities with cat and monkey afferents, human FAI, FAII, SAI, and SAII fibres are presumed to terminate in Meissner corpuscles, Pacinian corpuscles, Merkel disks, and Ruffini endings, respectively (Chambers, Andres, Duering, & Iggo, 1972; Iggo & Muir, 1969; Iggo & Ogawa, 1977; Jänig, Schmidt, & Zimmermann, 1968; Lindblom, 1965; Lindblom &

Lund, 1966; Lynn, 1969; Talbot, Darian-Smith, Kornhuber, & Mountcastle, 1968). However, Ruffini endings appear to be sparse or absent in the glabrous digital skin of monkeys (Paré, Smith, & Rice, 2002) and humans (Nolano, Provitera, & Crisci, 2003; Paré, Behets, & Cornu, 2003). Using immunofluorescence, Paré et al. (2003) observed several examples of Meissner corpuscles, Merkel disks, and Pacinian corpuscles, but only one Ruffini ending in the human digital skin. Given that microneurography (see Vallbo, Hagbarth, & Wallin, 2004 for review) studies have recorded impulses from the human glabrous hand that resemble those of FAI, FAII, SAI, and SAII afferents (Edin, Essick, Trulsson, & Olsson, 1995; Essick & Edin, 1995; Hulliger, Nordh, Thelin, & Vallbo, 1979; Johansson & Vallbo, 1979; Knibestöl &Vallbo, 1970), the results of Paré et al. (2003) suggest that primate SAII afferents may not always terminate in Ruffini endings.

The superficial skin location and small RFs of the type I units make them well suited for resolving fine spatial information (Johansson, 1978). The SAI units are the most sensitive to spatial patterns, providing the brain with a high quality image of stimuli contacting the skin (Johansson, Landström, & Lundström, 1982b; Phillips & Johnson, 1981). The FAI units, which are most sensitive to stimulus frequencies between 8-64 Hz (Johansson et al., 1982a), have been shown to support tactile motion perception. For example, Gardner and Sklar (1994) showed that humans readily perceived motion stimuli delivered by way of an OPTACON (OPTical-to-TActile CONverter; Telesensory Corp., Sunnyvale, CA), a reading assistance device for the blind that transforms spatial images into vibratory patterns. The OPTACON selectively activates the RA and PC units in monkeys (Gardner & Palmer, 1989). However, the PC units resolve OPTACON patterns poorly (Palmer & Gardner, 1990), suggesting that the RA units are sufficient for motion

perception. The deep skin location and large RFs of the type II units make them well suited for resolving coarse spatial information. In particular, the SAII units signal directional skin stretch that occurs during grasping (Chambers et al., 1972; Knibestöl & Vallbo, 1970; Knibestöl, 1975; Johansson et al., 1982a; Olausson, Wessberg, & Kakuda, 2000) and joint movement (Hulliger et al., 1979), whereas the FAII units are extremely sensitive to high frequency remote vibrations (64-400 Hz) like those transmitted via handheld tools (Johansson et al., 1982a).

The hairy skin, which covers more than 90% of the body surface (Halata, 1993), consists of five classes of mechanoreceptive units, namely SAI, SAII, FAII, hair follicle, and field units. FAI units are thought to be absent in the hairy skin. However, Johansson, Trulsson, Olsson, and Westberg (1988) reported that five of 24 mechanoreceptive units in the face that were not associated with hairs had response properties similar to those of the FAI units in the glabrous skin. On the other hand, FAII units are typically considered to be in both the glabrous and hairy skin, but psychophysics and microneurography research suggest that they are absent in the face (Barlow, 1987; Hollins, Delemos, & Goble, 1991; Johansson et al., 1988; Johansson & Olsson, 1976; Trulsson & Johansson, 2002). In addition, the FAII units have been shown to be absent (Olausson et al., 2000) or scarce (Vallbo et al., 1995) in the forearm. In humans, hair follicle and field units are both fast adapting and unique to the hairy skin (Järvilehto, Hämäläinen, & Laurinen, 1976; Vallbo et al., 1995). As the name implies, hair follicle units respond to hair displacement, with movement against the direction of the hair being more effective than movement with it (Vallbo et al., 1995). Hair follicle units have been described as the functional equivalent of the FAI units (Willis, 2008); that is, they are responsive to dynamic (or moving)

stimuli. Both the hair follicle and field units have relatively large irregular RFs with multiple high sensitivity spots. However, the field units respond to skin contact (not hair movement), are more densely packed, have larger RFs, and their structure is unknown (Vallbo et al., 1995).

In addition to the aforementioned A-fibres, the hairy skin contains unmyelinated slow-conducting C-fibres (see McGlone, Vallbo, Olausson, & Wessberg, 2007 for review). In humans, the high-threshold C-fibres are nociceptors and thermoceptors, whereas the low-threshold C-fibres are mechanoreceptors (Johansson et al., 1988; Nordin, 1990; Olausson et al., 2002; Vallbo, Olausson, & Wessberg, 1999; Vallbo, Olausson, Wessberg, & Norrsell, 1993; Wessberg, Olausson, Fernström, & Vallbo, 2003). The C-mechanoreceptors adapt to sustained stimulation at an intermediate rate and respond to slow moving stimuli like gentle brush stroking (Nordin, 1990; Vallbo et al., 1993; Vallbo et al., 1999). Evidence from a patient with selective loss of the large diameter A-fibres suggests that the C-fibres are involved in emotional, not discriminative, touch. For example, the A-fibre deafferented patient reported a faint sensation of pleasant touch in response to brush stroking of the hairy skin, but was unable to discriminate the direction of motion (Olausson et al., 2002). Moreover, fMRI activation in response to brush stroking in this patient was observed exclusively in the insular cortex, which is associated with emotion recall (Phan, Wager, Taylor, & Liberzon, 2002), whereas control subjects showed activation in the insular cortex as well as in the primary and secondary somatosensory cortices (Olausson et al., 2002), which are described in the next section.

1.1.2 Organization of somatosensory cortex

Sensory information from the mechanoreceptive units ascends to the cerebral cortex via the dorsal column-medial lemniscal pathway (Dreyer, Schneider, Metz, & Whitsel, 1973), synapsing twice along the way. The first-order mechanoreceptive afferents terminate in the gracile (lower body) or cuneate (upper body) nucleus of the caudal medulla. The second-order afferents decussate on their way to the thalamus, synapsing in either the ventral posterior lateral nucleus (VPL) in the case of the body or ventral posterior medial nucleus (VPM) in the case of the face. The third-order afferents terminate in the postcentral gyrus (PCG) of the parietal lobe.

The PCG is also referred to as the primary somatosensory cortex (SI) because it is the first cortical synapse for tactile information. It is located posterior to the central sulcus, or Rolandic fissure, and consists of four functionally and cytoarchitecturally distinct subregions, namely Brodmann's areas (BA) 3a, 3b, 1, and 2 that are arranged in sequence from anterior to posterior (Kaas, Nelson, Sur, Lin, & Merzenich, 1979). Within each subregion there is a topographic map of the body that reflects the innervation density of the skin (Gardner & Kandel, 2000). The medial part of the PCG represents the lower limb and lower trunk, the middle third represents the arm and hand, and the lateral third the face and head.

Areas 3b and 1 receive input from the cutaneous mechanoreceptive units, whereas areas 3a and 2 receive input from the deep muscle and joint units (Iwamura et al., 1993; Jones & Porter, 1980; Phillips, Powell, & Wiesendanger, 1971; Recanzone, Merzenich, & Jenkins, 1992; Schwarz, Deecke, & Fredrickson, 1973; Taoka et al., 1998; Wiesendanger & Miles, 1982). The neocortex consists of six cytoarchitecturally distinct

layers, which are traversed by columns (Mountcastle, 1957; Hubel & Wiesel, 1959). In area 3b, each cortical column processes information from a particular skin area and class of mechanoreceptive units. Specifically, there are two types of columns, one for FA unit input and one for SA unit input (Sur, Wall, & Kaas, 1981, 1984). The complexity and size of the RFs has been shown to increase from anterior (area 3) to posterior (areas 1, 2, and 5) in the PCG (Hyvärinen & Poranen, 1978; Iwamura, Iriki, & Tanaka, 1994; Iwamura, Tanaka, Sakamoto, & Hikosaka, 1983; Sur, Garraghty, & Bruce, 1985; Sur, 1980), suggesting information is processed in a hierarchical fashion (see Iwamura, 1998 for review). In accordance, motion sensitive neurons are found throughout SI, with the majority being in 3b, whereas direction selective neurons (i.e., neurons that respond to motion in a particular direction, but much less to motion in the opposite direction) are concentrated in areas 1 and 2 (Costanzo & Gardner, 1980; Gardner, 1988; Hyvärinen & Poranen, 1978; Warren et al., 1986; Whitsel et al., 1972).

SII is located along the superior bank (i.e., parietal operculum) of the lateral sulcus, or Sylvian fissure (Woolsey, Erickson, & Gilson, 1979), and is reciprocally connected to ipsilateral SI (Friedman, Murray, O'Neill, & Mishkin, 1986). The majority of projections to SII originate from SI, as evidenced by the fact that SII is unresponsive following lesions to SI (Pons, Garraghty, Friedman, & Mishkin, 1987; Pons, Garraghty, & Mishkin, 1992). However, there are also some projections directly from the thalamus to SII (Friedman & Murray, 1986). SII neurons have larger, often bilateral, and more complex RFs than those in SI (Iwamura, 1998). Further, the majority of these neurons are more responsive to moving tactile stimuli than stationary stimuli (Whitsel et al., 1969), and are thought to play an important role in texture perception (Pruett, Sinclair, &

Burton, 2000). Multiple SII subregions have been identified; however, the precise number is unclear. Research on monkeys has identified two (Burton, Videen, & Raichle, 1993; Whitsel et al., 1969) to three (Fitzgerald, Lane, Thakur, & Hsiao, 2004) somatotopically-organized subregions. There is recent evidence that human SII consists of four cytoarchitecturally distinct regions (OP 1-4), each subserving a different functional role (Eickhoff, Schleicher, Zilles, & Amunts, 2005).

The PPC is located caudal to SI and consists of two anatomical subregions, namely the superior (SPL, BA 5 and 7) and inferior (IPL, BA 39 and 40) parietal lobules. Neurons in areas 5 and 7 are often direction selective and have large (often bilateral) RFs that cover entire limbs or the whole body (Leinonen et al., 1979; Sakata et al., 1973). The SPL and IPL are separated by the intraparietal sulcus (IPS). In both monkeys and humans, the IPS consists of five functionally defined subregions (see Grefkes & Fink, 2005 for review). One of these regions, the ventral intraparietal area (VIP), receives visual input from middle temporal area (MT) as well as somatosensory input from multiple areas (Jones & Powell, 1969; Lewis & van Essen, 2000; Maunsell & van Essen, 1983b; Ungerleider & Desimone, 1986). The majority of VIP neurons are direction selective and respond to visual and tactile stimuli near the head and face (Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998).

Human functional neuroimaging studies have supported the involvement of the aforementioned parietal regions in unilateral tactile motion processing. For example, Summers et al. (2009) observed activation in the contralateral SI, bilateral SII, and bilateral PPC in response to unilateral vibrotactile motion on the fingertip. Similar parietal cortex activation patterns have been reported in response to airflow (Bremmer et

al., 2001), brush strokes (Polonara et al., 1999; Hagen et al. 2002; Maihöfner et al., 2004; Yoo et al., 2003), and moving patterns (Burton et al., 1997; Nakashita et al., 2008). Selective attention tasks have shown that SII and PPC process higher-level features of tactile stimuli; SII is preferentially activated by microgeometric features of tactile stimuli like texture, whereas PPC is preferentially activated by macrogeometric features like shape (Bodegård, Geyer, Grefkes, Zilles, & Roland, 2001; Burton, Abend, MacLeod, Sinclair, Snyder, & Raichle, 1999; Kitada, Kochiyama, Hashimoto, Naito, & Matsumura, 2003; Ledberg, O'Sullivan, Kinomura, & Roland, 1995; O'Sullivan, Roland, & Kawashima, 1994; Roland, O'Sullivan, & Kawashima, 1998). Area VIP processes multi-sensory information in a head-centered frame of reference. Bremmer et al. (2001) showed that airflow on the forehead activated VIP more than rest. However, there is also evidence that VIP processes tactile motion signals away from the head. Specifically, Hagen et al. (2002) observed IPS activation in response to brush strokes to the forearm and palm compared to rest, and suggested it may correspond to VIP.

1.2 PSYCHOPHYSICAL RESEARCH ON THE MAE

1.2.1 Brief review of the visual MAE

The visual MAE occurs when prolonged exposure to a continuously moving stimulus in one direction makes subsequently presented stationary stimuli appear to move in the opposite direction (Wohlgemuth, 1911). For example, stationary rocks appear to float upward when preceded by prolonged viewing of downward flowing water (Addams, 1884; Thompson, 1880). In vision, the MAE is a robust illusion, effectively observed in all individuals. Further, it has been reported in several nonhuman species, including

rhesus monkeys (Scott & Powell, 1963), insects (Srinivasan & Dvorak, 1979), cats (Berkley, 1990), and most recently pigeons (Xiao & Güntürkün, 2008).

The first scientific report of the visual MAE was the now landmark monograph of Wohlgemuth (1911). In a typical experiment, subjects view a moving (or 'adapting') stimulus for a fixed period of time followed by a stationary (or 'test') stimulus. The subjects' task is to report the duration for which they perceive the MAE. The visual MAE duration is approximately the square root of the adapting duration (Hershenson, 1989, 1993). Thus, an adapting duration of 60 s would yield an MAE of approximately 8 s. However, the illusion can be postponed or "stored" if the subjects close their eyes or a blank screen is inserted between the adapting and test stimuli (Culham et al., 2001; Spigel, 1960; Thompson & Wright, 1994; Verstraten, Fredericksen, Grusser, & van de Grind, 1994; Wohlgemuth, 1911). In fact, there are reports that the MAE can be stored for more than 25 hours following 15 minutes of adaptation (Hershenson, 1985; Masland, 1969)!

Several theoretical accounts have been put forward to explain the visual MAE (see Mather & Harris, 1998 for review). One prominent explanation is that the illusion results from the adaptation of direction selective neurons (Sutherland, 1961). In support of this view, it has been shown that exposure to continuous motion in one direction decreases the responsiveness of MT neurons (see 1.3.1 for details of MT) in non-human primates that are sensitive to that direction (Petersen, Baker, & Allman, 1985). This results in an imbalance of spontaneous activity such that a subsequently presented stationary stimulus evokes a larger response from the unadapted neurons that are sensitive to the opposite direction. However, this model cannot account for certain

findings, including the storage effect (Anstis, Verstraten, & Mather, 1998). Mather et al. (1998) detail alternative explanations.

1.2.2 Tactile MAE

The first known attempt to induce the tMAE was by Wohlgemuth (1911) in the final experiment of his monograph on the visual MAE. Using a cord knotted at fixed intervals, the volar aspect of the forearm was adapted at several unspecified rates and durations. Although the tMAE was not observed, Wohlgemuth concluded that it was worthy of further investigation.

In a series of 10 experiments Thalman (1922) continued the pursuit of the tMAE. In nine of the experiments the volar aspect of the forearm was adapted at several speeds using corrugated materials, such as a muslin belt with regularly spaced cloth strips adhered to it. Although the prevalence of the illusion was relatively low when averaged across all experiments (approximately 25%), Thalman did generate a set of conditions that reliably induced the tMAE in each of the four subjects. In particular, the tMAE was reported on over 90% of the trials when the belt corrugated at 4 cm intervals: 1) moved in a longitudinal direction across the entire length of the arm, 2) adapted the arm for 120 s at relatively fast rates of speed (39 and 109 cm/s), and 3) remained in stationary contact with the skin during the test phase. In addition, Thalman successfully induced the illusion on the calf of the leg.

The tMAE did not appear in the literature again for almost 50 years. Using a belt corrugated at 5 cm intervals and moving across the skin at 75 cm/s, Hazlewood (1971) adapted the glabrous and hairy skin, namely the fingertips, palm, and forearm. Several

manipulations were tested, such as including a stationary surround, telling the subjects to expect motion, and adapting the skin transversely or longitudinally. No matter the condition, there were very few reports of the tMAE, and of those reported, approximately half were in the unexpected (positive) direction.

More recently, Hollins and Favorov (1994) investigated the effectiveness of different test stimuli (Experiment 1) and adapting durations (Experiment 2). In both experiments the apparatus was a 9 cm diameter cylindrical drum with smooth fibrous ridges adhered at regular intervals parallel to the axis of rotation. During the adapting phase the subjects cupped their right hands excluding the thumb on the upper surface of the cylinder as it rotated at 60 rpm. In Experiment 1, the adapting phase lasted 120 s and three test conditions were examined: 1) Lift hand and hold in air, 2) Lift hand into air, then immediately lower back onto stationary cylinder, and 3) Lift hand into air, then immediately lower onto terrycloth-covered cylinder. Overall, the subjects reported the tMAE on at least 73% of the trials, and all subjects perceived the MAE during each condition. The vividness ratings did not differ across conditions, suggesting that the test stimulus (or lack thereof) was not critical for the perceived strength of the tMAE. Interestingly, the judgments of tMAE direction varied across subjects: Three subjects consistently reported the illusion in the negative direction, one consistently reported it in the positive direction, and one reported it in both directions across trials (i.e., positive in the initial trials and negative in the later trials). In Experiment 2, five adapting durations were tested: 30, 60, 90, 120, and 180 s, and the terrycloth-covered cylinder served as the test stimulus. The subjects were instructed to verbally mark the offset of the tMAE; the time that elapsed between the end of adapting period and the tMAE offset was measured.

Overall, the tMAE was reported on more than 98% of trials, and lasted between 9 and 92 s. The mean tMAE duration and vividness ratings increased as a function of adapting duration, and the judgments of direction were the same as in the previous experiment (i.e., four subjects reported the illusion in the negative direction and one in the positive direction). Taken together, these experiments were interpreted as evidence for the existence of a robust tMAE.

To date, only two studies have examined the effect of adapting duration on the tMAE (Hollins & Favorov, 1994; Thalman, 1922), and the relationship between adapting speed and the tMAE has yet to be assessed. As such, Experiment 2 of Chapter 2 tested the effect of adapting speed on the prevalence, duration, and vividness of the tMAE. Chapter 3 followed up this experiment by manipulating adapting speed and duration, thereby allowing the interaction between the two variables to be assessed.

Lerner and Craig (2002) attempted to replicate Hollins and Favorov (1994) using both a cylinder and an OPTACON. While the cylinder likely activates all of the mechanoreceptive units to some degree (Greenspan & Bolanowski, 1996), the OPTACON has been shown to selectively activate the FA units in monkeys (Gardner & Palmer, 1989). Thus, the inclusion of the OPTACON would indicate whether SA unit activation is critical for the perception of the tMAE. The fingers and palm including the thumb were adapted using a cylinder rotating at 60 rpm for 120 s. During the test phase, the hand was lifted into the air, and then placed back on the stationary cylinder. The OPTACON adapted the distal pad of the index finger by activating successive rows, creating the sensation of distal-to-proximal motion at a rate of 28 cm/sec. The subjects held their finger in the air during the test phase. No matter the adapting device, tMAEs

were reported on approximately half of the trials. Given that the prevalence did not differ between the cylinder and OPTACON, the tMAE does not appear to depend on the activation of SA units. However, it is not clear which FA unit(s) underlie the tMAE. Chapter 4 investigated this issue by adapting areas of the glabrous and hairy skin that differ in their composition of FA units.

The apparatuses and procedures of Hollins and Favorov (1994) and Lerner and Craig (2002) were virtually identical, and yet the former reported the tMAE on 98% of trials and the latter on only 50%. Lerner and Craig suggested that slight differences in the cylinder apparatuses (i.e., size of ridges and the type of adhesive tape covering) between the two studies might account for the discrepancy. However, another methodological difference was overlooked in their discussion; namely, the inclusion of the thumb. Hollins and Favorov adapted the hand excluding the thumb, whereas Lerner and Craig adapted the hand including the thumb. It is possible that this seemingly minor difference caused the divergent results. Experiment 1 of Chapter 2 addressed this question by adapting three skin areas, namely the fingers excluding the thumb, palm and fingers including the thumb, and palms and fingers excluding the thumb.

Recently, the poor reproducibility of the tMAE gained the attention of Watanabe and colleagues who argued that the discrepant findings were due to the non-optimal combination of adapting and test stimuli (Watanabe et al., 2007). That is, the rotating cylinder in the adapting phase primarily activates FA units, whereas the stationary cylinder in the test phase primarily activates SA units. However, the incompatibility between adapting and test stimuli cannot explain why Lerner and Craig (2002) were unable to replicate Hollins and Favorov (1994). Both studies used nearly identical

apparatuses and procedures, and yet Hollins and Favorov reported the illusion on over 90% of the trials, and Lerner and Craig on only 50%. Neither study should have observed robust tMAEs if activating the same class of mechanoreceptive units during the adapting and test phases is necessary. Nevertheless, Watanabe et al. (2007) activated the same class of mechanoreceptive units by presenting moving stimuli in the adapting and test phases. Specifically, they used vibrotactile pins to induce apparent motion on the glabrous surface of the right index finger, and then presented the pins again as test stimuli. There were three conditions: No adaptation, Upward adaptation, and Downward adaptation. The test stimuli were presented at various interstimulus onset intervals (ISOIs) ranging from –120 (upward motion) to 120 s (downward motion). The subjects' task was to indicate the direction of the test stimuli. The results showed that there were fewer "upward" responses when adaptation was in the upward direction. Likewise, there were fewer "downward" responses when adaptation was in the downward direction. The authors concluded that tactile motion adaptation influenced the perceived direction of the test phase motion such that the number of responses corresponding to the opposite direction systematically increased. Thus, when the FA units were activated in both phases, tMAEs were reliably observed.

1.3 MOTION PROCESSING AND AREA MT+

1.3.1 Visual motion processing and MT+

The neural basis of visual motion processing was first described in the early 1970s. In particular, neurons in area MT, also known as V5, of the monkey extrastriate cortex were shown to be sensitive to motion (Allman & Kaas, 1971; Dubner & Zeki,

1971; Zeki, 1978). The majority of monkey MT neurons are direction selective (Albright, 1984; Bisley, Zaksas, Droll, & Pasternak, 2004; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Maunsell & van Essen, 1983a), and injury to this region has been shown to impair visual motion processing (Cowey & Marcar, 1992; Marcar & Cowey, 1992; Newsome, Wurtz, Dürsteler, & Mikami, 1985; Newsome & Paré, 1988; Schiller, 1993). In addition to MT, the adjacent medial superior temporal area (MST) contains direction selective neurons that are particularly responsive to complex motion, such as rotation and expansion/contraction (Lagae et al., 1994). Tracer research in monkeys has shown that area MT is reciprocally connected to visual areas V1, V2, V3, V4, and MST, and parietal area VIP. In addition, subcortical areas, such as the claustrum, pulvinar nucleus of the thalamus, and basal ganglia, receive projections from MT (Maunsell & van Essen, 1983b).

The motion-sensitive homologue in humans is believed to include MT and its satellite area MST (see Huk, Dougherty, & Heeger, 2002 for review), and is thusly referred to as MT+. Although there is considerable inter-individual variability in the location of MT+, it is generally believed to be in the ascending limb of the inferior temporal sulcus (Bundo, Kaneoke, Inao, Yoshida, Nakamura, & Kakigi, 2000; Dumoulin et al., 2000; Wilms et al., 2005). Neuroimaging research has shown that MT+ is more responsive to visual motion than static images (McCarthy, Spicer, Adrignolo, Luby, Gore, & Allison, 1995; Tootell et al., 1995b; Watson et al., 1993; Zeki, Watson, Lueck, Friston, Kennard, & Frackowiak, 1991). Not only is MT+ activation associated with visual motion stimuli, but it is necessary for motion perception to occur. As in the monkey, lesions to this region selectively impair visual motion perception (Vaina,

Lemay, Bienfang, Choi, & Nakayama, 1990; Zihl, von Cramon, & Mai, 1983; Zihl, von Cramon, Mai, & Schmid, 1991; see Zeki, 1991 for review). Further, virtual lesions induced by transcranial magnetic stimulation (TMS) have been shown to disrupt motion perception when delivered over MT, but not control areas, compared to the perception of static stimuli (Beckers & Hömberg, 1992; Beckers & Zeki, 1995; Stewart, Battelli, Walsh, & Cowey, 1999).

1.3.2 MAE and MT+

In addition to being responsive to natural visual motion, neuroimaging research has shown that MT+ is activated by apparent motion (Goebel, Khoram-Sefat, Muckli, Hacker, & Singer, 1998; Kaneoke, Bundou, Koyama, Suzuki, & Kakigi, 1997; Muckli, Kriegeskorte, Lanfermann, Zanela, Singer, & Goebel, 2002), implied motion (Fawcett, Hillebrand, & Singh, 2007; Kim & Blake, 2007; Kourtzi & Kanwisher, 2000; Senior et al., 2000), motion imagery (Goebel et al., 1998; but see also Blake et al., 2004), and the MAE (Berman & Colby, 2002; Culham et al., 1999; Hautzel et al., 2001; He et al., 1998; Taylor et al., 2000; Tootell et al., 1995a; but see also Huk et al., 2001).

Using fMRI Tootell et al. (1995a) were the first to investigate the central neural basis of the visual MAE in humans. These authors observed greater MT activation in response to static rings preceded by unidirectionally moving rings (MAE condition) than static rings preceded by oscillating rings (no MAE condition). In addition, the decay of MT activation was shown to correlate with the decay of the perceptual MAE. This relationship, which has been corroborated by other groups (Berman & Colby, 2002; He et al., 1998), suggests that MT responds to perceived as well as natural visual motion.

Culham et al. (1999) used fMRI and the storage effect to further investigate the correspondence between MAE perception and MT+ activation. The results showed that MT+ was not effectively activated during the storage period, but emerged when the static test pattern was presented. This is strong evidence that MT+ activation corresponds to perceived visual motion. MT activation has also been reported by others as part of a broad network supporting the visual MAE (Hautzel et al., 2001; Taylor et al., 2000).

Attention has been shown to modulate MT+ activation (Beauchamp, Cox, & DeYoe, 1997; Berman & Colby, 2002; O'Craven, Rosen, Kwong, Treisman, & Savoy, 1997; Rees, Frith, & Lavie, 1997). In fact, Huk et al. (2001) argued that the increased MT+ activation observed during MAE experiments might be due to differences in attentional demands between the MAE trial and its control. That is, a moving stimulus is inherently more interesting and attracts more attention than its stationary counterpart, and it is this increased attention that leads to MT+ activation. To test this hypothesis, these researchers replicated the results of earlier MAE studies, and then went on to control for attention. The addition of the attention task removed the MT+ activation observed previously, suggesting that attention, and not perceived motion, accounts for the increased MT+ activation during the visual MAE. However, neuronal disinhibition following adaptation may explain the increased MT+ activation (Krekelberg, Boynton, & van Wezel, 2006).

The general conclusion of neuroimaging research that MT+ underlies the visual MAE has been supported by stimulation techniques. Specifically, TMS over MT+, and not control areas, has been shown to disrupt the visual MAE when delivered either early in the storage phase or during MAE perception itself (Stewart et al., 1999; Théoret et al.,

2002). Similar results have been obtained using transcranial direct current stimulation (Antal et al., 2004).

1.3.3 Multi-sensory motion processing and MT+

MT+ is traditionally regarded as a unisensory visual motion processing area. Consistent with the view, Zihl et al. (1983) showed that a patient with bilateral lesions to MT+ had deficits in visual motion processing, but not auditory or tactile motion processing. However, there is currently debate, primarily driven by neuroimaging research, about whether MT+ is a multi-sensory motion processing area. For example, Poirier and colleagues observed a greater MT+ response to moving sounds compared to static sounds in both sighted (Poirier et al., 2005) and blind subjects (Poirier et al., 2006). Further, Berman and Colby (2002) showed that MT+ activation in response to visual motion could be modulated by both visual and auditory attention. In contrast, others have failed to observe differential MT+ activation to moving and stationary auditory stimuli (Bremmer et al., 2001; Smith et al., 2004, 2007), or have reported negative MT+ activation in response to auditory motion (Lewis et al., 2000). The results of tactile motion studies are also mixed, with some groups reporting MT+ activation (Blake et al., 2004; Hagen et al., 2002; Ricciardi et al., 2007; Summers et al., 2009) and others reporting no activation (Bremmer et al., 2001) or negative activation (Bodegård et al., 2000; Nakashita et al., 2008). Using positron emission tomography (PET), Hagen et al. (2002) observed an increase in blood flow to MT+ bilaterally in response to tactile motion (i.e., brush stroke along the volar surface of the forearm and palm) compared to rest. These foci overlapped with the areas activated by radial visual motion. However, it

should be noted that subjects kept their eyes closed during the tactile motion scans, thus raising the possibility that they visualized the motion (Sathian & Lacey, 2007). However, Blake et al. (2004) showed that MT+ activation did not differ significantly between visualizing a rotating globe and rest, suggesting that MT+ activation during tactile motion tasks is not solely due to visual imagery.

Recently, Ricciardi et al. (2007) addressed the issue of whether visual imagery is responsible for the MT+ activation observed during tactile motion tasks. Specifically, sighted subjects were presented with static or moving dots either visually or tactually to the right or left hand (middle and index finger) while brain activity was measured using fMRI. In addition, congenitally and early blind subjects participated in the tactile conditions. In sighted subjects, visual motion activated MT+ and tactile motion selectively activated the more anterior portion of this region, perhaps corresponding to MST. In both the early and congenitally blind subjects, tactile motion activated more or less the entire MT+ region, including the area activated by visual motion in the sighted. Given that MT+ activation was observed in the early and congenitally blind subjects, the authors argued that visual imagery could not account for the robust MT+ activation by tactile motion in the sighted subjects. However, it may be that the anterior portion of MT+ is activated by visual motion and visual motion imagery (not tactile motion) in sighted subjects, whereas MT+ activation in blind subjects is the result of crossmodal plasticity. For example, neuroimaging studies have shown that tactile stimuli activate visual cortex in the blind (Sadato et al., 1996) and visual stimuli activate auditory cortex in the deaf (Finney, Fine, & Dobkins, 2001). Nevertheless, Ricciardi et al. concluded that visual experience serves to segregate MT+ into an anterior region, which processes tactile

and visual motion, and a posterior region, which processes visual motion only. In support of this functional segregation, Beauchamp, Yasar, Kishan, and Ro (2007) showed that SII and MST, but not MT, responded to rapidly presented vibrotactile stimulation to the hands and feet. Another area within the ventro-occipital region, namely the lateral occipital complex (LOC), is similarly segregated. In general, LOC is activated more by images of objects than scrambled images; however, a subregion of LOC, the so-called lateral occipital tactile-visual (LOtv) area, is activated by objects presented visually or tactually (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; Amedi, Malach, Hendler, Peled, & Zohary, 2001).

In summary, several parietal areas are involved in tactile motion processing. In addition, there is evidence that MT+ is responsive to real auditory, visual, and tactile motion and illusory visual motion. As such, it may also respond to illusory tactile motion, namely the tMAE. Chapter 5 will investigate the central neural basis of tactile motion perception and the tMAE using fMRI.

CHAPTER 2

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The tactile motion aftereffect revisited

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Abstract

In two experiments, we measured the direction, duration, frequency, and vividness of the tactile motion aftereffect (MAE) induced by a rotating drum with a ridged surface. In Experiment 1, we adapted the: 1) Fingers and palm, including the thumb, 2) Fingers and palm, excluding the thumb, and 3) Fingers only, excluding the thumb. In each condition the drum rotated at 60 rpm for 120 s. There was no difference in duration, frequency, or vividness between the skin surfaces tested. In Experiment 2, we tested several adapting speeds: 15, 30, 45, 60, and 75 rpm. At each speed the fingers and palm, excluding the thumb, were adapted for 120 s. The duration, frequency, and vividness of the tactile MAE increased linearly with adapting speed. Overall, the tactile MAE was reported on approximately half of the trials, suggesting that it is not as robust as its visual counterpart.

The tactile motion aftereffect revisited

Under certain conditions, adaptation (i.e., decreased sensitivity following prolonged stimulation) to a continuously moving stimulus in one direction makes subsequently presented stationary stimuli seem to move in the opposite direction -- the so-called motion aftereffect (MAE). In vision, a well-known example of the MAE is the "waterfall illusion," in which prolonged viewing of downward flowing water makes subsequently viewed stationary rocks appear to float upward (Addams 1834; Thompson 1880). The visual MAE has been studied extensively both behaviorally and physiologically. However, relatively little attention has been given to its tactile analogue.

The first attempt to induce a tactile MAE was reported by Wohlgemuth (1911) in his landmark monograph. After conducting a lengthy series of experiments on the visual MAE, Wohlgemuth attempted to induce a tactile MAE by adapting the forearms of subjects with silk cord, knotted at fixed intervals. The vague account of the procedure noted that the adapting period lasted between 1 and 3 minutes, and that the cord either remained in contact with the skin as it came to a stop or it dropped off the arm while it was still in motion. The adapting speeds were not reported. Based on the results of these manipulations, Wohlgemuth (1911) concluded that, "under the given experimental conditions, no analogous after-effect of movement exists in the case of touch." p.88. He states later, however, that the possibility of a tactile MAE warrants further investigation.

Thalman (1922) continued to pursue the tactile MAE, and was the first to report positive results. In nine of 10 experiments, the ventral forearms of four subjects were adapted at several speeds using corrugated surfaces (e.g., a muslin belt with cloth strips sewn on at regular intervals). Subjects were given a verbal signal at the end of the

adapting period, at which point they paid attention to any resultant aftersensations and verbally reported them. Across all of the experiments, subjects reported the MAE on 16% of the trials in which the belt was removed from the arm during the test phase and on 25% of the trials in which the belt remained in contact with the arm during the test phase. However, Thalman (1922) was able to generate a set of conditions that reliably induced the tactile MAE in all of the subjects. In particular, subjects reported the tactile MAE on over 90% of the trials when the belt: 1) moved in a longitudinal direction across the entire length of the arm, 2) adapted the arm for 120 s at a fast (39 cm/sec) or very fast (109 cm/sec) rate of speed, and 3) remained in contact with the arm, in a stationary position, during the test phase.

These initial contradictory findings led Hazlewood (1971) to investigate the occurrence of tactile MAE further. The fingertips or forearms of relatively large samples of subjects were adapted for 120 s at 75 cm/sec using a corrugated surface. Subjects were instructed to report any illusory movement of the apparatus following the adapting period. Several manipulations were tested, such as including a stationary surround, telling the subjects to expect motion, and adapting the skin transversely or longitudinally. No matter the condition, there were very few reports of the MAE, and of those reported, around half were in the unexpected (positive) direction.

The tactile MAE did not make another appearance in the literature until almost 25 years later when Hollins and Favorov (1994) studied the effectiveness of different postadapting (or test) stimuli (Experiment 1) and adapting durations (Experiment 2). The apparatus was a 9 cm diameter cylindrical drum with smooth fibrous ridges affixed at regular intervals parallel to the axis of rotation. Five subjects placed their right hand,

excluding the thumb, palm down on the upper surface of the drum as it rotated at 60 rpm (or 28 cm/sec). In Experiment 1, three post adapting conditions were tested: 1) Lift hand into air, 2) Lift hand into air, then lower back onto stationary drum, and 3) Lift hand into air, then lower onto terrycloth-covered drum. Following the adapting period, subjects attended to, and verbally reported, any resultant aftersensations. Overall, the subjects reported the MAE on at least 73% of the trials, and all subjects perceived the MAE during each condition. However, the judgments of direction varied across subjects: Three subjects consistently reported the illusion in the negative direction, one consistently reported it in the positive direction, and one reported it in both directions across trials (i.e., positive in the initial trials and negative in the later trials). The vividness ratings did not differ across the conditions, suggesting that the test stimulus (or lack thereof) is not critical for the induction of the tactile MAE. In Experiment 2, five adapting durations were tested: 30, 60, 90, 120, and 180 s, and the terrycloth-covered drum served as the test stimulus. Subjects were instructed to verbally mark the offset of the MAE, and the time that elapsed between the end of adapting period and the offset of the MAE was measured. The tactile MAE was reported on more than 98% of trials, and lasted between 9 and 92 s. The judgments of direction were the same as in the previous experiment: Four subjects reported the illusion in the negative direction and one in the positive direction. The duration, which was assessed by subjects verbally reporting the onset and offset of the illusion, increased linearly across the first 2 minutes, with only a modest gain between 120 and 180 s. The vividness ratings also increased as a function of adapting duration. Taken together, these findings suggest that the tactile MAE is quite robust and lasts much

longer than its visual counterpart, which generally increases as a square-root function of the adapting duration (Hershenson 1989, 1993).

To investigate the physiological basis of the illusion Lerner and Craig (2002) used a drum nearly identical to that of Hollins and Favorov (1994) and an Optacon (OPTical-to-TActile CONverter; Telesensory Corp., Sunnyvale, CA), a vibratory assistance device for the blind. Unlike the drum, which stimulates all of the mechanoreceptors to some degree (Greenspan and Bolanowski 1996), the Optacon does not activate the slow adapting (SAI) fibres, and it likely does not activate the SAII fibres (Gardner and Palmer 1989). Thus, the inclusion of the Optacon would indicate whether the activation of the SA fibres is critical for the perception of the tactile MAE. In the first phase of the experiment fifty subjects completed a series of trials using the drum and another series using the OPTACON. The drum adapted the fingers and palm, including the thumb, for 120 s at 60 rpm (or 28 cm/sec). During the test phase the hand was lifted into the air, and then placed back on the stationary drum. The OPTACON adapted the distal pad of the index finger by activating successive rows, creating the sensation of distal-to-proximal motion at a rate of 28 cm/sec. The finger was held in the air during the test phase. Subjects then filled out a response sheet, which included a checklist of adjectives and space to write descriptions or list other sensations that may have occurred. No matter the adapting apparatus, MAEs were reported on approximately half of the trials. There were more reports of positive than negative MAEs on the drum, but the frequency of the direction judgments did not differ on the OPTACON. It was not stated whether the direction judgments were consistent within subjects. Given that the frequency of the

tactile MAE did not differ between the drum and Optacon, it does not appear to depend on activation of the SA fibres.

The apparatuses and procedures used by Hollins and Favorov (1994) and Lerner and Craig (2002) were virtually identical, and yet the former reported the tactile MAE on 98% of trials and the latter on only 50%. Lerner and Craig (2002) suggested that slight differences in the size of their ridges and the tape that covered the drum might account for the discrepancy. However, another procedural difference was overlooked in their discussion; namely, the inclusion of the thumb. Hollins and Favorov (1994) adapted the hand, excluding the thumb, whereas Lerner and Craig (2002) adapted the hand, including the thumb. It is possible that this seemingly minor difference led to their discrepant findings. For example, when resting on a drum, the conformation of the hand causes the thumb to be at a slight angle relative to the axis of rotation; that is, the thumb is not completely parallel to the other fingers.

EXPERIMENT 1

The purpose of Experiment 1 was to determine whether the duration, frequency, and vividness of the tactile MAE differ between adapted regions of the volar right hand. In particular, we adapted the: 1) Fingers and palm, including the thumb, 2) Fingers and palm, excluding the thumb, and 3) Fingers only, excluding the thumb. If the inclusion of the thumb weakens the tactile MAE, we would expect to observe a lower frequency in the fingers and palm, including the thumb, condition compared to the other two conditions that do not adapt the thumb.

Methods

Subjects

Twenty-four right-handed volunteers (mean age, 20.71 ± 0.67 years; 20 female, 4 male) served as subjects. All subjects provided written informed consent for the procedures in this experiment, which were approved by the Research Ethics Board at Wilfrid Laurier University. To avoid issues with an unequal number of data points across conditions, only the 11 subjects (mean age, 21.55 ± 1.14 years, 8 female, 3 male) who perceived the tactile MAE in each condition were included in the duration and vividness analyses.

Apparatus

The experimental apparatus was a custom-built cylindrical plastic drum connected to a .33 HP Leeson AC Gearmotor via a pulley system. In particular, there was a pulley connected to the motor and another to the drum. The two pulleys were connected to each other via a thin rope belt that was approximately 180 cm in length. When engaged the motor rotated the pulley attached to it, which in turn caused the drum to rotate.

The motor was controlled by an AC Tech MC1000 series variable frequency drive, which was connected to an Apple Powerbook G4 computer via a National Instruments interface. The speed of the drum was set manually on the drive console and the direction and on / off duration of the drum were controlled by code written in Matlab. It took approximately 100 ms for the drum to ramp up to, and down from, its target speed.

The drum was 20.3 cm long and 9 cm in diameter. The surface consisted of flexible ridges made of mounting tape (two-sided adhesive tape with a fibrous core) affixed at regular intervals parallel to the axis of rotation. The ridges were 3 mm high, 1.2 cm wide, 17.8 cm long, and spaced approximately 1.35 cm apart. Broad strips (5.1 cm wide) of transparent smooth adhesive tape covered the ridges, closely following the square-wave pattern. Previous research has shown that a smooth tape covering results in less tingling than microtextured materials (e.g., corduroy, felt; Thalman 1922; Hollins and Favorov 1994), thus making the sensations of motion more discernible.

A custom-made plunger-style button was connected to the computer via the USB port. The Matlab program recorded the button presses (see Procedure for details).

Procedure

Throughout each session, the subject was seated comfortably at a table in front of the drum. Baby powder was applied (and re-applied, as necessary) to the volar surface of the right hand of subjects to reduce friction with the drum. To mask the sound emitted by the motor, subjects wore earplugs and listened to white noise via circumaural headphones. The experimenter sat to the immediate right of the subject in front of the computer.

At the beginning of each trial, the subject cupped his or her right hand and positioned it palm down just above the drum. The drum was engaged via the Matlab program and the subject closed his or her eyes. The experimenter then tapped the subject lightly on the right shoulder, indicating that he or she should lower the right hand onto the rotating drum. The drum rotated in a proximal to distal direction. After 2 minutes of

stimulation at 60 rpm (or 28 cm/sec), the experimenter tapped the subject on the shoulder again, at which point the subject lifted his or her hand into the air, and then immediately lowered it back onto the now stationary drum. Note that the hand was not in contact with the drum as it came to a stop. Subjects kept their hands on the stationary drum for at least one minute whether they perceived the illusion or not, as it has been reported previously that the illusion may not appear immediately (Hazlewood 1971) and it may also recur (Hollins and Favorov 1994).

Subjects were instructed to pay attention to any sensations they perceived on or in their right hand when they placed it back onto the stationary drum. In particular, they were asked to note whether any resultant sensations were directional, no matter the direction. To measure the duration of the MAE, subjects pressed a plunger-style button with their left thumb when the sensation started and again when it ended. If the MAE recurred, its onset and offset were also marked with button presses. Subjects were instructed to keep their hand on the drum until the experimenter turned off the white noise, at which point they were asked to describe the MAE in their own words, report its direction, and rate its vividness on a 10-point scale (1 = not vivid, 10 = very vivid), if applicable. The experimenter entered the responses into the computer. The subsequent trial began after a 2-minute rest period or when any tingling subsided, whichever came last.

There were 3 adapting conditions: 1) Fingers and palm, including the thumb, 2) Fingers and palm, excluding the thumb, and 3) Fingers only, excluding the thumb. The fingers were defined as the volar surface of the hand distal to the metacarpophalangeal joint. The hand included the volar surface distal to the base of the thenar eminence. The

experiment proper consisted of 3 sessions (one per condition) with 5 trials in each. Only one session was run per day. The order of the conditions was counterbalanced across subjects. A pre-testing session was held to familiarize the subjects with the apparatus and procedure.

Results

The tactile MAE was reported on 43% of the fingers and palm, excluding the thumb trials, 45% of the fingers and palm, including the thumb trials, and 48% of the fingers only, excluding the thumb trials. A repeated-measures analysis of variance (ANOVA) performed on these data showed no difference in frequency between the three conditions, $F(2, 46) = .24, p = .784$.

Reports of direction were categorized into positive, negative, and other. Trials were categorized as 'other' when motion was described as lateral (left-to-right or right-to-left), radial, spiral, zigzag, both positive and negative, etc. Overall, the tactile MAE was reported on 45% of the trials: 22% in the positive direction, 18% in the negative direction, and 5% in 'other' direction.

The duration and vividness data from the subjects who experienced the tactile MAE in each of the three conditions (n = 11) are shown in Figures 1 and 2, respectively. Repeated-measures ANOVAs performed on these data showed that neither duration, $F(2, 20) = .26, p = .776$, or vividness, $F(2, 20) = .66, p = .528$, differed across the conditions.

EXPERIMENT 2

Experiment 2 measured the direction, duration, frequency, and vividness of the tactile MAE at several adapting speeds; namely, 15, 30, 45, 60, and 75 rpm (or 7, 14, 21, 28, and 35 cm/sec). Previous research has measured the frequency of the tactile MAE at several adapting speeds (Thalman 1922), but the relationship has not been described systematically. More recently, it has been shown that 60 rpm (or 28 cm/sec) is moderately (Lerner and Craig 2002) to very effective (Hollins and Favorov 1994) at inducing the illusion. Additionally, it has been suggested that 30 rpm (or 14 cm/sec) is ineffective at inducing the illusion (Lerner and Craig 2002).

Methods

Subjects

Twenty new right-handed volunteers (mean age, 19.55 ± 0.57 years; 14 female, 6 male), including one of the authors (PJP), participated in Experiment 2 after providing written informed consent. The tactile MAE was only reported on 12% of the 15-rpm (or 7-cm/sec) trials. Given the relative lack of data in this condition, it was excluded from the duration and vividness analyses. Ten subjects (mean age, 19.2 ± 0.44; 6 female, 4 male) who reported the tactile MAE at each of the remaining adapting speeds were included in the duration and vividness analyses.

Apparatus

The same apparatus from Experiment 1 was used in Experiment 2.

Procedure

On each trial the right fingers and palm, excluding the thumb, were adapted for 2 minutes. Five adapting speeds were tested: 15, 30, 45, 60, and 75 rpm (or 7, 14, 21, 28, and 35 cm/sec). During each of the five sessions, subjects completed five trials, one per adapting speed. The trials were presented in a random order. All other procedures were identical to Experiment 1.

Results

Figure 3 shows the frequency data as a function of adapting speed. Overall, the tactile MAE was reported on 40.4% of the trials: 19.8% in the positive direction, 12.8% in the negative direction, and 7.8% in 'other' direction. The direction of the tactile MAE was fairly consistent within subjects; no matter the adapting speed, subjects reported the tactile MAE as occurring in a particular direction.

A repeated-measures ANOVA revealed a significant difference in frequency across the adapting speeds, $F(4, 76) = 15.94, p < .001$; the frequency of the tactile MAE increased linearly with adapting speed.

Figure 4 shows the mean duration of the tactile MAE as a function of adapting speed. A repeated-measures ANOVA performed on these data showed a significant effect of adapting speed on mean duration, $F(3, 27) = 4.8, p = .008$; the mean duration of the tactile MAE increased as a function of adapting speed, with a sharp increase between 45 and 60 rpm and only a modest increase between 60 and 75 rpm.

The mean vividness ratings as a function of adapting speed are displayed in Figure 5. A repeated-measures ANOVA showed that the mean vividness ratings differed

significantly across the adapting speeds, $F(3, 27) = 15.2, p < .001$; the mean vividness ratings increased linearly as a function of adapting speed.

Discussion

Experiment 1 showed that there were no differences in the duration, frequency, and vividness of the tactile MAE across the adapted regions of the right hand. Thus, the discrepant frequencies between Hollins and Favorov (1994) and Lerner and Craig (2002) cannot be accounted for by the latter study's adaptation of the thumb along with the hand. In fact, it has been shown that the tactile MAE can be readily induced on other regions of the body, namely the leg (Thalman 1922).

Overall, the tactile MAE was reported on approximately half of the trials, which is akin to the results of Lerner and Craig (2002). To date, two studies have reported robust tactile MAEs (Thalman 1922; Hollins and Favorov 1994) and three have reported weak MAEs or unsuccessful attempts to induce it (Wohlgemuth 1911; Hazlewood 1971; Lerner and Craig 2002). The two successful studies tested few subjects (4-5), whereas at least two of the three unsuccessful attempts tested larger samples (17-50). Note that Wohlgemuth (1911) did not report how many subjects he tested. Like the other less than successful attempts to induce the illusion, we tested approximately 20 subjects in each of our experiments. There were considerable individual differences in the reports of the tactile MAE – some subjects reported it on every trial, others only on some trials, and others never reported it. Thus, the few subjects in the successful studies may have been those who are more prone to perceiving the illusion.

It is possible that differences in mechanoreceptor density may account for the variability in reporting the tactile MAE between individuals. The fast adapting (FAI) afferent fibers, which terminate in Meissner corpuscles (Lindblom 1965), signal motion across the glabrous skin (Essick and Edin 1995; Gardner and Palmer 1989; Gardner and Sklar, 1994; Srinivasan, Whitehouse and LaMotte, 1990). Anatomical studies have reported cases in which Meissner corpuscles were absent in the glabrous skin of humans. For example, Dillon, Haynes, and Henneberg (2001) reported that there were no Meissner corpuscles in the fingers of one of the 28 cadavers, and Schimrigk and Ruettinger (1980) reported that two of the 30 cadavers contained no Meissner corpuscles in their big toes. Thus, approximately 3-7% of the cadavers were missing Meissner corpuscles. Interestingly, 9% of the subjects in Experiments 1 and 2 never reported experiencing the tactile MAE. Perhaps this inability to induce the illusion was due to a lack of Meissner corpuscles.

The context in which the trials were presented may have also influenced the frequency of the MAE. Consider that when the hand, excluding the thumb, was adapted at 60 rpm, 25% of the subjects reported the illusion on 80% or more of the trials in Experiment 1, but 45% of the subjects reported the illusion on 80% or more of the trials in Experiment 2.

Differences in contact force and response bias do not seem to impact the frequency of the MAE, and therefore they cannot explain the individual differences. As indicated by Lerner and Craig (2002), the stimulation delivered by the Optacon is less intense than that delivered by the drum. Despite this, both apparatuses induced the illusion on approximately the same number of trials. In terms of response bias, Lerner

and Craig (2002) informed subjects of the purpose of the experiment between Phases 1 and 2, and this did not lead to a substantial increase in their reports of the MAE.

Experiment 2 showed that the duration, frequency, and vividness of the tactile MAE increased linearly with adapting speed. While Thalman (1922) measured the frequency of the tactile MAE at a few speeds, Experiment 2 was the first to characterize the relationship, and also to measure the duration and vividness of the illusion at several speeds. Hollins and Favorov (1994) reported the mean duration of the tactile MAE to be approximately 50 s when the fingers and palm, excluding the thumb, were adapted for 120 s at 60 rpm. However, at the same adapting speed and duration, the mean MAE duration was approximately 8 s in Experiment 1 and 5 s in Experiment 2, suggesting that the tactile MAE is relatively short lasting. The discrepancy in duration between the present experiments and that of Hollins and Favorov (1994) may be the result of different methods of measurement. Specifically, subjects in Hollins and Favorov (1994) verbally reported the end of the MAE, and its duration was calculated as the time that elapsed between the end of actual stimulation and the end of the MAE. In the present experiments, subjects marked the onset *and* offset of the MAE with a button press, and the duration was calculated by subtracting the time of the first press from the time of the second press. Given that the MAE did not always start immediately upon the cessation of actual stimulation, it is possible that the duration measurements of Hollins and Favorov (1994) were inflated by not taking this into account.

The frequency, duration, and vividness of the tactile MAE increase with adapting duration (Hollins and Favorov 1994) and also adapting speed (Experiment 2). In both cases, the independent variable is confounded with the total number of revolutions. That

is, when adapting duration is held constant and adapting speed is increased, the total number of revolutions increases. When adapting speed is held constant and adapting duration is increased, the total number of revolutions also increases. Therefore, it is not clear whether increases in tactile MAE frequency are due to increases in speed and duration or the total number of revolutions. Future research should hold the total number of revolutions constant to investigate this possibility.

Thalman (1922) showed that the ideal stimulus for inducing the tactile MAE was a low spatial frequency square wave pattern. Similarly, Hollins and Favorov (1994) attributed their high induction rate to the stiff fibrous ridges covered with smooth tape, and suggested that more textured materials cause tingling that may obscure the MAE. However, the present experiments and Lerner and Craig (2002) employed a virtually identical apparatus to Hollins and Favorov (1994), and in the absence of the MAE, subjects often reported a stationary tingle or numbness in the adapted region.

When motion was reported, it was described using a variety of terms, with the most common being "tingle". Other descriptors included wave, pulse, light touch, tickle, and moving drum. This variety of tactile MAE descriptors has been noted previously (Thalman 1922; Hollins and Favorov 1994; Lerner and Craig 2002). Typically, the MAE was localized to the region (or a sub-region) of adaptation. Surprisingly, however, there were a few reports of motion extending into the forearm or occurring on the hairy surface of the hand. There were no reports of a recurrence of the tactile MAE.

The tactile MAE was reported in positive, negative, and 'other' directions. 'Other' trials included lateral, radial, and spiral motion. Previously, the tactile MAE has been reported in the negative and positive directions (Hazlewood 1971; Hollins and Favorov

1994; Lerner and Craig 2002) as well as 'other' directions (Lerner and Craig 2002). Hollins and Favorov (1994) explained their results using the model of somatosensory cortical dynamics (Whitsel et al, 1989, 1991), which can account for both negative and positive MAEs. However, it cannot account for three findings reported in the present experiments: 1) lateral, radiating, and spiral MAEs, 2) MAEs in unadapted regions (e.g., arm) and 3) the low frequency rate of MAEs. Clearly, much needs to be done before we have a clear understanding of this phenomenon.

Acknowledgements

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Figure Captions

Figure 1. Mean duration of the tactile MAE as a function of adapted skin surface. Error bars represent the standard errors of the mean. Note that only the 11 subjects who reported the tactile MAE in all conditions are displayed.

Figure 2. Mean vividness ratings of the tactile MAE as a function of adapted skin surface. Error bars represent the standard errors of the mean. Note that only the 11 subjects who reported the tactile MAE in all conditions are displayed.

Figure 3. Frequency of the tactile MAE as a function of adapting speed (n = 20). Error bars represent the standard errors of the mean.

Figure 4. Mean duration of the tactile MAE as a function of adapting speed. Error bars represent the standard errors of the mean. Note that 15 rpm is omitted and that only the 10 subjects who reported the tactile MAE at the four remaining adapting speeds are displayed.

Figure 5. Mean vividness ratings of the tactile MAE as a function of adapting speed. Error bars represent the standard errors of the mean. Note that 15 rpm is omitted and that only the 10 subjects who reported the tactile MAE at the four remaining adapting speeds are displayed.

Figure 1.

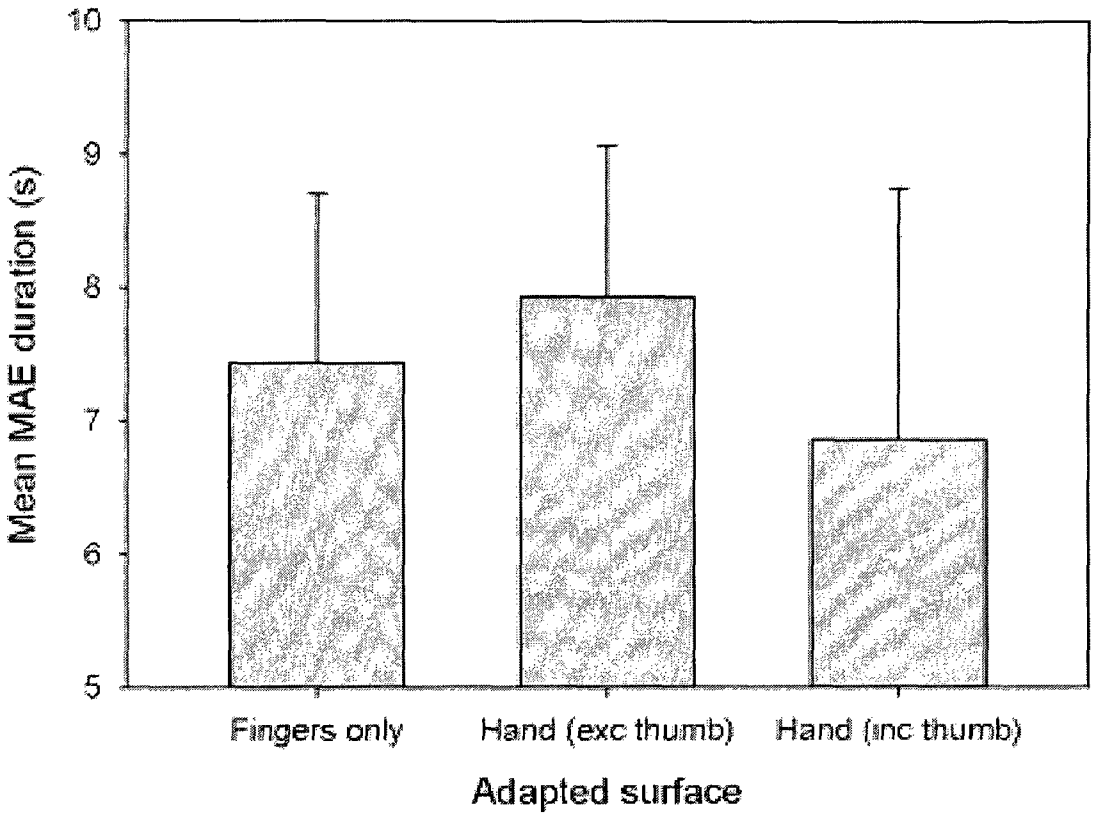

10
9
8
7
6
5
Mean MAE duration (s)
Fingers only
Hand (exc thumb)
Hand (inc thumb)
Adapted surface

Figure 2.

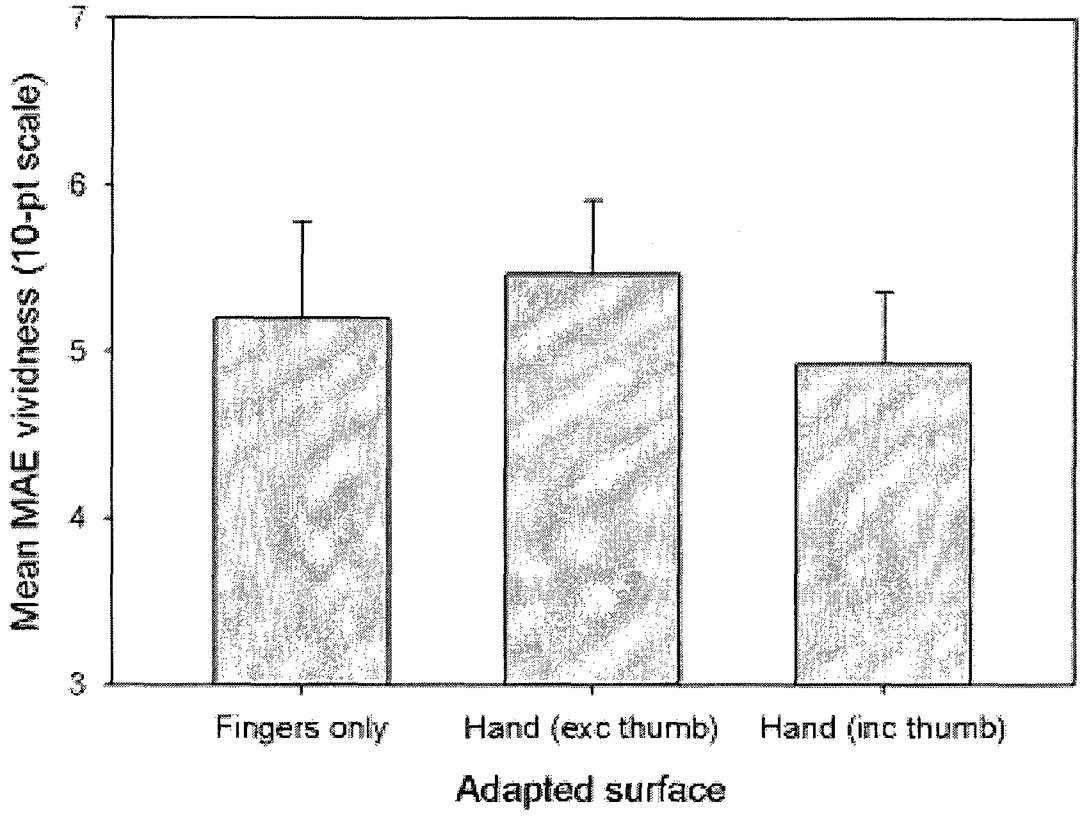

Mean MAE vividness (10-pt scale)
7
6
5
4
3
Fingers only
Hand (exc thumb)
Hand (inc thumb)
Adapted surface

Figure 3.

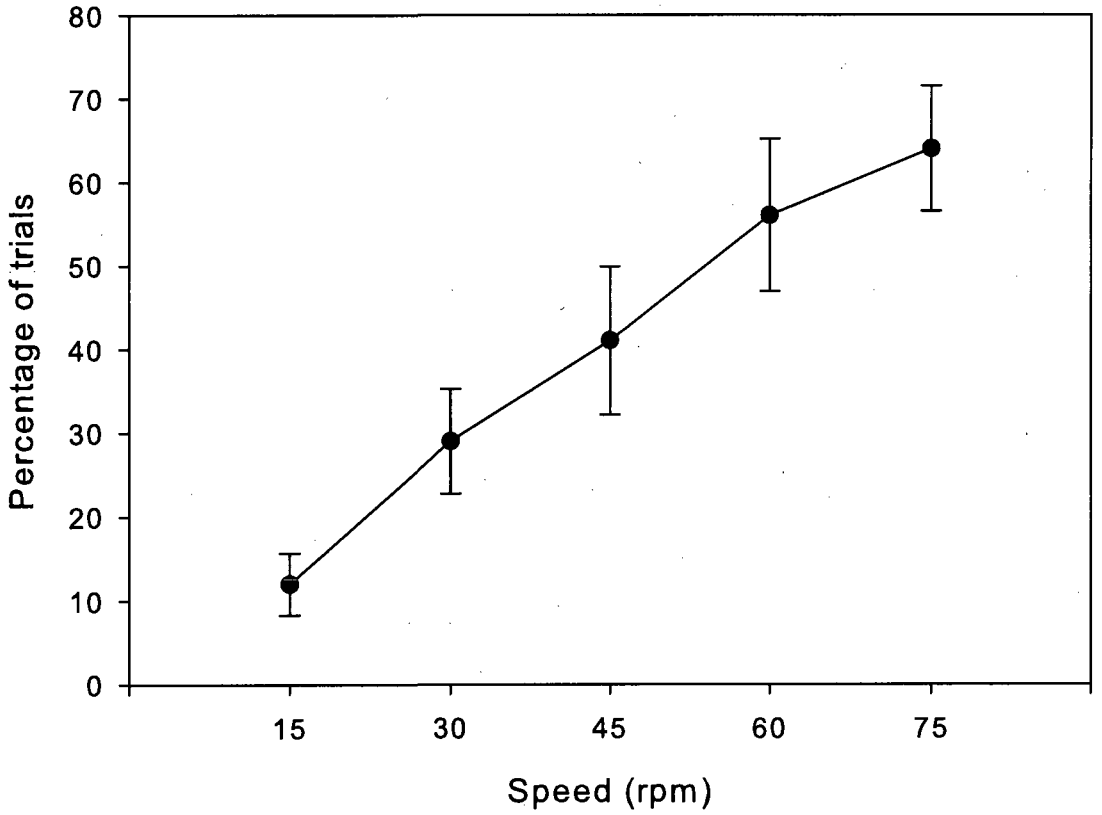
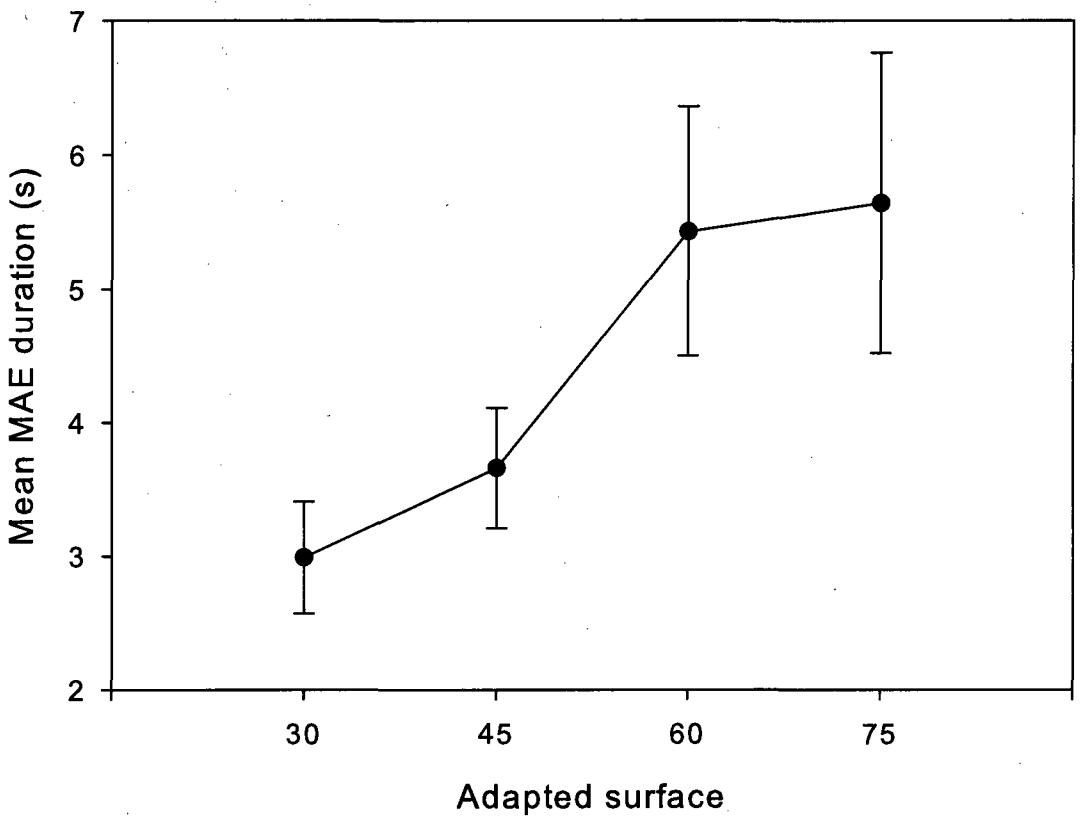
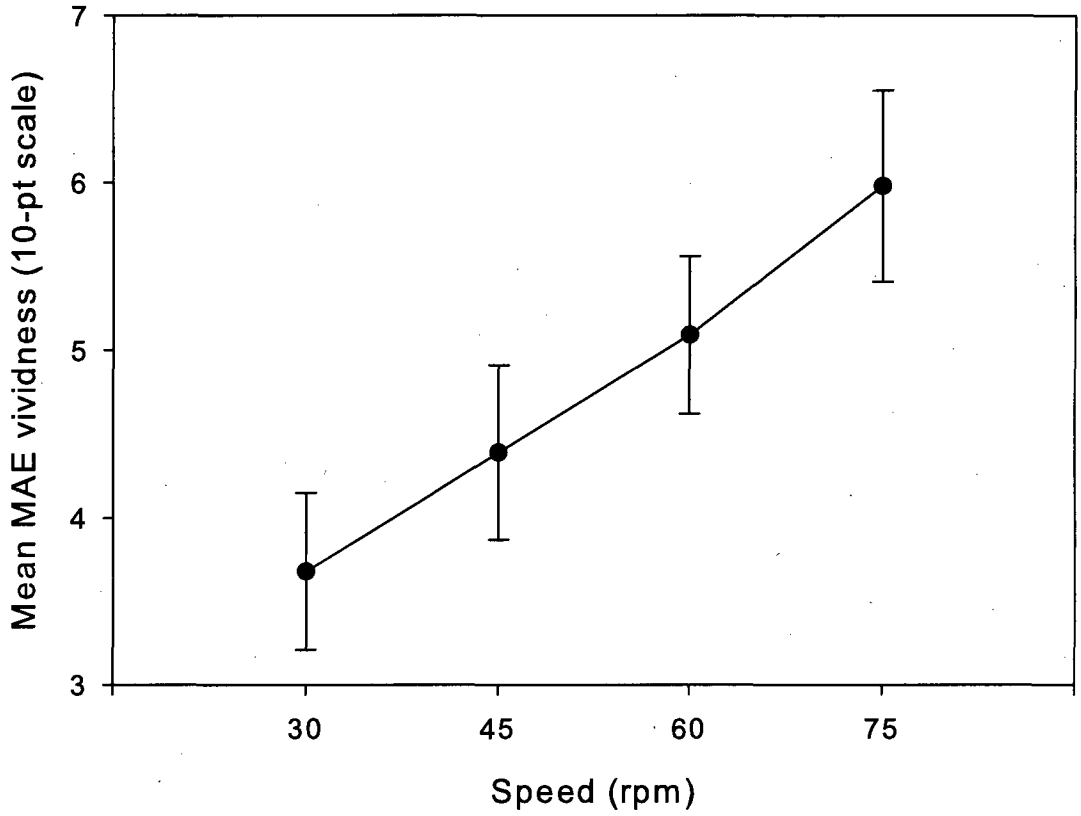

80
70
60
50
40
30
20
10
0
Percentage of trials
15
30
45
60
75
Speed (rpm)

Figure 4.



Note: x-axis should read "Speed (rpm)"

Figure 5.



CHAPTER 3

The effect of adapting speed, duration, and distance on the tactile motion aftereffect

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Abstract

We investigated the effect of adapting speed, duration, and distance on the prevalence, duration, and vividness of the tactile motion aftereffect (tMAE). Using a cylindrical drum we adapted the volar surface of the right hand at two speeds (14 and 28 cm/s) and three durations (60, 120, and 240 s). Combinations of the speed and duration parameters allowed us to examine the effect of distance on the tMAE. The results showed that the prevalence, duration, and vividness of the tMAE increased with adapting speed. There was also a positive relationship between adapting duration and the prevalence, but not the duration or vividness, of the illusion. Distance was only a factor when it came to the duration of the tMAE. Taken together, these results show the importance of adapting parameters, particularly speed, on the tMAE.

Introduction

Following prolonged exposure to a continuously moving tactile stimulus in one direction, a stationary tactile stimulus may feel as though it is moving. This illusion is known as the tactile motion aftereffect (tMAE), and has been induced by several researchers using a cylindrical drum with flexible ridges affixed to it at regular intervals parallel to the axis of rotation (Hollins and Favorov 1994; Lerner and Craig 2002; Planetta and Servos 2008). Typically, the subjects cup their right hand around the upper portion of the drum, which rotates at a fixed speed during the adapting phase and is stationary (or absent) during the subsequent test phase.

Using such an adapting procedure on the volar surface of the hand, the dependence of the tMAE on adapting speed and duration has been investigated in two separate studies. Hollins and Favorov (1994) showed that there is a positive relationship between adapting duration and the duration and vividness of the tMAE; as adapting duration increased, the tMAE duration and vividness also increased. It should be noted that the prevalence of the illusion did not differ across conditions; it was consistently at or around 100%. Recently, we showed that the prevalence, duration, and vividness of the tMAE increased with adapting speed (Planetta and Servos 2008). However, given that speed * duration = distance, increasing either speed or duration also increases distance. As such, it is not clear which parameter(s) caused the observed increase in the prevalence, duration, and vividness of the tMAE.

To date, only one study has manipulated adapting speed and duration in the same study. Over 85 years ago Thalman (1922) attempted to find compulsory conditions for inducing the tMAE by adapting the volar surface of the forearm using a corrugated belt.

Across the series of experiments, the illusion was reported most reliably when the belt was corrugated at 4 cm intervals, adapted the entire length of the arm in a longitudinal direction at fast speeds (39-109 cm/s) and longer durations (~120 s), and maintained stationary contact during the test phase. However, no statistical analyses were performed on the data and Thalman himself noted that that there were too few trials (and only four subjects) to draw definitive conclusions. In addition, Thalman only tested the hairy skin, which differs from the glabrous skin in terms of its motion-sensitive mechanoreceptive units (i.e., fast adapting type I units in glabrous surface of the hand and hair follicle and field units in the forearm; Knibestöl and Vallbo 1970; Vallbo et al. 1995). Thus, the effect of adapting speed and duration on the prevalence of the tMAE (especially on the glabrous skin) is not well understood, nor is their effect on the duration and vividness of the resultant tMAE.

The present experiment investigated the effect of adapting speed, duration, and distance on the prevalence, duration, and vividness of the tMAE. To this end, we adapted the volar surface of the right hand using a cylindrical drum at two adapting speeds (14 and 28 cm/s or 30 and 60 rpm, respectively) and three adapting durations (60, 120, and 240 s). The interaction between adapting speed and duration will give us a better understanding of the influence of distance on the tMAE. In particular, two distance values (1680 and 3360 cm) were examined in the interaction between adapting speed and duration. If distance affects the tMAE prevalence, duration, or vividness, we would expect there to be no significant difference between the two 1680 cm distance values or the two 3360 cm distance values. On the other hand, if distance does not affect the

dependent variables, we would expect there to be significant difference between these values.

Methods

Subjects

Fifteen healthy right-handed volunteers (mean age, 23.60 ± 0.80 years; 9 women, 6 men) served as subjects. Eight of these subjects, including the first author, participated in previous work on the tMAE. One additional subject withdrew prior to completion of the study, and is not discussed any further. All subjects (except PJP) were compensated financially for their participation and provided written informed consent for the experimental procedures, which were approved by the Research Ethics Board at Wilfrid Laurier University. To avoid issues with missing data points, only the 13 subjects who reported the tMAE in each of the six conditions were included in the duration and vividness analyses.

Apparatus

The tMAE was induced using a custom-made plastic cylindrical drum that was 20.3 cm in length and 9 cm in diameter. The surface of the drum had strips of mounting tape (double-sided adhesive tape with a fibrous center) attached to it at regular intervals parallel to the axis of rotation. In particular, the strips of mounting tape were 3 mm in height, 1.2 cm in width, 17.8 cm in length, and spaced approximately 1.35 cm apart. Sheets of transparent smooth adhesive tape (5.1 cm in width) were used to cover the

surface of the drum, closely following the square-wave pattern created by the mounting tape.

A 0.33 HP Leeson AC Gearmotor powered the drum via a belt and pulley system. In particular, there was a pulley wheel connected to the motor and another to the drum. A thin rope that was approximately 180 cm in length ran between the pulleys. When the motor was engaged it rotated the pulley wheel attached to it, which in turn caused the drum to spin.

The motor was controlled by an AC Tech MC1000 series variable frequency drive, which was connected to a computer via a National Instruments interface. The speed of the drum was controlled by a switch selectable speed control that was added to the drive console and the on / off duration of the drum was controlled by a Matlab program (The MathWorks, Natick, MA) using the Psychophysics Toolbox (Brainard 1997). The drum took approximately 100 ms to ascend to and descend from its target speed.

A custom-made plunger-style button was connected to the computer via the USB port. The Matlab program recorded the time of the button responses (see Procedure for details)

Procedure

During each session the subjects were tested individually with only the experimenter in the room. The subjects were seated at a table directly in front of the drum, and the experimenter sat to their immediate right. The skin surface adapted by the drum was always the right palm and fingers including the thumb. Prior to contacting the drum the

subjects applied hypoallergenic baby powder to their right hand to reduce the friction between their hand and the drum. In addition, they wore earplugs and listened to white noise via headphones to mask the sound of the motor.

Each trial consisted of two phases, the adapting phase and the test phase. Prior to the adapting phase the subjects positioned their right hand just above the stationary drum. They were instructed to keep their eyes closed throughout the entire trial and to lower their hand onto the moving drum when they felt a light tap on their right shoulder. At the end of the adapting phase the drum came to a stop. Note that the hand was in contact with the drum as it came to a stop. The test phase refers to the period of time when the subjects had their hand on the stationary drum. During the test phase, which lasted at least 30 s to ensure the illusion had the opportunity to present itself, the subjects: 1) attended to any sensations felt in or on their right hand, 2) pressed the plunger-style button with their left thumb to mark the onset and offset of the tMAE, if it occurred, and 3) kept their right hand on the drum until the experimenter turned off the white noise.

Following the test phase of each trial, the experimenter turned off the white noise, indicating the trial was complete. The subjects who pressed the button were then asked to describe the tMAE (including its direction) in their own words and rate its vividness on a 10-pt scale (1 = not vivid, 10 = very vivid). The experimenter typed the verbal responses into the computer. There was a break period lasting several minutes after each trial to allow any tingling to dissipate. The subjects who did not press the button proceeded immediately to the break period.

We tested two adapting speeds (14 and 28 cm/s or 30 and 60 rpm, respectively) and three adapting durations (60, 120, and 240 s) for a total of six conditions. The

interaction between adapting speed and duration resulted in four different distances – 840, 1680, 3360, and 6720 cm. There were two conditions with a distance of 1680 cm and two with a distance of 3360 cm. To investigate the effect of distance on each dependent variable we preplanned comparisons between the 14 cm/s * 120 s condition and the 28 cm/s * 60 s condition (both 1680 cm distance) and the 14 cm/s * 240 s condition and the 28 cm/s * 120 s (both 3360 cm distance). The experiment consisted of 15 sessions, each of which was held on a different day. In each session there were six trials, one per condition, which were presented in a random order. Thus, each subject completed a total of 90 trials over the course of the experiment.

The data were analyzed using repeated measures analysis of variance and paired samples t-tests. The Bonferroni method was used to correct for multiple comparisons.

Results

The direction of the tMAE was categorized as positive (i.e., proximal to distal or same direction as the adapting motion), negative (i.e., distal to proximal or opposite direction as the adapting motion), or 'other'. Trials were classified as 'other' when the subjects reported the motion as both positive and negative (i.e., positive motion followed by negative motion or vice versa), radiating outward (and then sometimes contracting back inward), indescribable, and so on.

Overall, the tMAE was reported on 63% of the trials: 30% in the positive direction, 29% in the negative direction, and 4% in the 'other' direction. As can been seen in Figure 1 ($n = 15$) this pattern was true for each adapting a) speed and b) duration, except for 60 s in which there were more reports of negative than positive tMAEs. Only

six subjects were consistent in their reports of direction across the conditions; three subjects reported the illusion only in the negative direction and three only in the positive direction. No one consistently reported the illusion in the 'other' direction.

Figure 2 (n = 15) displays the prevalence of the tMAE for each adapting speed as a function of adapting duration. The main effect of adapting speed was highly significant, $F(1, 14) = 30.85, p < 0.001$; the illusion was reported more frequently at 28 cm/s than 14 cm/s. There was also a highly significant main effect of adapting duration, $F(2, 28) = 29.00, p < 0.001$; the prevalence of the illusion increased with adapting duration. More specifically, the three adapting durations differed significantly from each other (all ps < 0.005). The interaction between adapting speed and duration was not significant, $F(2, 28) = 0.585, p = 0.564$, suggesting that distance does not affect the prevalence of the tMAE. Pre-planned comparisons of the conditions with the same distance supported this conclusion. In particular, the comparison of 14 cm/s at 120 s and 28 cm/s at 60 s (i.e., 1680 cm distance) was significant, $t(14) = -2.90, p = 0.024$, as was the comparison of 14 cm/s at 240 s and 28 cm/s at 120 s (i.e., 3360 cm distance), $t(14) = -2.93, p = 0.022$. If distance were a factor, we would have expected the prevalence rates in the two conditions with constant distances to be comparable.

The mean duration of the tMAE for each adapting speed as a function of adapting duration is shown in Figure 3 (n = 13). There was a significant effect of adapting speed, $F(1,12) = 9.82, p = 0.009$; the illusion was longer at 28 cm/s than 14 cm/s. There was also a significant effect of adapting duration, $F(2, 24) = 14.65, p = 0.045$. However, none of the pairwise comparisons were significant (all ps > 0.08), suggesting that the effect of duration was only significant for the 28 cm/s speed. This is supported by the significant

interaction between adapting speed and duration, $F(2, 24) = 10.60$, $p = 0.046$. The preplanned comparison of 14 cm/s at 120 s and 28 cm/s at 60 s (i.e., 1680 cm distance) was not significant, $t(12) = 0.10$, $p = 1.00$, whereas the comparison of 14 cm/s at 240 s and 28 cm/s at 120 s (i.e., 3360 cm distance) was significant, $t(12) = -3.00$, $p = 0.022$. This suggests that distance may have an effect on the tMAE duration at the shorter distance, but not the longer one.

Figure 4 displays the mean vividness of the tMAE for each adapting speed as a function of adapting duration (n = 13). The effect of adapting speed was highly significant, $F(1, 12) = 35.56$, $p < 0.001$; the illusion was rated as more vivid at 28 cm/s than 14 cm/s. There was also a significant effect of adapting duration, $F(2, 24) = 3.62$, $p = 0.042$; pairwise comparisons showed that there were no significant differences between 60 s and 120 s ($p = 1.00$) or 60 s and 240 s ($p = 0.155$), but that there was a marginally significant difference between 120 s and 240 s ($p = 0.052$). The interaction between adapting speed and duration was not significant, $F(2, 24) = 3.00$, $p = 0.069$, and the preplanned distance comparisons were significant (both ps < 0.009). Taken together, these results suggest that distance does not significantly affect the vividness of the illusion.

Discussion

The present study was the first to investigate how adapting speed, duration, and distance affect the prevalence, duration, and vividness of the tMAE on the glabrous skin. The results showed that as the adapting speed increased so did the prevalence, duration, and vividness of the illusion. The prevalence of the illusion also increased with adapting

duration. However, there was not a positive relationship between adapting duration and the duration and vividness of the tMAE. The shorter distance (i.e., 1680 cm) may have affected the duration of the illusion but not its prevalence or vividness. The adapting speed seems to be particularly important for the prevalence of the illusion in that all 28 cm/s conditions were higher than all 14 cm/s conditions.

In previous research the effects of adapting speed and duration on the tMAE have been investigated separately. First, Hollins and Favorov (1994) showed that there was a positive relationship between adapting duration and the duration and vividness of the tMAE. In particular, the mean duration of the illusion increased from just over 20 s to approximately 55 s as the adapting duration increased from 30 to 180 s. Note that the adapting speed was always 60 rpm. Although we also observed a positive relationship between adapting duration and the duration of the tMAE, it certainly was not as dramatic. In fact, at the 60 rpm our mean tMAE duration increased from 4 to just less than 7 s across the adapting durations. In addition, Hollins and Favorov reported that the prevalence of the illusion did not depend on adapting duration; it was around 100% across all of the adapting durations (30 to 180 s). Given the fact that all subsequent studies using a comparable adapting apparatus have not observed such high prevalence rates (Lerner and Craig 2002; Planetta and Servos 2008) or such long durations (Planetta and Servos 2008), the results of Hollins and Favorov are questionable. Second, we have shown previously that the prevalence, duration, and vividness of the tMAE increased with adapting speed (Planetta and Servos 2008). In particular, as adapting speed increased from 7.5 to 35 cm/s (or 15 to 75 rpm, respectively), the prevalence of the illusion increased from around 10 to 65% and the its duration increased from around 3 to

5.5 s. Both of these findings are consistent with the present study. Further, the ineffectiveness of relatively slow moving adapting apparatus at inducing the tMAE has been corroborated recently in a study of illusory motion reversals (Holcombe and Seizova-Cajic 2008). In particular, there were only a few reports of short-lived (i.e., less than 3 s) tMAEs following adaptation of the fingertips to a drum with a textured surface rotating at approximately 15-20 rpm.

Interestingly, some subjects in the present study and some of our previous studies spontaneously reported illusory motion reversals during adaptation. However, we are unable to comment on the relationship between adapting speed and duration and the prevalence and duration of illusory reversals of tactile motion for two reasons. First, we did not reliably document their occurrence. Second, the subjects were not asked to report whether they experienced motion reversals during adaptation, and thus, they may have perceived it but simply did not report it. Given that there was some evidence of illusory motion reversals, it is possible that the positive and negative directions reported by subjects are a function of this. Future research should investigate this possibility.

The only other study to simultaneously test the effects of adapting speed and duration on the prevalence of the tMAE was done over 85 years ago on the hairy skin (Thalman 1922). In general, the illusion was more prevalent at faster adapting speeds and longer durations. However, the duration of the illusion was not measured, there were few subjects, and statistics were not performed on the data. In addition, we recently showed that the prevalence of the tMAE is much lower on the hairy skin than the glabrous skin (Planetta and Servos unpublished data). As such, further research is necessary to

determine how adapting speed and duration affect the prevalence, duration, and vividness of the tMAE on the hairy skin.

In summary, the present study showed the importance of adapting duration and speed on the tMAE. These results will be used to develop an effective induction protocol so that the brain activation associated with the tMAE can be measured using functional magnetic resonance imaging.

Acknowledgments

We thank Sarah Illman for assistance with data collection and Rudy Eikelboom and Dwayne Keough for helpful discussions. This study was funded by the Natural Sciences and Engineering Research Council of Canada (PS) and the Canada Research Chairs program (PS).

Declaration of interest

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

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Figure Captions

Figure 1. Percentage of trials that resulted in positive, negative, and 'other' MAEs for a) each adapting speed and b) each adapting duration (n = 15).

Figure 2. Percentage of trials in which the tactile MAE was reported for each adapting speed as a function of adapting duration (n = 15).

Figure 3. Mean duration (in seconds) and SEM of the tactile MAE for each adapting speed as a function of adapting duration (n = 13)

Figure 4. Mean vividness (on a 10-pt scale) and SEM of the tactile MAE for each adapting speed as a function of adapting duration (n = 13).

Figure 1.

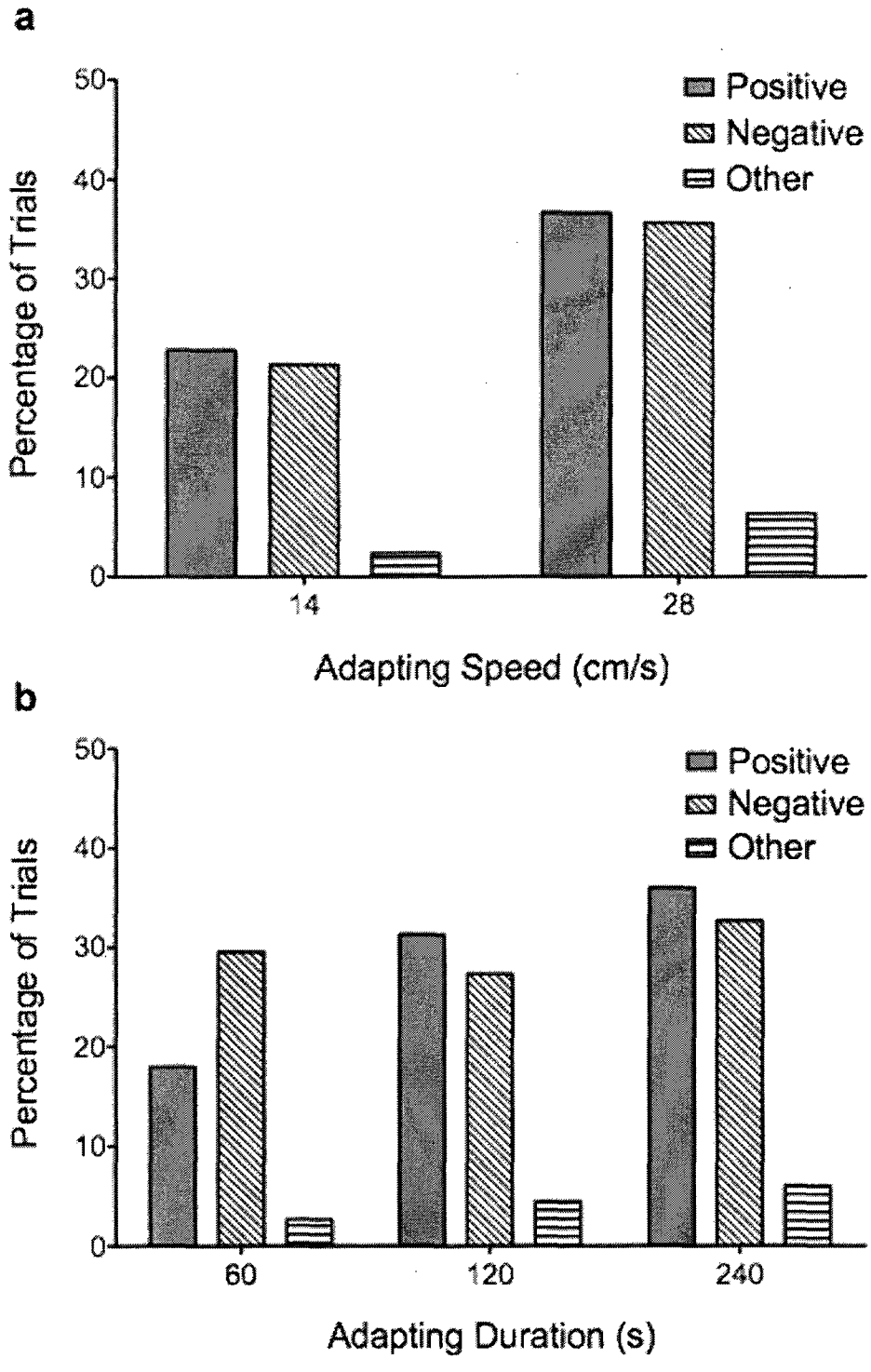

a
Positive
Negative
Other
Percentage of Trials
50
40
30
20
10
0
14
28
Adapting Speed (cm/s)
b
Positive
Negative
Other
Percentage of Trials
50
40
30
20
10
0
60
120
240
Adapting Duration (s)

Figure 2.

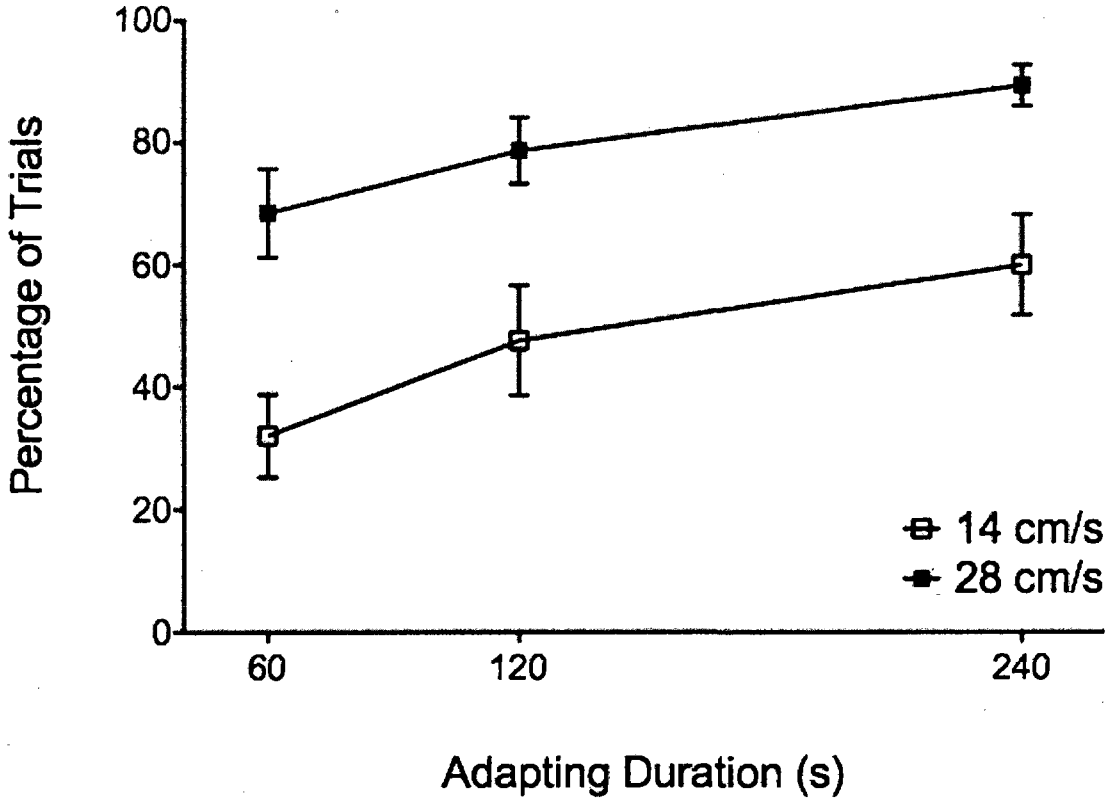

100
80
60
40
20
0
Percentage of Trials
60
120
240
Adapting Duration (s)
14 cm/s
28 cm/s

Figure 3.

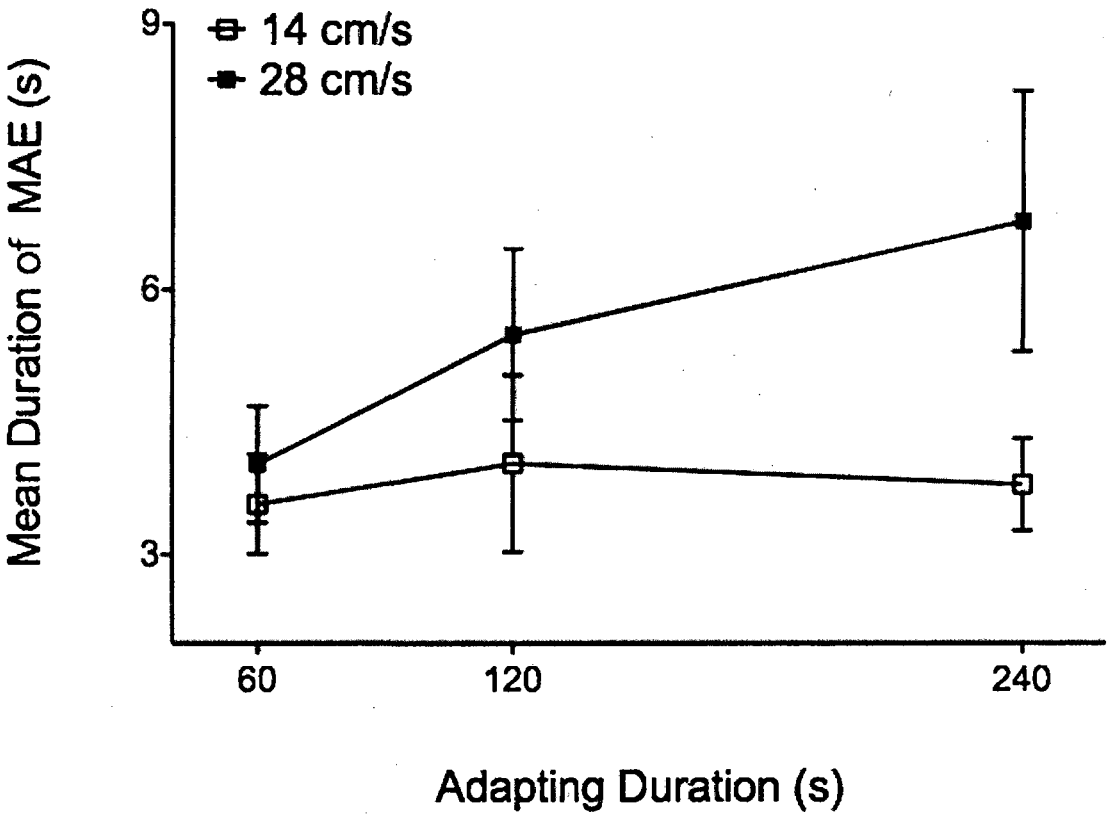
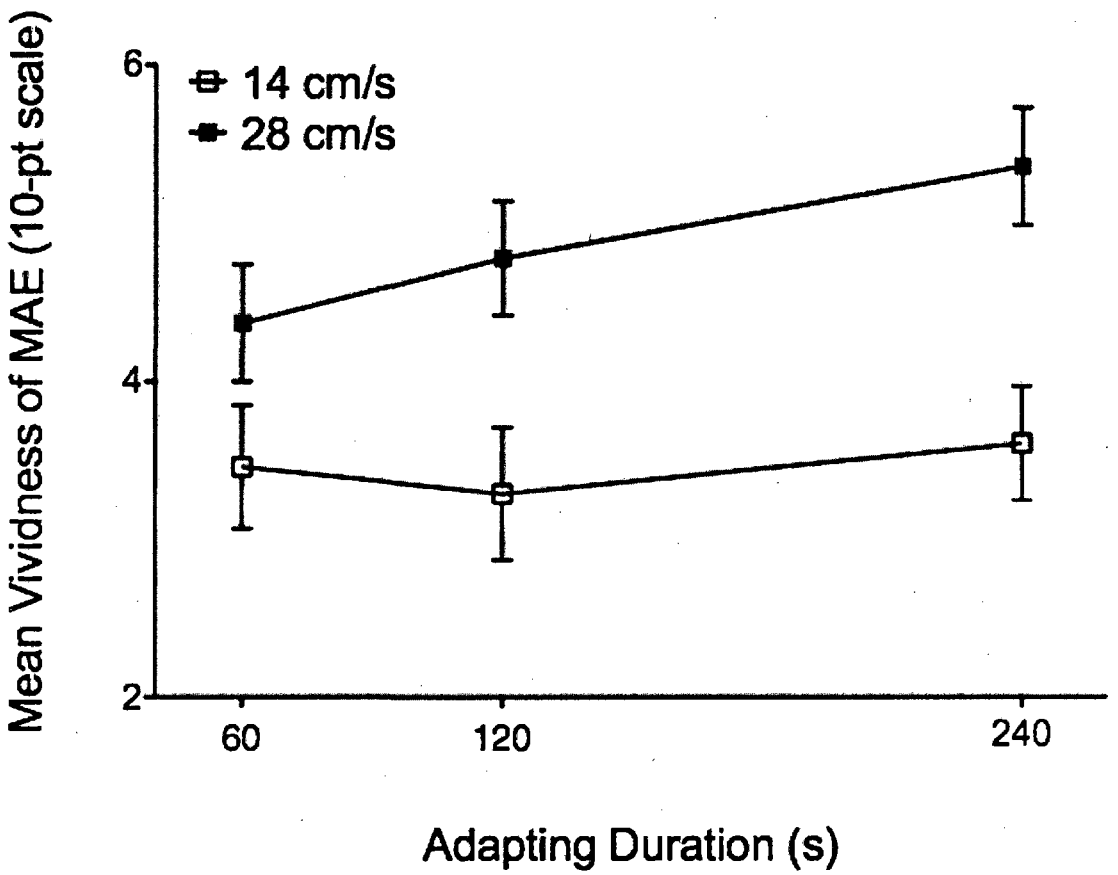

14 cm/s
28 cm/s
Mean Duration of MAE (s)
9
6
3
60
120
240
Adapting Duration (s)

Figure 4.


Mean Vividness of MAE (10-pt scale)
6
4
2
14 cm/s
28 cm/s
60
120
240
Adapting Duration (s)

CHAPTER 4

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Site of stimulation effects on the prevalence of the tactile motion aftereffect

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Abstract

The motion aftereffect (MAE) refers to the apparent motion of a stationary stimulus following adaptation to a continuously moving stimulus. There is a growing consensus that the fast adapting (FA) rather than the slowly adapting afferent units mediate the tactile version of the MAE. The present study investigated which FA units underlie the tactile MAE by measuring its prevalence, duration, and vividness on different skin areas that vary in their composition of FA units. Specifically, the right cheek, volar surface of the forearm, and volar surface of the hand were adapted using a ridged cylindrical drum, which rotated at 60 rpm for 120 s. Although there was no difference in duration or vividness between the skin surfaces tested, the tactile MAE was reported twice as often on the hand compared to the cheek and forearm, which did not differ significantly from one another. This suggests that the FA I units in the glabrous skin and the hair follicle units and/or the FA I and field units in the hairy skin contribute to the tMAE.

Keywords: cutaneous afferents, mechanoreceptors, motion aftereffect, perceptual illusion, sensory adaptation, tactual perception

Introduction

Our sense of touch provides us with pain, pressure, and thermal information about our immediate environment, enabling us to successfully and safely navigate and interact with the world around us. One aspect of touch that is particularly important is motion perception – the ability to track potentially interesting stimuli on the surface of the skin and predict their future position. Psychophysical research on the ability of humans to detect and discriminate between moving tactile stimuli dates back over a century (Hall and Donaldson 1885).

As in the visual system, illusory motion phenomena have been observed in the tactile system. In the current paper we examine one such illusion, the tactile motion aftereffect (MAE), in which adaptation to a unidirectionally moving stimulus on the skin causes the apparent motion of a subsequently presented stationary stimulus. Relatively little attention has been given to the tactile MAE. Moreover, the results of the few studies that have been conducted are not conclusive; the illusion was successfully induced on the majority of trials in three studies (Hollins and Favorov, 1994; Thalman 1922; Watanabe et al. 2007), whereas it was less consistently observed in four other studies (Hazlewood 1971; Lerner and Craig 2002; Planetta and Servos 2008; Wohlgemuth 1911).

To our knowledge, only two papers have investigated the peripheral basis of the tactile MAE. Lerner and Craig (2002) induced the illusion using a drum and an OPTACON (OPTical-to-TActile CONverter; Telesensory Corp., Sunnyvale, CA), a vibratory reading assistance device for the blind. While the corrugated drum surface activates the fast adapting (FA), and to a lesser extent the slowly adapting (SA), mechanoreceptive units (Greenspan and Bolanowski 1996), the OPTACON has been

shown to selectively activate the FA units in monkeys (Gardner and Palmer 1989). Thus, the inclusion of the OPTACON would indicate whether the SA units contribute significantly to the tactile MAE. In the first phase of the experiment the subjects completed a set of trials using the drum and another set using the OPTACON. Each device was used to adapt the left and right hand for 120 s on separate trials. The drum adapted the volar surface of the hand including the thumb at 60 rpm (or 28 cm/s). During the test phase the hand was lifted into the air while the drum came to a stop, and then was immediately placed back onto the stationary drum. The OPTACON adapted the distal pad of the index finger by activating successive rows, creating the sensation of distal-to-proximal motion at a rate of 28 cm/s. The finger was held in the air during the test phase. Regardless of the adapting apparatus, the tactile MAE was reported on approximately half of the trials. Given that the prevalence of the tactile MAE did not differ between the drum and OPTACON conditions, it was concluded that the illusion depends primarily on the activation of the FA units.

Recently, Watanabe et al. (2007) provided further evidence that the FA units underlie the tactile MAE by testing the hypothesis that the poor reproducibility of the illusion across studies was due to the non-optimal combination of adapting and test stimuli. In previous research, the adapted skin surface was either held motionless in the air or was placed on a stationary surface during the test phase. Thus, FA (and sometimes SA, depending on the stimulus) units were activated during the adapting phase (moving stimulus), whereas SA units (motionless stimulus) or no units (no stimulus) were activated during the test phase. To test the importance of stimulus compatibility on the tactile MAE these researchers activated the FA units during both the adapting and test

phases. Specifically, the volar surface of the right index finger was adapted using three vibrating metal pins spaced 5 mm apart that were activated sequentially with an interstimulus onset interval (ISOI) of 100 ms, giving the perception of apparent motion. There were three adapting conditions: No adaptation (i.e., stationary pins), upward adaptation, and downward adaptation. Following adaptation, the pins were presented again in either the downward or upward direction at various ISOIs, ranging from 0 to 120 ms. The task was to judge the direction of the test stimulus as upward or downward. Overall, the results showed that there were fewer "upward" responses when adaptation was in the upward direction than when there was no adaptation. Likewise, there were fewer "downward" responses when adaptation was in the downward direction than when there was no adaptation. Thus, by activating the FA units in both the adapting and test phases, Watanabe et al. observed a robust tactile MAE. Similarly, it has been shown that the perceived speed of a moving test stimulus on the fingertips was reduced following adaptation to motion in the same direction (Hazlewood 1971).

Taken together, these studies show the importance of the FA units in the perception of the tactile MAE. However, the human skin consists of four types of FA units, namely the FA type I (FA I), FA type II (FA II), hair follicle, and field units, and thus it remains unclear which of these units are important for the tactile MAE. Although the FA units are located throughout the entire surface of the skin, they are not distributed uniformly. The FA I units are located at the dermal-epidermal border, have relatively small receptive fields with several high sensitivity spots, innervate the skin densely, and are described as being exclusive to the glabrous (or non-hairy skin), whereas the FA II units are located in the dermis and subcutaneous tissue, have relatively large receptive

fields with a single high sensitivity spot, innervate the skin sparsely, and are located in both the glabrous and hairy skin (Johansson 1976, 1978; Johansson and Vallbo 1979; Vallbo and Johansson 1984; Vallbo et al. 1995). However, note that there is one report of FA I units in the facial skin (Johansson et al. 1988) and convergent evidence that FA II units are absent in the face (Barlow 1987; Darian-Smith 1973; Hollins et al. 1991; Johansson and Olsson 1976; Johansson et al. 1988). Further, FA II units have poor spatial resolution and are not considered important for motion perception (Johnson 2001). Hair follicle and field units are unique to the hairy skin, with the former responding to hair displacement and the latter responding to skin contact (Vallbo et al. 1995). Both the hair follicle and field units have large irregular receptive fields with multiple high sensitivity spots, but the field units are more densely packed (Vallbo et al. 1995). Relatively little is known about the structure and function of human field units, which have only been reported in the volar surface of the forearm (Vallbo et al. 1995).

With their known role in motion signaling, the FA I (and not the FA II) units likely underlie the tactile MAE on the glabrous skin. That is, both FA I and hair follicle units transmit information relevant to motion perception. Given that the hair follicle units have been described as the functional equivalent of FA I units (Willis 2008), it is possible that adapting the hairy skin will also induce the tactile MAE. To date, there have only been a few attempts to induce the tactile MAE on the hairy skin, with the first appearing in the seminal monograph on the visual MAE by Wohlgemuth (1911). Specifically, the volar surface of the forearm was adapted at several rates and durations using a cord knotted at fixed intervals. The results were always negative; the tactile MAE was not observed. However, Thalman (1922) continued to pursue the tactile MAE on the hairy

skin, and was able to establish a set of conditions under which it could be induced reliably on the volar surface of the forearm. In particular, the tactile MAE was reported on the majority of trials when the belt corrugated at 4 cm intervals adapted the entire length of the arm in a longitudinal direction at fast speeds (39-109 cm/s), and then maintained stationary contact during the test phase. More recently, however, Hazlewood (1971) was unsuccessful at inducing the illusion on the glabrous and hairy skin (i.e., fingertips and forearm, respectively) using a belt corrugated at 5 cm intervals that moved at 75 cm/s during the adapting phase and was stationary during the test phase.

Across studies the reproducibility of the tactile MAE on both the glabrous and hairy skin has been quite poor, with the only successful attempt on the hairy skin appearing over 85 years ago (Thalman 1922). As such, it is not clear whether the tactile MAE can be induced only on the glabrous skin or on both the glabrous and hairy skin. By adapting skin surfaces that differ in their composition of FA units we can gain insight into the relative importance of these units in the tactile MAE. To this end, the present study used a cylindrical plastic drum with a patterned surface to adapt the right: 1) cheek (FA I and hair follicle units), 2) volar surface of the forearm (FA II, field, and hair follicle units), and 3) volar surface of the hand excluding the thumb (FA I and FA II units). Using a within-subjects design, we compared the prevalence, duration, and vividness of the tactile MAE across conditions.

Methods

Subjects

Thirty right-handed volunteers (mean age, 22.67 ± 0.78 years; 25 women, 5 men) provided written informed consent to participate in the experiment. Four subjects participated in a previous experiment on the tactile MAE. One subject was the first author; the rest received partial course credit or financial compensation for their participation. All experimental procedures were approved by the Research Ethics Board at Wilfrid Laurier University. To avoid issues with an unequal number of data points across conditions, only the 15 subjects (mean age, 23.33 ± 1.09 years; 10 women, 5 men) who reported the tactile MAE in each of the three conditions (see Procedure for details) were included in the duration and vividness analyses.

Apparatus

Fig. 1, left panel, shows the adapting apparatus, a custom-built cylindrical plastic drum that was 20.3 cm in length and 9 cm in diameter. The surface of the drum had ridges made of mounting tape (two-sided adhesive tape with a fibrous core) affixed to it parallel to the axis of rotation. The right panel shows the geometry of the ridges, which were 3 mm in height, 1.2 cm in width, 17.8 cm in length, and spaced approximately 1.35 cm apart. The ridges' corners were dull and their radius of curvature (c = 1/r) was 0.21 cm-1. Broad strips (5.1 cm in width) of transparent smooth adhesive tape covered the ridges, closely following the square-wave pattern.

The drum was powered by a 0.33 HP Leeson AC Gearmotor via a belt and pulley system. Specifically, there were two pulleys, one attached to the motor and another to the drum. The two pulleys were connected to each other via a thin rope belt that was

approximately 180 cm in length. When the motor was engaged it rotated the pulley attached to it, which in turn caused the drum to rotate.

The motor was controlled by an AC Tech MC1000 series variable frequency drive, which was connected to a computer via a National Instruments interface. The speed of the drum was set manually on the drive console, whereas the direction and on / off duration of the drum were controlled by a program written in Matlab (The MathWorks, Natick, MA) using the Psychophysics Toolbox (Brainard 1997). The drum took approximately 100 ms to ramp up to and down from its target speed.

A custom-built plunger-style button was connected to the computer via the USB port. The Matlab program recorded the button presses (see Procedure for details).

Procedure

During each session the subjects sat comfortably at a table directly in front of the drum. The experimenter sat to the immediate right of the subject, directly in front of the computer.

Hypoallergenic baby powder was applied (and re-applied, as necessary) to the skin to minimize friction with the drum. To avoid any visual or auditory signals from influencing tactile perception, the subjects closed their eyes, wore earplugs, and listened to white noise via stereo speakers throughout each trial.

There were three conditions, each corresponding to the skin region adapted on the right side of the body, namely the cheek (midway between the tragus and the corner of the mouth), the volar surface of the forearm (midway between the elbow and wrist), and the volar surface of the hand (palm and fingers). On the forearm and hand trials the

subjects simply extended their right arms forward to make contact with the drum. On the cheek trials the drum was rotated 90 degrees into the vertical position and secured to a custom-built wooden stand. This allowed the subjects to remain seated in the upright position and simply turn their heads slightly to the left to make contact with the drum.

At the beginning of each trial the subject placed the appropriate skin area next to the drum and closed his or her eyes. The Matlab program was then used to set the drum in motion and the experimenter tapped the subject lightly on the right shoulder, indicating that he or she should place their skin onto the rotating drum. The drum rotated in a proximal to distal direction (in the case of the cheek trials the drum rotated upward). Following 2 minutes of adaptation at 60 rpm (or 28 cm/s), the experimenter tapped the subject on the shoulder again, at which point the subject lifted his or her skin off of from the rotating drum, and then immediately lowered it back onto the now stationary drum. Thus, the subjects were not in contact with the drum as it came to a stop.

The subjects were instructed to pay attention to any sensations they perceived on or in their skin when they placed it onto the stationary drum. Specifically, they were asked to note whether any after-sensations were directional, regardless of the direction. If the MAE occurred (i.e., directional motion was perceived), the subjects pressed a plunger-style button with their left thumb to mark its onset and offset. Following the second button press, the white noise was turned off and the subjects were asked to describe the MAE in their own words, report its direction, and rate its vividness on a 10-point scale (1 = not vivid, 10 = very vivid). The responses were typed into the computer by the experimenter. Following each trial there was a rest period lasting approximately 2 minutes.

To ensure that the MAE had sufficient time to present itself, the subjects maintained contact with the stationary drum for at least 20 s per trial. If the MAE did not occur, as indicated by no button presses, the experimenter turned off the white noise and proceeded directly to the rest period.

Five subjects were randomly assigned to each of the six possible orderings of the three conditions. In each of the three sessions the assigned ordering was repeated five times. Thus, each subject completed a total of 45 trials (15 per condition). Only one session was run per day.

Results

The tactile MAE was reported on 36% of the cheek trials, 29% of the forearm trials, and 62% of the hand trials (n = 30). A repeated-measures analysis of variance (ANOVA) performed on these data revealed a significant difference between the conditions, $F_{2, 58} = 13.74$, $p < 0.001$. Paired samples t-tests (corrected for multiple comparisons using the Bonferroni method) showed that the hand condition differed significantly from both the cheek, $t_{59} = 4.05$, $p = 0.001$, and forearm conditions, $t_{59} = 4.86$, $p < 0.001$, but the cheek and forearm conditions did not differ significantly from one another, $t_{59} = 0.96$, $p = 1.00$.

Fig. 2a and 2b display the means (and standard errors) of the duration and vividness data from the subjects who experienced the tactile MAE in each of the three conditions (n = 15), respectively. Repeated-measures ANOVAs performed on these data showed that neither duration, $F_{2, 28} = 2.06$, $p = .146$, nor vividness, $F_{2, 28} = 2.95$, $p = 0.69$, differed significantly between the conditions.

Fig. 3 shows the percentage of trials for each adapted skin surface that resulted in positive MAEs, negative MAEs, and 'other' MAEs (n = 30). Trials were categorized as 'other' when the motion was described as lateral (left-to-right or right-to-left), radial, spiral, zigzag, both positive and negative, etc. Only six subjects were consistent in their reports of direction across the conditions. Specifically, two subjects reported the MAE only in the negative direction, four only in the positive direction, and two only in the 'other' direction.

The subjects used several different terms to describe the MAE, including moving drum, pressure, tingle, wave, pulse, sweep, and warmth. Additionally, it should be noted that approximately 11% of the trials classified as MAEs were movement aftereffects. That is, the subjects reported that their body part, or in some cases their entire body, felt as though it was moving following adaptation. Given that the movement aftereffects were reported fairly equally across the conditions (i.e., 3% cheek, 4% forearm, 3% hand), removing them would not change the overall pattern of results. Like the MAEs, the movement aftereffects were reported in the positive, negative, and 'other' direction.

Discussion

By adapting different regions of the skin the present study was able to assess the relative importance of the FA units in the prevalence, duration, and vividness of the tactile MAE. We showed that the tactile MAE can be induced by adapting the glabrous or hairy skin, but that its prevalence is significantly higher on the glabrous skin. In particular, the illusion was successfully induced twice as often on the hand than the cheek and forearm, which did not differ significantly from one another.

In terms of its peripheral basis, these results suggest that the FA I units underlie the tactile MAE observed on the glabrous skin, whereas the hair follicle (cheek and forearm) units and/or the FA I (cheek) and field (forearm) units underlie the tactile MAE observed on the hairy skin. It has been suggested that the hair follicle units provide relatively unreliable spatio-temporal information (Olausson et al. 2000), which may explain why the prevalence of the illusion was much higher on the glabrous skin than the hairy skin.

To further investigate the importance of the FA I units, future research should attempt to induce the tactile MAE on the tongue. Aside from the absence of FA II units in the tongue, the tongue and glabrous hand consist of similar mechanoreceptive units and comparable ratios of fast adapting to slowly adapting units (Johansson and Vallbo 1979; Trulsson and Essick 1997). Thus, the prevalence, duration, and vividness of the tactile MAE on the tongue and glabrous hand should be comparable if the FA I units underlie the tactile MAE.

Previously we showed that the duration and vividness of the tactile MAE did not differ between regions of the glabrous skin, namely the fingers, hand excluding the thumb, and hand including the thumb (Planetta and Servos 2008). In the present study we showed that the duration and vividness of the tactile MAE did not differ between regions of the hairy and glabrous skin, namely the volar surface of the hand including the thumb, volar surface of the forearm, and cheek. Taken together, these results suggest that the duration and vividness of the illusion do not depend on the type or density of FA units adapted.

Anatomical studies have reported that approximately 3-7% of human cadavers lack Meissner corpuscles, the end organ of the FA I afferent (Lindblom 1965), in the index and ring fingers (Dillon et al. 2001) and big toe (Schimrigk and Rüttinger 1980). It has been shown by the present and previous research that 7-9% of subjects never report the tactile MAE on the hand (Planetta and Servos 2008). Thus, one interesting possibility is that these individuals lack FA I units.

While the presence of the FA I units may be critical for the tactile MAE on the glabrous skin, the density of FA I units appears to be less important. Given that the density of the FA and SA units decreases substantially from the distal to the intermediate finger and again from the base of the fingers to the palm (Johansson and Vallbo 1979), we would expect to observe a decrease in the prevalence of the tactile MAE across these regions if density was important. However, it has been shown that the tactile MAE does not differ between the distal finger pad and volar surface of the palm and fingers (Lerner and Craig 2002) or between the volar surface of the fingers and the volar surface of the palm and fingers (Planetta and Servos 2008). The difference in the ratio of SA to FA units between the skin regions may provide an explanation. In particular, the ratio of SA to FA in the forearm (Vallbo et al. 1995) and face (Johansson et al. 1988) are both approximately 2:1, whereas the opposite pattern is true for the hand (Johansson and Vallbo 1979). Further, the ratio of densities is fairly constant across the hand (Johansson and Vallbo 1979).

Interestingly, there were some reports of apparent limb and body movement following adaptation. Previously it has been shown that such kinesthetic illusions can be induced by stretching the skin (cutaneous afferents) and/or vibrating the muscle (muscle

spindle afferents) (Collins et al. 2005). Given that the adapting apparatus in the present study consisted of corrugations that, when run across the skin, caused some vibration of the body as well as stretching of the skin, it is not clear which type of afferent(s) caused the illusion of movement.

Consistent with previous research using a moving adapting stimulus and stationary test stimulus, there were more reports of positive than negative MAEs (Lerner and Craig 2002; Planetta and Servos 2008). Two other papers have reported positive MAEs, though not as many (Hazlewood 1971; Hollins and Favorov 1994). A detailed explanation of negative and positive tactile MAEs has been provided by Hollins and Favorov (1994). In brief, they noted that the only subject who consistently reported positive MAEs also reported illusory motion reversals during the adapting phase; the subjects who reported negative MAEs did not report such reversals. Interestingly, a few subjects in our present and previous research on the tactile MAE have spontaneously reported that they perceived illusory motion reversals. While these reports were anecdotal, Holcombe and Seizova-Cajic (2008) studied illusory tactile motion reversals directly and showed that they occur reliably during stimulation of the fingertips using a drum with a textured surface rotating unidirectionally at approximately 15 to 20 rpm. Typically, continuous motion in one direction causes the neurons tuned to that direction to adapt. The result is an imbalance of spontaneous neural activity in favor of the reverse direction (i.e., a negative MAE). However, illusory motion reversals may shift the balance of spontaneous neural activity in favor of the veridical direction (i.e., positive MAE). The cause of 'other' MAEs (Lerner and Craig 2002; Planetta and Servos 2008) remains unclear.

In addition to explaining negative and positive MAEs, illusory motion reversals may help explain the low prevalence of the illusion. Specifically, the subjects who did not report the tactile MAE may have perceived the drum as rotating equally often in both directions (i.e., veridical and reverse) during the adapting phase. In this case, neurons selective to each direction of motion would adapt, and thus there would be no imbalance of activity to induce the MAE. Further, the less reliable spatio-temporal information provided by the hair follicle units (Olausson et al. 2000) may make such reversals more likely to occur on the hairy skin than the glabrous skin. Of course, we cannot make any definitive conclusions, given that our subjects were not instructed to continuously report on the direction of motion during the adapting phase. It will be up to future research to determine whether there is a relationship between illusory motion reversals and the direction and prevalence of the tactile MAE on both the glabrous and hairy skin.

In summary, the present research showed that the patterned surfaced cylinder induced the tMAE twice as often on the glabrous skin than the hairy skin. This result provides some insight into the specificity of the tactile MAE, namely that it can be induced by adapting the FA I units in the glabrous skin and the hair follicle units and/or FA I and field units in the hairy skin. Currently we are investigating the central basis of the tactile MAE by adapting the glabrous surface of the hand.

Acknowledgements

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Figure Captions

Fig. 1

The drum apparatus set up for the hand condition. Refer to the Procedure for details about the experimental setup in the cheek and forearm conditions. Left panel shows the front view. Note that the pulley is attached to the right side of the drum and is covered by a plastic case for safety purposes. Right panel shows the side view and details the geometry of the ridges

Fig. 2

Mean a) duration and b) vividness of the tactile MAE as a function of adapted skin surface. Error bars represent the standard errors of the mean. There were no significant differences. Note that only the 15 subjects who reported the tactile MAE in all three conditions are displayed

Fig. 3

Percentage of trials for each adapted skin surface that resulted in positive MAEs, negative MAEs, and 'other' MAEs (n = 30)

Fig. 1

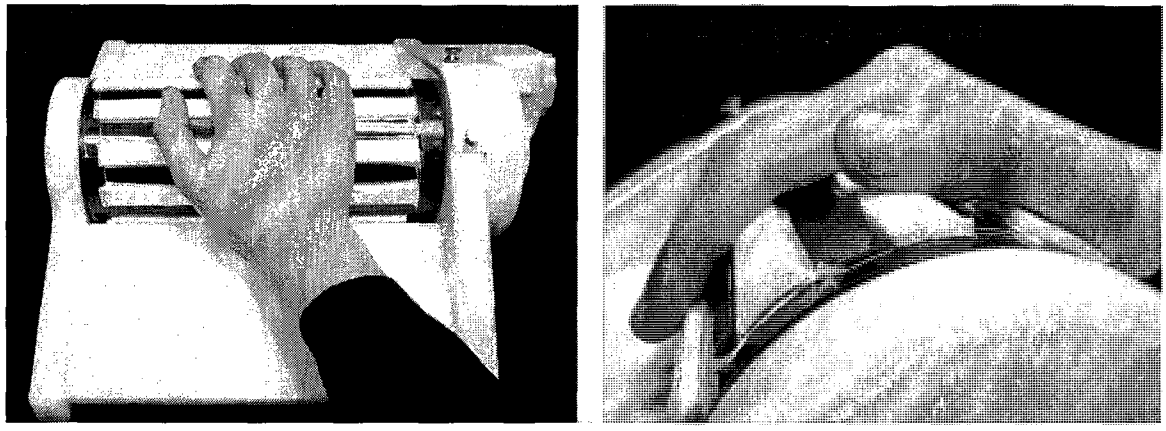


Fig. 2

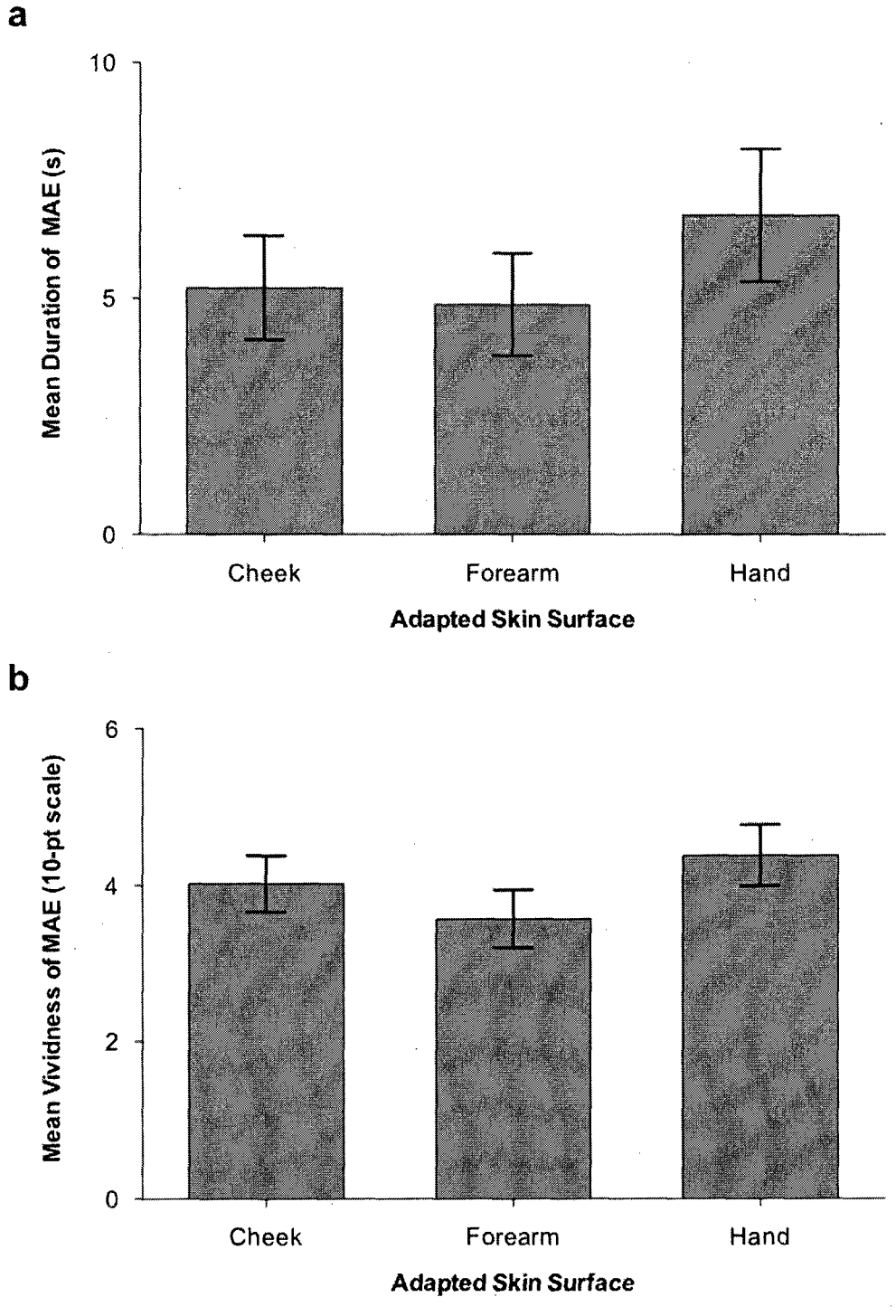
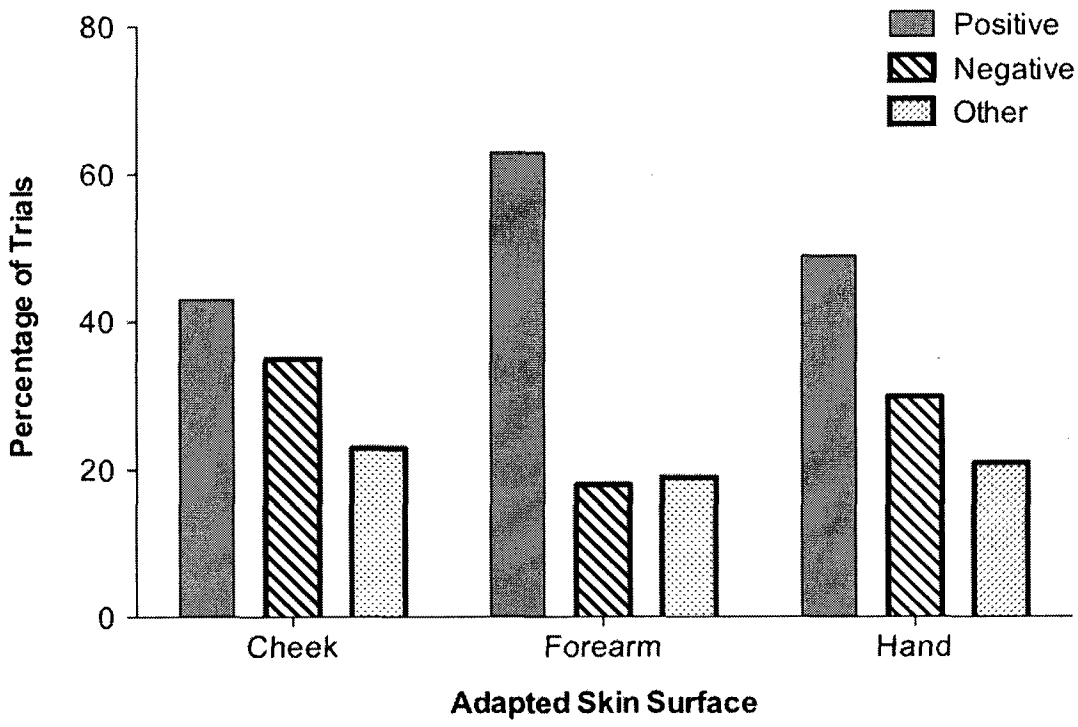

a
10
5
0
Mean Duration of MAE (s)
Cheek
Forearm
Hand
Adapted Skin Surface
b
6
4
2
0
Mean Vividness of MAE (10-pt scale)
Cheek
Forearm
Hand
Adapted Skin Surface

Fig. 3


Positive
Negative
Other
80
60
40
20
0
Percentage of Trials
Cheek
Forearm
Hand
Adapted Skin Surface

CHAPTER 5

The neural basis of the tactile motion aftereffect

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Abstract

The tactile motion aftereffect (tMAE) is a perceptual illusion in which a stationary stimulus feels as though it is moving when presented following adaptation to a unidirectionally moving tactile stimulus. Using functional magnetic resonance imaging (fMRI), we localized the brain areas responsive to tactile motion, and then investigated whether these areas underlie the tMAE. Tactile stimulation was delivered to the glabrous surface of the right hand by means of a plastic cylinder with a square-wave patterned surface. In the tactile motion localizer, we contrasted periods in which the cylinder rotated at 15 rpm with periods of rest (stationary contact). Activation was observed in the contralateral (left) thalamus, postcentral gyrus, and parietal operculum. To induce the tMAE, the cylinder rotated at 60 rpm for 2 minutes. It was expected that the subjects would perceive illusory motion for several seconds following the offset of stimulation. In the control sequence the cylinder rotated for 2 minutes but at a relatively slow speed (15 rpm) that is unlikely to induce the tMAE. Of the areas activated by the tactile motion localizer, only the postcentral gyrus showed a sustained fMRI response following the offset of the illusion sequence (but not the control sequence), presumably reflecting the illusory perception of motion.

Introduction

Historically, illusions have been used to gain insight into the normal perceptual system. One illusion that has been used extensively to study visual motion perception is the motion aftereffect (MAE) -- following prolonged viewing of a unidirectionally moving stimulus, a stationary stimulus appears to move in the opposite direction (Wohlgemuth, 1911). This phenomenon is typically explained by the imbalance of spontaneous activity caused by the adaptation of direction sensitive neurons (Sutherland et al., 1961). Single cell recordings in the middle temporal (MT) area of non-human primates support this view (Petersen et al., 1985). Human MT+ (MT and satellite area MST) is well established as a visual motion processing area, and many studies have shown that it underlies the visual MAE (Antal et al., 2004; Berman and Colby, 2002; Culham et al., 1999; Hautzel et al., 2001; He et al., 1998; Taylor et al., 2000; Théoret et al., 2002; Tootell et al., 1995; but see Huk et al., 2001).

In contrast, the tactile MAE (tMAE) has garnered little attention, and to our knowledge its neuroanatomical basis has yet to be investigated. One candidate area is the postcentral gyrus, or primary somatosensory cortex (SI). In non-human primates, SI consists of motion and direction sensitive neurons (Warren et al., 1986). Functional neuroimaging studies of humans have shown that several areas within the parietal cortex are responsive to unilateral tactile motion. Most recently, Summers et al. (2009) reported activation in the contralateral SI, bilateral parietal operculum or secondary somatosensory cortex (SII), and bilateral posterior parietal cortex (PPC) in response to unilateral vibrotactile motion on the fingertip. Similar parietal activation patterns have been reported by others to brush strokes (Polonara et al., 1999; Hagen et al. 2002; Maihöfner et

al., 2004; Yoo et al., 2003), airflow (Bremmer et al., 2001), and moving patterns (Burton et al., 1997; Nakashita et al., 2008). Selective attention tasks have shown that SII and PPC process higher-level features of tactile stimuli; SII is preferentially activated by stimulus texture and duration, whereas PPC is preferentially activated by stimulus shape (Bodegård et al., 2001; Burton et al., 1999; Ledberg et al., 1995; O'Sullivan et al., 1994; Roland et al., 1998).

In addition, there is currently debate about whether MT+ is a unisensory visual motion processing area or multisensory motion processing area. Several studies have reported MT+ activation in response to tactile motion (Hagen et al., 2002; Blake et al., 2004; Ricciardi et al., 2007; Summers et al., 2009), while others have either failed to observe MT+ activation (Bremmer et al., 2001) or have reported negative activation (Bodegård et al., 2000; Nakashita et al., 2008). If MT+ is responsive to tactile motion, then it may also mediate the tMAE.

In the present study, we used functional magnetic resonance imaging (fMRI) to localize tactile motion responsive brain areas, and then investigated whether these areas mediate the tMAE. To both ends, tactile stimulation was delivered to the glabrous surface of the right hand using a cylinder with a patterned surface.

Materials and Methods

Subjects

Ten healthy right-handed adults (mean age, 25.0 ± 1.0 years; seven females, three males) participated in exchange for payment. Two of these subjects were excluded from the MAE analyses (see Procedure for details), one subject for consistently reporting the

illusion on the control sequences, and the other for not reporting the tMAE on at least 10 illusion sequences. All subjects reliably reported the tMAE in previous research, were screened carefully for MRI compatibility, and provided written informed consent for the procedures in this study. The Research Ethics Boards at St. Joseph's Healthcare Hamilton and Wilfrid Laurier University approved the experimental protocol.

Apparatus

The experimental apparatus was a custom-built plastic cylinder powered by a 0.33 HP Leeson AC Gearmotor. The motor was controlled by an AC Tech MC1000 series variable frequency drive, which was connected to an Apple Powerbook G4 computer via an A/D board (National Instruments NI-DAQCard-DIO-24). The speed of the cylinder was controlled by a switch selectable speed control that was added to the drive console, and the on / off duration and direction of the cylinder were controlled by a Matlab program (The MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard 1997). It took approximately 100 ms for the cylinder to ascend to and descend from its target speed.

The cylinder was 20.3 cm in length, 9 cm in diameter, and was supported by a plastic frame. Eleven strips of mounting tape (two-sided adhesive tape with a fibrous center) were adhered to the surface of the cylinder parallel to the axis of rotation. The strips were approximately 3 mm in height, 1.2 cm in width, 17.8 cm in length, and spaced 1.35 cm apart. Pieces of smooth transparent packaging tape covered the cylinder and ridges, closely following the square-wave pattern. The cylinder sat atop a plastic table, which straddled the subject's waist.

Since ferromagnetic devices cannot be used in high magnetic fields, the motor was located in the MRI control room and the cylinder in the MRI exam room. They were connected to each other through a waveguide via a rope and pulley system. In particular, there were four pulleys: one mounted to the motor, one to the cylinder, and two in between that allowed the rope to be angled toward the center of the bore. For safety purposes there was a plastic cover over the pulley attached to the cylinder and the rope was encased in tent poles (i.e., hard inflexible sections of plastic tubing that fit together) between each pulley. The distance between each pulley, starting at the motor, was approximately 1.75, 3.0, and 2.5 m. When the motor was engaged it rotated the pulley mounted to it, causing the rope to move, and finally the cylinder to rotate.

An MRI-compatible plunger-style button, which the subjects used to mark the offset of the illusion (if applicable), was connected to the computer via the USB port. The Matlab program recorded the time of the button presses.

Procedure

There were two scan sessions per subject. Each session was held on a different day (10 ± 2.8 days apart) and consisted of two experiments: the tactile motion aftereffect (MAE) and the tactile motion localizer (ML). The anatomical scan was always first, followed by the MAE experiment, and finally the ML experiment. Throughout the functional experiments the subjects fixated a cross on the top of the bore and cupped their right hand over the upper portion of the cylinder. Note that the glabrous surface of the hand (i.e., fingers and palm) made contact with the cylinder. As the subject lay supine in the

scanner, the cylinder was angled acutely in the frontal plane atop the table to maximize comfort. Foam padding was used to support the arm and wrist.

The MAE experiment consisted of two sequence types, illusion and control. In both sequences the cylinder rotated from proximal to distal (i.e., head to toe). The illusion sequences proceeded as follows: 30 s period of hand on stationary cylinder, 2 min period of hand on cylinder rotating at 28 cm/s (or 60 rpm), 30 s period of hand on stationary cylinder. It was expected that the rotating cylinder would induce the tMAE during the second stationary period. The control sequences proceeded as follows: 30 s period of hand on stationary cylinder, 2 min period of hand on cylinder rotating at 7.5 cm/s (or 15 rpm), 30 s period of hand on stationary cylinder. It was expected that the subjects would not perceive the tMAE during the second stationary period given that the prevalence of the illusion is negligible at 15 rpm (Planetta and Servos, 2008). In both the illusion and control sequences, the subjects pressed the plunger-style button with their left thumb to indicate when the illusory motion ceased, if applicable.

In each session the illusion and control sequences were presented in alternation six times, and the sequence order was counterbalanced across subjects; that is, half of the subjects started with the illusion sequence and half with the control sequence in each session. The total run time of the MAE experiment was 36 min (12 sequences x 3 min per sequence). However, due to hardware limitations on the amount of data that could be collected in a single functional run, the MAE experiment was collected in four back-to-back runs of three sequences each (9 min). Note that over both sessions six subjects were run in one to three additional MAE sequences. Further, one subject was run in a third session. This was done to try to obtain a sufficient number of useable sequences (i.e.,

illusion sequences in which the tMAE was reported and control sequences in which the tMAE was not reported) for the analyses.

The ML experiment consisted of 30 s periods of tactile motion (hand on cylinder rotating at 7.5 cm/s or 15 rpm) alternated with 30 s periods of rest (hand on stationary cylinder). No response was required. The direction of the cylinder changed every cycle (i.e., proximal to distal or distal to proximal), and the order of the blocks was counterbalanced across subjects in each session; that is, half of the subjects started with the tactile motion period and half with the rest period. In total there were six cycles, for a total run time of 6 min.

fMRI data acquisition

All images were acquired with a 3.0T short-bore MR scanner (Signa Excite, General Electric Healthcare, Waukesha, WI) and an eight-channel phased array, receive-only head coil. Foam padding was placed between the subject's head and the coil to restrict movement. T1-weighted sagittal scout images were used to select 18 contiguous 4-mm thick axial oblique slices covering most of the parietal and occipital cortices. Blood oxygenation level dependent (BOLD) contrast was measured using a single-shot, two-dimensional, gradient-recalled echo-planar (GR-EPI) pulse sequence (repetition time (TR) = 1,200 ms, echo time (TE) = 35 ms, flip angle (FA) = 80°, matrix = 64 x 64, field of view (FOV) = 240 mm). Thus, the resulting functional voxel size was 3.75 × 3.75 × 4 mm. For each experiment, the first 12 volumes were discarded due to unstable magnetization. The remaining 1,800 volumes in each MAE experiment (4 runs x 450 volumes each) and 300 volumes in each ML experiment were recorded. Prior to

functional imaging, T1-weighted anatomical images of the whole brain were acquired axially with a three-dimensional fast spoiled gradient-recalled echo (FSPGR) pulse sequence (TR = 9.036 ms, TE = in phase, FA = 12°, matrix = 512 x 512, FOV = 240 mm, slice thickness = 2.0 mm).

fMRI data analysis

Image preprocessing and analyses were performed using BrainVoyager QX software (Brain Innovation, Maastricht, The Netherlands). The anatomical and functional images for each subject were co-registered, isovoxelled (1 mm^3 anatomical, 3 mm^3 functional), and spatially normalized into stereotaxic space (Talairach and Tournoux, 1988). The spatially normalized anatomical images were averaged to account for variation in cortical anatomy across the subjects. Functional pre-processing included motion correction, linear trend removal, and slice timing correction. No spatial or temporal smoothing was performed on the data.

ML data

All 10 subjects were included in the ML analyses. However, the first ML run for one subject was excluded due to technical problems (i.e., poor signal quality).

The voxel-wise statistical analyses of the changes in the BOLD signal were based on the application of the random-effects multi-subject general linear model (GLM) with a boxcar waveform (ON/OFF) convolved with a two-gamma hemodynamic response function. The data from each subject were z-normalized and concatenated before the GLM computation. The number of comparisons was reduced by restricting the group

analyses to the brain tissue. In particular, a mask of each subject's normalized anatomical scan was generated, and then these masks were combined. Activation clusters had to meet a threshold of at least $p < 0.05$ (corrected for multiple comparisons using the false discovery rate method, FDR; Genovese et al., 2002).

Due to the inter-subject variability in the location of MT+ (Wilms et al., 2005), we also examined the statistical maps of each subject, which were thresholded at an FDR of 0.05. Individual brain masks were used to restrict the statistical tests to the brain tissue. MT+ is often located around the inferior temporal sulcus-ascending limb of the inferior temporal sulcus junction (Dumoulin et al., 2000). As such, activation clusters in this general area were defined as regions of interest (ROIs).

MAE data

Eight of the 10 subjects were included in the MAE analysis; one subject was excluded for consistently reporting the illusion on the control sequences and the other for not reporting the illusion on at least 10 illusion sequences. For each of the eight subjects 10 illusion sequences (longest reported illusion duration) and 10 control sequences (no illusion reported) were analyzed.

The activation clusters from the group ML analyses were used as ROIs in the MAE analyses. For each ROI we extracted the mean BOLD percent signal change time courses in both the illusion and control sequences. Note that the 30 s period of rest (i.e., hand on stationary drum) prior to each stimulation period served as its baseline. Next, the 10 illusion time courses for each subject were averaged, as were the 10 control time courses. The time course data were then divided into 15 s windows, and the mean of each

time window was calculated for each subject. We performed a 2 (sequence type) x 11 (time window) repeated measures analysis of variance (ANOVA) on the mean percent signal change for each ROI. This was done to assess whether the amplitude differed between the sequence types during the stimulation period. For the 15 s period following the offset of stimulation, we calculated the area under the illusion and control sequence curves for each subject and ROI. One-way ANOVAs compared the illusion and control sequence area under the curve (AUC) data for each ROI. The AUC calculations were performed using the trapezoid rule, as implemented in Prism (GraphPad Software, La Jolla, CA).

For subjects with focal activation in the vicinity of MT+ we extracted the mean percent signal change time courses as described earlier. However, due to the small sample size (see Results for details), statistical comparisons were not performed on these data.

Results

Overall, the tMAE was reported on 90.7% of the illusion trials. The mean tMAE duration of the analyzed illusion sequences was 9.21 ± 1.44 s.

ML data

Table 1 lists the stereotaxic coordinates, sizes, and mean *t* values of the clusters. All activation (positive BOLD) clusters were observed in the contralateral (left) hemisphere, namely the thalamus, postcentral gyrus, and parietal operculum (Figure 1). In addition,

several deactivation (negative BOLD) clusters were observed, including the ipsilateral (right) postcentral gyrus, cuneus, and precentral gyrus and contralateral (left) precuneus.

In the individual subject analyses, we observed focal activation in the vicinity of MT+ in five subjects (four contralaterally, one bilaterally). Two others showed large areas of interconnected activation in occipital cortex. Of the remaining three subjects, one showed no activation near MT+ and two showed large interconnected occipital deactivation.

MAE data

Figure 2 shows the mean ± SEM BOLD signal change time courses of the illusion and control sequences for each ROI. The top panel shows the postcentral gyrus, the middle panel the parietal operculum, and the bottom panel the thalamus. For each ROI, there was a significant effect of stimulation time window (all $ps < 0.05$), no significant effect of sequence type and no significant interaction between stimulation time window and sequence type (all $ps > 0.05$). The main effect of stimulation time window was likely driven by the strong BOLD response to both sequence types at onset of stimulation. Importantly, there was no difference between the two sequence types, suggesting that stimulation speed did not affect the amplitude of the BOLD signal.

For the 15 s period following the offset of stimulation, the control sequence response promptly returned to baseline in the postcentral gyrus ROI, whereas the illusion sequence response remained high for several seconds (even increasing slightly) and then returned to baseline. A paired samples t-test showed that the AUC was significantly greater for the illusion sequences (M = 13.72 ± 1.66) than the control sequences (M =

8.55 ± 0.92), $t(7) = 2.53$, $p = 0.039$. In the parietal operculum ROI, the illusion and control sequences did not show any differential activation following the offset of stimulation. Moreover, the AUC for the illusion (M = 8.89 ± 1.69) and control (M = 7.93 ± 2.06) sequences did not differ significantly, $t(7) = 0.45$, $p = 0.668$. Note that both sequences showed a slight increase following the offset of stimulation. However, there was great deal of inter-subject variability in this effect, as evidenced by the large standard error bars. In the thalamus ROI, there was no differential activation following the offset of stimulation, and the AUC for the illusion (M = 3.32 ± 0.72) and control (3.02 ± 0.63) sequences did not differ significantly, $t(7) = 0.33$, $p = 0.751$.

Given that only seven of the 10 subjects showed activation in the vicinity of MT+, but all reported the tMAE, it seems unlikely that this area plays a critical role in the illusion. Nevertheless, we examined the time courses of the five subjects who showed focal activation, and there was no differential activation between the illusion and control sequences at the offset of stimulation.

In summary, the contralateral thalamus, postcentral gyrus, and parietal operculum were activated by tactile motion. Of these regions, only the postcentral gyrus showed evidence of the tMAE, namely sustained activation following the offset of stimulation in the illusion sequences and not the control sequences.

Discussion

In the present study, we observed activation in several known somatosensory areas in response to tactile motion on the glabrous surface of the right hand. Specifically, our contrast of moving tactile stimulation (rotating cylinder with patterned surface) with

stationary tactile stimulation (same cylinder but stationary) revealed activation in the contralateral (left) thalamus, postcentral gyrus (presumably SI), and parietal operculum (presumably SII). Moreover, we provided the first evidence regarding the neural basis of the tMAE -- a sustained BOLD response in the postcentral gyrus when the subjects perceived the tMAE compared to when they did not. None of the other tactile motion responsive areas showed this differentiation.

Tactile motion perception

The involvement of the thalamus, postcentral gyrus, and parietal operculum in tactile information processing is well established (Gardner and Kandel, 2000). In accordance with the ascending somatosensory pathway, we observed thalamic activation focused around the intersection of the ventral posterior lateral nucleus (VPL) and pulvinar. Previously, activation of the ventral posterior nucleus in the thalamus has been reported using fMRI in response to stroking of the hand with a wooden instrument (Davis et al., 1998).

While some studies have reported bilateral SI activation in response to unilateral tactile stimulation (Blatow et al., 2007; Sutherland and Tang, 2006; Yoo et al., 2003), we observed contralateral activation and ipsilateral deactivation. The activation cluster encompassed cytoarchitectonic areas 3, 1, and 2 (with the center of gravity likely corresponding to area 2), whereas the two smaller deactivation clusters likely correspond to area 3. In non-human primates, area 3 consists of motion sensitive neurons, whereas areas 1 and 2 consist of direction sensitive neurons (Warren et al., 1986). Using fMRI, Hlushchuk and Hari (2006) also observed ipsilateral SI (area 3b) and primary motor

cortex deactivation to pulsatile tactile stimulation to the fingers, and suggested it was the result of interhemispheric inhibition.

In non-human primates, the neurons in SII have relatively large receptive fields, some of which are bilateral (Whitsel et al., 1969; Robinson and Burton, 1980). We only observed contralateral SII activation. Ipsilateral SII activation is less correlated with the hemodynamic response function than contralateral SII (Blatow et al., 2007). Given that our contralateral activation cluster was fairly small (i.e., 14 mm^3), any ipsilateral activation may not have reached significance. The contralateral activation was located midway between the lip and fundus of the lateral sulcus. This finding is consistent with previous human neuroimaging research on the somatotopic location of the hand within SII (Disbrow et al., 2000; Malinen et al., 2006; Ruben et al., 2001). In addition, the SII (and absence of PPC) activation supports previous research indicating that SII is preferentially activated by tactile texture, or microgeometry, whereas the PPC is preferentially activated by shape, or macrogeometry (Bodegård et al., 2001; Burton et al., 1999; Ledberg et al., 1995; O'Sullivan et al., 1994; Roland et al., 1998). PPC activation has been reported when attention to the macrogeometric features of a moving tactile stimulus is required (Kitada et al., 2003; Nakashita et al., 2008). For example, Kitada et al. (2003) showed that the PPC was activated when moving tactile stimuli presented to two fingers on the right hand required integration compared to when they did not. In our study, there was no experimental task and the cylinder shape was the same in both conditions (moving vs. stationary). As such, the subjects may have selectively attended to the patterned surface of the cylinder moving across the skin. An earlier fMRI report suggests that the somatotopy of human SII has a lower spatial resolution than SI (Ruben

et al., 2001). Taken together, our SII activation may reflect the integration of fast patterned stimulation across the fingers and hand.

Tactile motion aftereffect

The tMAE prevalence was higher and duration was longer in the present study than in our previous work (Planetta and Servos, 2008). This is not surprising given that we recruited subjects who reliably reported the illusion for relatively long durations in previous studies. The purpose of this recruitment strategy was to increase our likelihood of capturing the neural basis of the transient tMAE using fMRI.

The thalamus, postcentral gyrus, and parietal operculum were examined as candidate areas for the tMAE. Following the offset of stimulation, the thalamus and parietal operculum responses did not differ between the illusion and control sequences. However, the postcentral gyrus response did differ; the illusion sequence lasted longer than the control sequence. One interpretation of this difference is the perception of the tMAE. Presumably, exposure to the relatively fast (but not slow) moving cylinder adapted neurons sensitive to a particular direction, creating an imbalance of activation in favor of the neurons sensitive to the opposite direction.

One difference between the illusion and control sequence was the stimulation speed. Magnetoencephalography research has shown that the SI response increases with stimulus intensity (Torquati et al., 2002). However, in the present study the BOLD response amplitude did not differ between the illusion (60 rpm) and control (15 rpm) sequences during the stimulation period for any ROI. Similarly, Bodegård et al. (2000) showed that there were no activation differences between high- and low-speed tactile

discrimination intervals. Thus, the sustained BOLD response to the illusion sequence at the offset of stimulation cannot be accounted for by an amplitude difference during the stimulation period.

Absence of MT+ activation

Our group-level analysis did not reveal any occipital activation. To ensure that the absence of group-level activation was not caused by the heterogeneous location of MT+ (Wilms et al., 2005), we also examined the individual statistical maps of each subject. While seven subjects showed activation in the general area of MT+, the remaining three subjects either lacked activation or showed deactivation in this region. This inter-subject variability would explain the lack of group-level activation, and suggests that MT+ is not critical for tactile motion perception. Nevertheless, we examined the illusion and control sequence time courses for the focal MT+ clusters, and observed no evidence of the tMAE; that is, there was no differential activation following the offset of the illusion and control sequences.

These results are consistent with previous research that showed MT+ is a unisensory visual motion processing area. For example, Zihl et al. (1983) showed that a patient with bilateral lesions to area MT+ had deficits in visual motion processing, but not auditory or tactile motion processing. Similarly, Bremmer et al. (2001) observed MT+ activation in response to visual motion, but not auditory or tactile motion. Moreover, some researchers have reported MT+ deactivation (Bodegård et al., 2000; Nakashita et al., 2008), which may be the result of selective attention to the relevant incoming tactile information (Haxby et al., 1994).

While some groups have reported MT+ activation in response to tactile motion (Hagen et al., 2002; Blake et al., 2004; Ricciardi et al., 2007; Summers et al., 2009), it has been argued that visual imagery may be responsible (Sathian and Lacey, 2007). That is, MT+ activation may be caused by visualizing the moving tactile stimulus. Goebel et al. (1998) showed that visualizing moving dots led to increased MT+ activation compared to fixation, but this activation was only half of that observed in the real and apparent motion conditions. On the other hand, Blake et al. showed that activity in MT+ did not differ significantly between visualizing a rotating globe and rest, suggesting that MT+ activation during tactile motion tasks is not solely due to visual imagery. Recently, Ricciardi et al. provided further evidence against the imagery account in a study of tactile motion perception in the sighted, early blind, and congenitally blind. In sighted individuals, visual motion activated MT+ and tactile motion selectively activated the more anterior portion of this region. In the early and congenitally blind individuals, tactile motion activated more or less the entire MT+ region, including the area activated by visual motion in the sighted. However, it may be that the anterior portion of MT+ is activated by visual motion and visual motion imagery (not tactile motion) in sighted subjects, whereas MT+ activation in blind subjects is the result of crossmodal plasticity (Sadato et al., 1996; Finney et al., 2001). Nevertheless, the authors argue that visual experience serves to segregate MT+ into an anterior region that processes tactile and visual motion and a posterior region that processes visual motion only. In support of this functional segregation, Beauchamp et al. (2007) showed that SII and MST, but not MT, responded to rapidly presented vibrotactile stimulation to the hands and feet.

Conclusion

To our knowledge, this study was the first to investigate the neural basis of the tMAE. We showed that there was a sustained BOLD response in the contralateral postcentral gyrus when subjects perceived the tMAE, perhaps reflecting the adaptation of direction sensitive neurons. However, these findings do not preclude the involvement of other areas. For example, a higher-level area that is not responsive to tactile motion may be involved in the tMAE.

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Figure Legend

Figure 1. Statistical map of the group ML analysis (n = 10) thresholded at a false discovery rate of $p < 0.05$ and overlaid on the averaged spatially normalized anatomical image. The left side of the image corresponds to the right side of the brain. Activation clusters are shown in the contralateral 1) postcentral gyrus, 2) parietal operculum, and 3) thalamus.

Figure 2. The mean ± SEM BOLD signal time course (n = 8) for the illusion and control sequences from each group-level region of interest (ROI). Note that tactile stimulation started at 30 s and ended at 150 s. The only ROI to show evidence of the tMAE was the contralateral postcentral gyrus, in which there was a sustained BOLD response following the offset of the illusion sequence.

Figure 1.

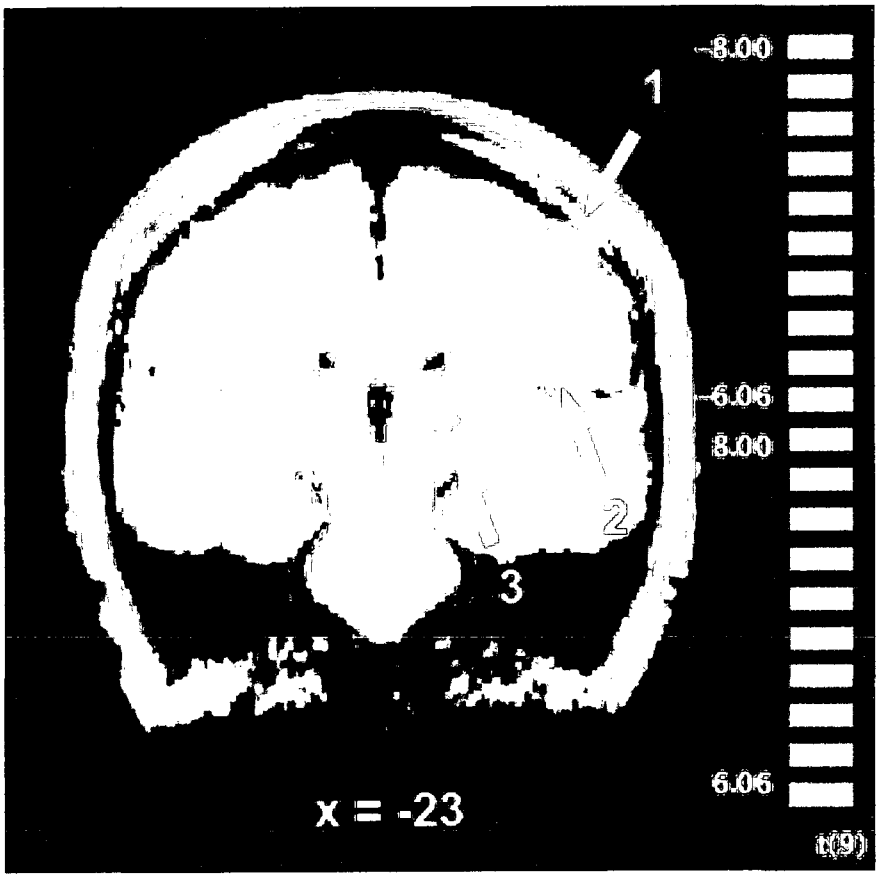

Figure 2.

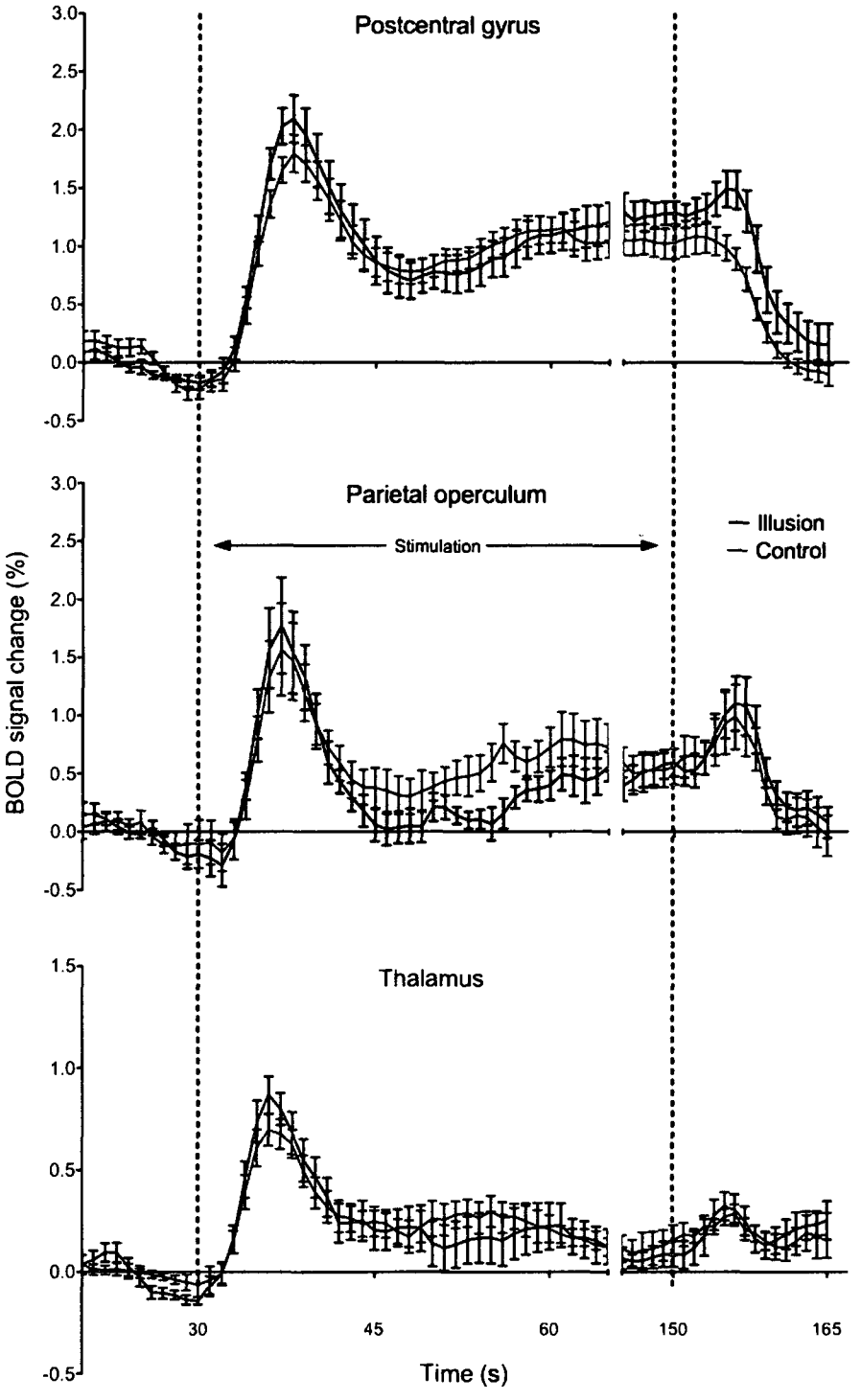
Postcentral gyrus
Parietal operculum
Stimulation
Illusion
Control
Thalamus
BOLD signal change (%)
Time (s)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
30
45
60
150
165

Table 1.

Brain regions activated in the group ML analysis (n = 10)

Region	Talairach coordinates			Cluster size	*t*-scores
	x	y	z		
Positive (activation)					
L parietal operculum	-44	-22	19	14	6.37
L postcentral gyrus	-42	-29	54	3,976	8.62
L thalamus	-16	-23	8	140	6.86
Negative (deactivation)					
L frontal lobe, subgyral	-30	-4	29	10	-7.00
L precuneus	-12	-71	37	58	-6.38
R cuneus	16	-78	36	101	-6.46
R temp lobe, subgyral	24	-66	23	19	-6.41
R precentral gyrus	32	-28	60	44	-6.47
R middle frontal gyrus	36	-1	40	7	-6.55
R postcentral gyrus	36	-30	58	4	-6.28
R postcentral gyrus	36	-25	47	124	-6.53
R superior temporal gyrus	51	-40	13	7	-7.01

L: left hemisphere, R: right hemisphere; Talairach coordinates refer to the cluster's center of gravity; cluster size is the number contiguous of 1 mm^3 voxels; *t*-scores are the mean activations of the cluster; $t(9) > 6.05, p < 0.05$ (corrected for multiple comparisons using the false discovery rate method)

CHAPTER 6

The purpose of the experiments described herein was to gain a better understanding of the tMAE. Chapters 2 (Experiment 2) and 3 showed that the prevalence, duration, and vividness of the tMAE increased with adapting speed (up to 75 rpm) and duration (up to 240 s). These findings were then used to design an effective stimulation protocol (i.e., one that would induce the illusion in most subjects for several seconds) for use in the fMRI scanner (Chapter 5).

To gain some insight into the basis of the tMAE at the periphery, Chapter 4 adapted skin areas that differ in their composition of FA units, which have previously been shown to support tactile motion perception (Gardner & Sklar, 1989) and the tMAE (Lerner & Craig, 2002). The tMAE was twice as prevalent on the glabrous surface of the hand (FAI, FAII units) than the cheek (FAI, hair follicle units) and volar surface of the forearm (FAII, field, hair follicle units), which did not differ significantly from one another. As such, it seems likely that the tMAE is primarily induced via the FAI and hair follicle units. Taken together, Chapters 2 to 4 showed that the best measure of tMAE strength, as induced by a patterned cylinder, is prevalence. The tMAE duration and vividness responses were highly variable and subjects anecdotally reported not being confident in these responses.

Chapter 5 showed that the contralateral (left) thalamus, PCG (presumably SI area 2), and parietal operculum (presumably SII) were responsive to tactile motion on the glabrous surface of the right hand. Previously, each of these areas has been shown to respond to unilateral tactile motion perception in monkeys and humans. Thalamic activation (i.e., ventral posterior nucleus) has been reported in response to motion along

the glabrous surface of the hand (Davis et al., 1998). In the monkey PCG, motion sensitive neurons are concentrated primarily in area 3b, whereas direction selective neurons are concentrated primarily in areas 1 and 2 (Costanzo & Gardner, 1980; Gardner, 1988; Hyvärinen & Poranen, 1978; Warren et al., 1986; Whitsel et al., 1972). SII neurons are also responsive to motion tactile stimuli (Whitsel et al., 1972), and serve to integrate information received from SI (Iwamura, 1998). Interestingly, MT+ activation was not observed reliably across subjects, suggesting that it is not critical for tactile motion perception. Thus, MT+ activation in earlier reports (Blake et al., 2004; Hagen et al., 2002; Ricciardi et al., 2007; Summers et al., 2009) may have been the result of visualizing the moving tactile stimulus (Heller, 1991; Sathian and Lacey, 2007). Of the three regions shown to be responsive to tactile motion, only the PCG showed evidence of the tMAE; that is, a continued response following the offset of the illusion trials and not the control trials. This suggests that the tMAE reflects the adaptation of direction selective neurons that are concentrated in the posterior PCG.

Two other groups have studied the tMAE using a comparable cylinder adapting apparatus. Hollins and Favorov (1994) reported high tMAE prevalence rates following adaptation of the glabrous surface of the right hand including the thumb. While the prevalence was consistently high (around 100%), the duration and vividness of the illusion increased with adapting duration. Using similar methodology, however, Lerner and Craig (2002) reported prevalence rates around 50% following adaptation of the glabrous surface of the right hand including the thumb. Experiment 1 of Chapter 2 showed that the discrepant results of these two studies cannot be explained by the inclusion of the thumb by the former. Specifically, the prevalence, duration, and

vividness of tMAE did not differ between three adapted skin areas, namely the fingers and palm including the thumb, fingers and palm excluding the thumb, and fingers only excluding the thumb. Moreover, the present results were in agreement with Lerner and Craig, with prevalence rates just under 50%. This suggests that the high prevalence rates reported by Hollins and Favorov using a cylinder apparatus are anomalous, perhaps the result of their small sample size.

In a typical tMAE experiment the stimulus moves across the skin during the adapting phase and is stationary during the test phase. As a result, the FA and SA units are activated during the adapting phase, whereas the SA units are preferentially activated during the test phase. Watanabe et al. (2007) argued that the unreliability of the tMAE across studies is caused by this mismatch of activated units between the two experimental phases. In support of this view, robust tMAEs were observed on the glabrous surface of the finger when a vibrotactile stimulus simulated motion during the adapting and test phases, thus activating the FA units in both.

Using a paradigm similar to Watanabe et al. (2007), Konkle, Wang, Hayward, and Moore (2009) recently reported the existence of crossmodal MAEs. In particular, these authors showed that adaptation to visual motion induced the tMAE and adaptation to tactile motion induced the visual MAE. These results suggest that visual and tactile motion processing interact at the neural level. Currently, evidence suggests that MT+ supports the visual MAE (Antal et al., 2004; Berman and Colby, 2002; Culham et al., 1999; Hautzel et al., 2001; He et al., 1998; Taylor et al., 2000; Théoret et al., 2002; Tootell et al., 1995a), whereas SI supports the tMAE. However, this does not preclude

the possibility that these two adapted neural populations interact. It will be up to future researchers to investigate the site of such an interaction directly.

In summary, this dissertation increased our understanding of the relatively unexplored tMAE by studying it from several angles. In particular, Chapters 2 and 3 described the effect of different adapting parameters, namely speed, duration, and adapted skin area, on the tMAE, while Chapters 4 and 5 provided insight as to the peripheral and central neural basis of the illusion, respectively. Further, the development of the MRI-compatible cylinder will allow researchers to continue to study the central neural basis of tactile motion perception, as well as tactile texture processing.

CHAPTER 7

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CHAPTER 8

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