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ADAPTATION TO MOVING TACTILE STIMULI AND ITS EFFECTS ON PERCEIVED SPEED AND DIRECTION

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Candidate declaration

The research presented in this thesis was undertaken by the candidate while enrolled in a PhD program with the School of Psychology, University of Sydney. This work is original and has not been submitted for a higher degree to any other university or institution. Research was conducted at three locations: 1) Cumberland campus, Faculty of Health Sciences, University of Sydney, under the supervision of co-supervisor Dr Tatjana Seizova-Cajic; 2) Camperdown campus, School of Psychology, University of Sydney, under the supervision of co-supervisor A/Prof Alex Holcombe; 3) Neuroscience Research Australia (previously 'Prince of Wales Medical Research Institute'), under the supervision of external collaborator Dr Ingvars Birznieks. Ethics approval was obtained from the University of Sydney Human Research Ethics Committee for sites 1 and 2 (ref: 11067), and from the University of New South Wales Human Research Ethics Committee for site 3 (ref: 02179 and 11074). The candidate took primary responsibility for all aspects of the research including topic identification, study design, formulation of hypotheses, data collection, statistical analysis, interpretation of results and writing the thesis. The candidate was the primary author of the manuscript presented in this thesis, and major contributions from co-authors are as follows: Dr Tatjana Seizova-Cajic conceived Experiments 1 and 3, and conducted Experiment 3, and Dr Ingvars Birznieks provided expertise in microneurographic recording techniques to collect physiological data.

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Abstract

Like other senses, tactile perception is subject to adaptation effects in which systematic changes in the pattern of sensory input lead to predictable changes in perception. In this thesis, aftereffects of adaptation to tactile motion are used to reveal the processes that give rise to tactile motion perception from the relevant sensory inputs. The first aftereffect is the tactile speed aftereffect (tSAE), in which the speed of motion appears slower following exposure to a moving surface. Perceived speed of a test surface was reduced by about 30% regardless of the direction of the adapting stimulus, indicating that the tSAE is not direction sensitive. Additionally, higher adapting speeds produced a stronger tSAE, and this dependence on adapting speed could not be attributed to differences in temporal frequency or spatial period that accompanied the different adapting speeds. The second motion aftereffect that was investigated is the dynamic tactile motion aftereffect (tMAE), in which a direction-neutral test stimulus appears to move in the opposite direction to previously felt adapting motion. The strength of the tMAE depended on the speed of the adapting motion, with higher speeds producing a stronger aftereffect. Both the tSAE and the tMAE showed evidence of an intensive speed code in their underlying neural populations, with faster adapting speeds resulting in stronger aftereffects. In neither case was any evidence of speed tuning found, that is, neither aftereffect was strongest with a match between the speeds of the adapting and test stimuli. This is compatible with the response properties of motion sensitive neurons in the primary somatosensory cortex. Despite these shared features, speed and direction are unlikely to be jointly coded in the same neurons because the lack of direction sensitivity of the tSAE requires neural adaptation effects to be uniform across neurons preferring all directions, whereas the tMAE requires direction selective adaptation.

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Glossary

FA1: Fast Adapting type 1 mechanoreceptive afferent (human).

FA2: Fast Adapting type 2 mechanoreceptive afferent (human).

hMT+/V5: The human motion complex, a brain region of the occipital lobe.

PC: Pacinian mechanoreceptive afferent (monkey; equivalent to FA2 in humans).

PSE: Point of Subjective Equality.

RA: Rapidly Adapting mechanoreceptive afferent (monkey; equivalent to FA1 in humans).

RF: Receptive Field.

SP: Spatial Period.

SA: Slowly Adapting mechanoreceptive afferent (monkey; equivalent to SA1 in humans).

SA1: Slowly Adapting type 1 mechanoreceptive afferent (human).

SA2: Slowly Adapting type 2 mechanoreceptive afferent (human).

SI: The primary Somatosensory cortex.

TF: Temporal Frequency.

tMAE: Tactile Motion Aftereffect.

tSAE: Tactile Speed Aftereffect.

vMAE: Visual Motion Aftereffect.

Chapter 1: Background

1 .1 Introduction

The goal of this thesis is to discover the sensory processes that contribute to perception of motion across the skin, in particular perception of both its direction and speed. Tactile research has focused on detection, vibration perception and perception of surfaces more than motion. Those studies that have examined tactile motion perception have tended to focus on perceived direction, while perceived speed is relatively unexplored, as is the relationship between these two features. As with other senses, tactile perception is subject to adaptation, in which sustained exposure to a stimulus results in changes in how that stimulus and similar stimuli are perceived. In the experiments reported here, sensory adaptation is employed as a technique to uncover the mechanisms involved in tactile motion perception. Participants were exposed to sustained motion on the skin, and the resulting changes to perception were observed. Systematically varying the stimulus features, such as texture, speed and direction, can reveal the inputs that the tactile system is most sensitive to, exposing the underlying perceptual and neural mechanisms affected by adaptation. This chapter presents a review of the existing literature on the somatosensory system, the functional role of tactile motion perception and the perception of direction and speed. The use of adaptation as a tool for examining sensory systems is explained, with examples of how it has been used previously in the tactile and visual domains.

1 .2 The somatosensory system

The site of stimulation used in the experiments reported here is the volar surface of the fingers, usually the distal finger pad of the index finger. Primates have two different kinds of skin – hairy skin that covers most of the body, and glabrous (hairless) skin on the volar surface of the hands and fingers, the soles of the feet and the perioral region (lips). The hands and fingers are most commonly used for object and surface exploration, and the glabrous skin has some unique features that serve this function. The glabrous skin on the fingers is very sensitive to mechanical stimulation, with humans able to detect skin indentations as small as 10μm (Johansson & Vallbo, 1979b). It also has a high density of receptors with small receptive fields, providing high spatial resolution, particularly in the distal finger pads (Johansson & Vallbo, 1979a).

Mechanoreceptors are primary afferents that are sensitive to mechanical deformations of the skin, and are distinct from thermoceptors (signalling temperature) and nociceptors (signalling noxious stimuli, usually causing pain). Four types of mechanoreceptor afferents innervate the glabrous skin of the human hands and fingers (Johansson, 1978; Knibestöl & Vallbo, 1970; Knibestöl, 1975). When identified by their response properties, these units are labelled Slowly Adapting Type 1 and 2 (SA1, SA2) and Fast Adapting Type 1 and 2 (FA1 and FA2). A lot of research on primary afferents has been conducted in monkeys, who have a similar set of mechanoreceptive afferents, and inferences about human tactile function are commonly made from monkey studies. In contrast to humans, monkeys have only three types of mechanoreceptive afferents innervating the glabrous skin, which are usually referred to as SA (slowly adapting, with response properties similar to SA1 units in humans, RA (rapidly adapting, with response properties similar to FA1 units in humans) and PC (named for the underlying anatomical structure, Pacinian corpuscles, with response properties similar to FA2 units in humans).

The FA units respond only to transient stimulation, firing at the onset (and often the offset) of a pressure stimulus applied to the receptive field, but falling silent when pressure is sustained (Knibestöl & Vallbo, 1970). They continue firing when vibration is applied (Järvilehto, Hämäläinen, & Laurinen, 1976). The responses of human FA1 and monkey RA units are precisely phase-locked to the cycle of vibration (Johansson, Landström, & Lundström, 1982b; Johnson, 1974; Talbot, Darian-Smith, Kornhuber, & Mountcastle, 1968), or to the cycle of indenting features of a surface scanned across the receptive field (Darian-Smith & Oke, 1980; Morley & Goodwin, 1987). The SA units continue firing when pressure is sustained over the receptive field. The type 1 primary afferents have small receptive fields, with sharp borders that are relatively densely distributed, and have multiple points of maximal sensitivity (Knibestöl & Vallbo, 1970). The type 2 afferents have large receptive fields with diffuse borders that are relatively sparsely distributed (Knibestöl & Vallbo, 1970).

The primary somatosensory cortex (SI) is the main target site in the brain for ascending pathways in touch, with primary afferents mainly projecting via the dorsal column and the ventroposterior thalamic nuclei (for review, see Wall & Dubner, 1972). SI has two main organisational features. The first is a somatotopic arrangement, in which neighbouring regions of cortex respond to stimulation of neighbouring skin regions, creating a 'map' of the skin surface in the brain (Overduin & Servos, 2004; Penfield & Boldrey, 1937). The region of cortex representing the hand and fingers is large relative to the representation of the rest of the body, reflecting the functional importance of these skin regions for sensation. The second organisational feature is the division into cytoarchitectural Brodmann areas 3a, 3b, 1 and 2, and the neurons in these areas have different functional properties (discussed below). The somatotopic map appears to be orthogonal to the Brodmann areas, with observations that the hand and finger somatotopic maps are repeated in each area (Kaas, Nelson, Sur, Lin, & Merzenich, 1979; Merzenich, Kaas, Sur, & Lin, 1978; Nelson, Sur, Felleman, & Kaas, 1980; Pons, Garraghty, Cusick, & Kaas, 1985; Sanchez-Panchuelo et al., 2012).

When studying perceptual phenomena, researchers usually make the assumption that perceptual and neural phenomena are closely linked, that neural phenomena give rise to perceptual experience, and conversely that perceptual phenomena reflect the neural processes underlying them. Evidence for this comes from neurophysiological experiments in which direct electrical stimulation of some neurons results in distinct perceptual phenomena. For example, Penfield and Boldrey (1937) electrically stimulated areas of the somatosensory cortex in pre-operative epilepsy patients and noted the sensations that were produced.

Ochoa and Torebjörk (1983) similarly applied microstimulation to single mechanoreceptor primary afferents with receptive fields on the hand of their human participants. The stimulation evoked sensations at locations that matched the receptive fields. Stimulation of FA1 units evoked a sensation of 'intermittent tapping', PC units produced 'vibration or tickle' and SA1 units produced 'pressure'. Neural stimulation doesn't always result in sensory phenomena, however. When Ochoa and Torebjörk (1983) stimulated single SA2 units, they did not produce any percept in isolation, suggesting that not all neurons are equally involved in producing perceptual phenomena, and that in some cases sensory neurons might contribute to perception only in the context of a population response, such that the activity of multiple neurons would be required to exceed a perceptual threshold.

1 .3 The role of motion across the skin in perception of surfaces and objects

The sense of touch can be functionally divided into sensations related to the perception of the environment (e.g. a felt object or surface) and those related to the perception of the self and the condition of the skin and body (e.g. being touched at a certain skin location, itching). Early tactile researchers observed the qualitative difference in the sensations produced when two areas of skin touch each other, and one acts as a sense organ while the other is the felt object (Gibson, 1962; Krueger, 1970; Weber, 1905/1996). Weber described this sensation:

> *"We can touch one hand with the other, or touch the tip of our tongue with our teeth, or, vice versa, feel our teeth with the tip of our tongue in the mouth: in so doing we perceive them as external objects." – p148, Weber (1905/1996)*

Motion between the skin and the felt object or surface is beneficial when using tactile perception to obtain information about the environment, an observation made by Weber (1834/1996) and Katz (1925, cited in Krueger, 1970), and later confirmed experimentally by several researchers (Gibson, 1962; Meenes & Zigler, 1923; Morley, Goodwin, & Darian-Smith, 1983). Katz described the stationary hand as "beset with a partial anaesthesia" (p. 339, Katz, 1925; cited in Krueger, 1970). The importance of motion for tactile perception may reflect the greater responsiveness of primary afferents to motion across the skin. Without motion, both FA1 and FA2 afferent units are barely stimulated, and even SA units respond more strongly to dynamic than sustained stimulation (Johnson & Lamb, 1981).

Movement across the skin improves performance in several different tactile spatial judgment tasks. Weber (1834/1996) observed that two points contacting the skin with a small separation between them were perceived as only one point when they were applied to the finger simultaneously, but could be distinguished when moving the finger back and forth across the two points. At four different stimulation sites, Loomis and Collins (1978) found that the distance required for a water jet to travel across the skin to produce reliable direction discrimination was shorter than that needed for threshold performance on two static tests of spatial resolution on the same stimulation sites (Weinstein, 1968): the first static task, *two-point discrimination*, was to judge whether a single probe was presented or if two separate probes were presented simultaneously; the second task, *point localisation*, was to judge whether the probe was located at a previously presented reference point. Gould, Vierck and Luck (1979) also found that discriminating the orientation of lines was easier when an arc was rolled over the skin to define the line than when a stationary plastic edge was pressed into the skin. Similarly, when the line was defined by its two end-points, orientation discrimination was better when the end-points were presented sequentially rather than simultaneously (Gould et al., 1979).

In a study investigating the role of motion in surface perception, Morley, Goodwin and Darian-Smith (1983) had participants judge the roughness of fine textured surfaces. These surfaces were of a periodic "grating" form, with regular ridges. They found that if participants were free to tactually scan the surfaces, moving the index finger across it, they were able to discriminate small differences in the ridge-to-ridge distance, or spatial period (SP), of the surfaces. However, when the experimenter put barriers on either side of the finger to prevent tangential motion between the surface and the skin, performance dropped and participants required greater differences in SP to maintain the same discrimination performance. All of these observations suggest that the introduction of motion to static stimulus presentation improves the spatial resolution of tactile perception.

Active and passive touch

Weber (1834/1996) also observed that objects are felt more clearly when actively explored with the fingers. Gibson (1962) found that participants were better at identifying cookie cutters of different shapes when they were rotated on the palm than when they were simply placed there, while active exploration with the fingers yielded better performance again. This result provides some support for the notion that relative movement between the skin surface and an object aids identification, but it does not explain how. When comparing rotation on the palm with stationary placement, it could have been the presence of motion that improved performance, or it could be the increased amount of contact between different areas of skin and the different parts of the object. Improved performance with finger exploration could have been due to the active nature of the movement or to the better sensitivity of the fingertips than the palm.

Several further studies suggest that that passive motion across the surface is sufficient for object and surface identification, and that active touch is not necessary. Cronin (1977) conducted an experiment similar to Gibson's with better control over the differences between conditions, restricting contact to only the palm in all three conditions: no movement, active exploration, and passive touch with a moving object. Similar to Gibson, she found that object identification was worst when there was no movement between the skin and the object, but active exploration conferred no benefit when it was restricted to the same skin area as the passive movement condition. Schwartz, Perey and Azulay (1975) similarly found no difference between active and passive touch when shapes were felt with the finger. Active vs. passive touch also has little impact on perceptual discrimination of surface textures under most circumstances (Lamb, 1983; Yoshioka, Craig, Beck, & Hsiao, 2011), or on Braille reading speeds (Grunwald, 1966).

Apart from its importance for object and surface perception, tactile motion also plays a role in motor function and affect. For example, when holding an object, small slips trigger automatic grip force adjustments (Johansson & Westling, 1987), and slow movement of materials across the skin elicit reliably higher pleasantness ratings than when scanned at fast speeds (Essick, James, & McGlone, 1999).

Perception of tactile motion properties

It is clear that motion across the skin is important for several functions. What is not as obvious is why the properties of the motion itself are available to perception. That is, it is less clear what function is served by the human ability to make conscious judgments about the speed and direction of motion across the skin. When perceiving surfaces, scanning speed must be taken into account but it need not be perceived directly. It is not obvious that maintenance of grip should require a precise perception of the speed or direction with which something is slipping from the hand; a signal simply that it is slipping may be sufficient. In fact, it might not require any conscious perception at all. Reflex actions do not require conscious perception, and Dijkerman and de Haan (2007) have proposed, based on perceptual phenomena and neuroanatomical evidence, that separate somatosensory pathways serve conscious perception and perceptual-motor functions. For example, in a phenomenon called 'numbsense', patients with cortical or thalamic lesions are able to point to tactile stimulation applied to the impaired hand despite being unable to detect the stimulation, or verbally report its location (Aglioti, Beltramello, Bonazzi, & Corbetta, 1996; Paillard, Michel, & Stelmach, 1983; Rossetti, Rode, & Boisson, 1995).

One possible role for conscious perception of the speed and direction of a surface moving relative to the skin is to provide motor control feedback when scanning a surface. Motion perception might be needed to adjust hand movements to bring the relative speed between the skin and the surface within the optimal range for surface perception and object manipulation. However, speed and direction signals are still available to perception when there is no hand movement, e.g. when a surface is moved across the stationary fingers.

Simultaneous motion of the object and the finger can also be perceptually separated, and the speed and direction of either the hand or the object motion estimated (Gibson, 1962; Vitello, Ernst, & Fritschi, 2006). Nevertheless, our attention tends to be focused away from the motion, and towards the percept of a stable and persistent object or surface, even as the motion facilitates this percept. It is similar to some other important sensory inputs, such as the visual blur across the retina when the head moves – our attention remains on the external world, which appears stable. The vestibular system, used constantly to maintain balance, and proprioception, which provides information about our body position and movement, are two sensory systems that are so ignored that they do not even appear in the popular notion of the "five senses". Awareness of these inputs is not required for them to function, but conscious perception gives us information about the environment that may not trigger immediate action. For example, if an object slips from grasp, it is useful to be aware of that even if the grip is not adjusted. It is possible that the primary function of perceiving tactile motion cues is to serve higher-level decision-making processes.

1 .4 Perceived direction of tactile motion

Direction discrimination typically refers to one of two different tasks: the first one involves detecting a difference in the *trajectories* of two motion stimuli travelling across the skin, which differ by a certain angle. Thresholds for trajectory discrimination on the finger vary depending on the manner of stimulation (Drewing, Fritschi, & Zopf, 2005; Eves & Novak, 1998; Keyson & Houtsma, 1995; Salada, Vishton, Colgate, & Frankel, 2004; Tsagarakis, Horne, & Caldwell, 2005). While it isn't clear what the optimal conditions are, very low thresholds of 3.6° have been reported for a rough textured surface that slid across the finger at 100mms^{-1} (Salada, Vishton, Colgate & Frankel, 2004), while high thresholds were reported for a probe that laterally stretched the skin, traversing 1mm of the finger pad at 10mms^{-1} (Drewing et al., 2005). Intermediate thresholds have been reported with electrocutaneous apparent motion applied across multiple fingers (Eves & Novak, 1998), and a probe that stretched the finger pad skin, moving at 15-41mms^{-1} and traversing 3.25mm (Keyson & Houtsma, 1995).

Perceived direction is likely based on the population responses of direction selective neurons in the primary somatosensory cortex (SI). Costanzo and Gardner (1980) reported that 56% of the direction selective neurons that they sampled were broadly tuned (although narrow tuning was more prevalent on the hand area than the forearm). This broad tuning means that fine direction discrimination of direction trajectories observed in perceptual judgments requires analysis of the neural responses at the population level. One possible population code was suggested by Ruiz, Crespo and Romo (1995), who found that a population vector average, in which the preferred direction of each neuron is weighted according to its response intensity, was a good estimate of stimulus motion direction, although the site of such a computation is unknown.

The second task, which has been studied much more extensively, involves judging which of two *opposite directions* a single motion stimulus moved in, and the threshold is given by the distance required to reach a certain level of performance (usually 75% accuracy), known as the *critical traverse length*. The lowest discrimination thresholds tend to be observed with stimuli that stretch the skin, move at faster speeds (up to approximately 10mms^{-1}), and are applied to densely innervated skin regions (these factors are discussed in detail in the following sections). On the finger, the critical traverse length for discriminating opposite directions of motion is between 0.1mm and 3.3mm, depending on the manner of stimulation (Essick, Bredehoeft, McLaughlin, & Szaniszlo, 1991; Gleeson, Horschel, & Provancher, 2010; Loomis & Collins, 1978).

Compared to static tactile stimulation, moving stimuli appear to engage additional sensory processes. Judgments of some static stimuli placed on the skin may be poor, while dynamic stimuli with the same spatial extent are more clearly perceived. For example, trajectory discrimination is better than orientation discrimination of stationary bars pressed on to the skin (Gould et al., 1979), and the critical traverse length for discriminating the direction of two points sequentially applied to the skin is shorter than the distance required for discriminating two points of contact that are presented simultaneously to the skin (Loomis & Collins, 1978; Weinstein, 1968).

Two cues to direction of motion: stretch and successive positions

The tactile motion system takes advantage of two cues for direction that are present in a stimulus that moves across the skin. The first of these is lateral skin stretch, and the second is the stimulation of successive positions, in sequence, along the path of motion. Either one of these cues alone can signal direction, but both cues are frequently present in typical interactions with the environment. At the onset of motion between the skin and a surface, there is initially only skin stretch. When the force of lateral movement overcomes the friction between the skin and surface, a sliding motion begins, which additionally provides the successive positions cue. Switching between these two modes of motion is referred to as 'stick-slip' (Salada et al., 2004; Srinivasan, Whitehouse, & LaMotte, 1990).

Direction discrimination is very sensitive to how much the stimulus causes the skin to stretch, whereas the successive positions cue must be relied on when no skin stretch is present. Using a probe glued to the skin so that no successive positions cue is present, good discrimination of opposite directions has been observed on the forearm for excursions as small as 0.13mm (Olausson, Hamadeh, Pakdel, & Norrsell, 1998), and 0.2mm on the finger pad (Gleeson et al., 2010). Gould et al. (1979) reported that on the forearm, a frictionless air-stream stimulus that does not stretch the skin, providing only the successive positions cue, had a much higher critical traverse length (11.3mm) than a probe that provides both skin stretch and successive positions cues (2mm).

Norrsell and Olausson (1992) dragged a metal probe across the forearm and found that increasing the amount of skin stretch by increasing the vertical load (from 1 to 6g) resulted in a tenfold decrease in the critical traverse length (from 27.5mm to 2.5mm). This was unlikely to be due to other factors affected by vertical load because direction discrimination did not improve when the load of a frictionless air-stream stimulus was increased (by increasing the pressure with which it was forced through the nozzle; Norrsell & Olausson, 1992; Norrsell & Olausson, 1994). The air-stream did not stretch the skin, regardless of the load, so the discriminability of the stimulus did not change. Conversely, restricting how much the skin can be stretched, either by bracing the skin with plaster or by changing the posture of the arm (straight or bent at the elbow), results in a decline in direction discrimination of a moving probe (Norrsell & Olausson, 1992; Olausson & Norrsell, 1993).

The direction of skin stretch may already be coded in the primary afferents. Several studies have observed that SA2 units in human glabrous skin exhibit a sensitivity to skin stretch, and are often direction selective, showing large differences between responses to the preferred direction of stretch and the opposite direction (Essick & Edin, 1995; Johansson, 1978; Knibestöl & Vallbo, 1970; Knibestöl, 1975; Olausson, Wessberg, & Kakuda, 2000; Westling & Johansson, 1987). SA units in monkeys (equivalent of SA1 units in humans) show similar response properties (Srinivasan et al., 1990). Tangential forces that stretch the skin have also been shown to provoke direction selective responses in FA1 as well as SA1 and SA2 units in humans (Birznieks, Jenmalm, Goodwin, & Johansson, 2001), and in both RA (equivalent to FA1) and SA units in monkeys (Wheat, Salo, & Goodwin, 2010). Furthermore, the majority of the primary afferent units of all three types found in monkey glabrous skin (SA, RA and PC, equivalent of human SA1, FA1 and FA2) were found to be sensitive to the direction of a grating scanned across the receptive field (Goodwin & Morley, 1987a), a stimulus that provided both stretch and successive positions cues.

While skin stretch is unique to touch, the successive positions cue is also present in vision. This shared feature accounts for some similarities between the tactile and visual motion systems. For example, the aperture problem, a well known visual phenomenon, has also been observed in touch (Bicchi, Scilingo, Ricciardi, & Pietrini, 2008; Pei, Hsiao, & Bensmaïa, 2008). The aperture problem was first described for visual stimuli (Wallach, 1935; see also Adelson & Movshon, 1982), and occurs when a stimulus is perceived through an aperture that hides the end-points of a line (or grating). Motion is always perceived as orthogonal to the line because motion along the parallel axis doesn't change the stimulus. Bicchi et al. (2008) demonstrated the tactile aperture problem with a ridged grating felt by participants using the finger pad through an aperture, and used lubricant to reduce the stretch cues present in the stimulus. Without this step, the ridges would almost certainly have stretched the skin, providing an additional unambiguous cue to the real direction of motion. Pei et al. (2008) similarly demonstrated the aperture problem with a frictionless stimulus – they used a dense tactile array that can present tactile apparent motion gratings with effectors that move only perpendicular to the skin surface. It is the successive positions cue that is susceptible to the aperture problem, while stretch cues can be used to perceive motion components parallel to the stimulus, even when end points and other spatial cues are hidden by the aperture.

Surface texture is crucial for the successive positions cue, but not for stretch (though it plays a role in both). Srinivasan et al. (1990) found that when feeling a totally smooth glass surface move across the finger, participants could detect the initial portion of the motion (the 'stick' portion of its stick-slip motion) and were able to judge direction based on the initial stretch, despite the lack of any surface features. However, when the plate continued to slide across the skin afterwards, participants could not detect the motion because both stretch and successive positions cues failed. When the otherwise smooth surface had a single small protrusion (550μm across, 4μm high), the slip portion of the motion could be detected, and the protrusion could be tracked across the skin, indicating that it provided a successive positions cue. Participants were also able to detect the slip portion of the motion when the surface had a repeating pattern of even smaller protrusions (50μm across, 1μm high, 100μm SP), even though they could not track the individual elements. The stretch cue was likely to have failed in the slip portion of the motion for all three surfaces, as no differences were observed in the amount of skin stretch in this phase (it was monitored with a video camera). While surfaces with coarser features might cause more stretch even during slip motion, it seems likely that in this case, only the successive positions cue was present.

The responses of individual primary afferents are only minimally sensitive to direction when the stimulus produces little to no stretch (Gardner & Palmer, 1989; Pei, Hsiao, Craig, & Bensmaïa, 2010). In this case, successive activation of neighbouring afferents can provide the successive positions cues to direction (Darian-Smith & Oke, 1980; Srinivasan et al., 1990). The small receptive field sizes of SA1 and FA1 units provide high spatial resolution of an object moving across the skin, while the fast adapting nature of the FA1 and FA2 units provide high temporal resolution. The combination of high spatial and temporal resolution signals means that FA1 units probably play the dominant role in signalling the successive positions cue, although SA1 and FA2 units may also contribute.

Evidence for the role of RA and PC afferents in signalling successive positions was provided by Srinivasan et al. (1990) when they recorded the responses of single mechanoreceptor afferents in monkeys and their responses to the smooth, fine textured and single-protrusion surfaces moving across the skin (described above). Neither RA nor PC afferents responded during the slip portion of the motion to the smooth surface, the only surface that provided no successive positions cue. In contrast, the fine textured surface was signalled only by PC afferents, while the surface with a single protrusion elicited a brief response in RA mechanoreceptor units as the protrusion crossed the receptive field. RA units with neighbouring receptive fields would presumably be activated in sequence as the protrusion travelled across the skin.

The responses of primary afferents would need to feed in to a later comparator stage to produce direction discrimination from the successive positions cue. The dorsal column nuclei receive convergent inputs from the periphery (Jones, 2000; Wall & Dubner, 1972), and may play an important role in processing direction of motion. Lesions to the dorsal columns cause selective impairment of direction discrimination, while other tactile functions are preserved such as detecting the presence of motion or judging its speed, presumably via other pathways (Vierck, 1974; Wall & Noordenbos, 1977). The dorsal column nuclei project to the cortex via the thalamus.

The primary somatosensory cortex (SI) is the most obvious candidate as the neural basis for tactile direction coding. SI neurons have larger receptive fields than peripheral units, covering whole finger segments and sometimes the whole hand (Costanzo & Gardner, 1980), due to convergent inputs from the periphery (Gardner, Palmer, Hämäläinen, & Warren, 1992). About 38% of SI neurons respond better to motion across the receptive field than to simple punctate stimulation (Warren, Hamalainen, & Gardner, 1986), and a large number of these motion sensitive neurons (approx. 60%;

Warren et al., 1986) are direction selective (Hyvärinen & Poranen, 1978; Warren et al., 1986; Whitsel, Roppolo, & Werner, 1972).

There is evidence that motion is processed in different ways in the different areas of SI. Area 3b neurons show response inhibition when stimulation of the receptive field is accompanied by nearby stimulation outside the receptive field, and the magnitude of the inhibition depends on the relative location and timing of stimulation (Reed et al., 2010). This suggests spatio-temporal filtering of the type that would be required for processing of the successive positions cue. However, area 3b may be involved in a large variety of tactile tasks, and direction-selective neurons are found less commonly in area 3b than in areas 1 and 2 (Gardner, 1988; Hyvärinen & Poranen, 1978). Pei et al. (2010) found neurons in SI that signalled the direction of motion regardless of shape, speed and indentation amplitude. These pattern-independent neurons were mostly found in area 1, with a small number in area 2.

The receptor number hypothesis

In studies using critical traverse length as the threshold for direction discrimination, it is important to understand why increasing traverse length improves performance in direction discrimination tasks. The stimuli used are well above detection thresholds, so it is not the case that greater traverse lengths are required simply because they improve the chance to detect the presence of the stimulus. Furthermore, in all of these studies, traverse length was confounded with presentation duration. That is, as traverse length increased, so did presentation duration, and the researchers could have measured the ‘critical presentation duration’ with equal validity. However, there is evidence that suggests it is neither the traverse length nor the presentation duration per se, but rather the total amount of receptor activation, that determines direction discriminability.

The first indication of this is the observation that discrimination of two opposite directions shows regional inhomogeneity, with the critical traverse length varying widely between stimulation sites. Loomis and Collins (1978) measured the critical traverse length of a water jet stimulus at several sites. Sensitivity was best on the finger (0.1mm), followed by the forehead, the belly, and was worst on the back (3.5mm). Several other studies have shown similar variations in critical traverse length of a brush stroked across the skin at different sites (Dreyer, Hollins, & Whitsel, 1978; Essick et al., 1991; Whitsel, Dreyer, Hollins, & Young, 1979). For example, Essick et al. (1991) found that the critical traverse length increases as the stimulation site moved progressively from the finger (3.3mm) to the shoulder (28.1mm). The brush stimuli used in the latter studies provided both stretch and successive positions cues, indicating that regional inhomogeneity is observed even with rich motion stimuli.

In all of these studies, the most sensitive sites with the lowest critical traverse lengths tend to be the most densely innervated. A similar pattern is observed with static two-point discrimination and point localisation thresholds (Weinstein, 1968). This effect of innervation density suggests that direction discrimination depends on the amount of peripheral receptor recruitment elicited by the stimulus. That is, as more peripheral receptors respond to the stimulus, the more information becomes available with which to make direction judgments. Greater density of innervation affords greater spatial resolution for perceptual tasks, and would require a stimulus to cover a shorter distance to recruit the same number of receptors. Here, this is referred to as the *receptor number hypothesis*.

The receptor number hypothesis is also supported by studies in which the motion stimulus is discontinuous, contacting only some points on the skin along the motion path (Essick, McGuire, Joseph, & Franzén, 1992; Gardner & Sklar, 1994). Essick et al. (1992)

compared an uninterrupted brush stroke felt through a single aperture (7.5mm) to an interrupted brush stroke felt through two split apertures (2.5mm each). The split apertures produced motion with the same starting and end points as the single aperture, but with an area in the middle where skin contact was broken and the motion occluded. Direction sensitivity was lower when motion was partially occluded, suggesting that discrimination depends not only on the distance traversed, but that the intervening contact is also important.

The same effect was observed in a study by Gardner and Sklar (1994) who used apparent motion rather than real motion. Their tactile array was made up of spatially separated probes that can be independently controlled to indent the skin at the desired time (a 24x6 vibrotactile array, "Optacon"). By vibrating the skin at different locations in sequence an illusory sensation of motion across the skin is produced, known as *apparent motion*. Unlike real motion, apparent motion is discontinuous, with discrete stimulation occurring only at the location of the probes. Gardner and Sklar (1994) varied the distance between successively activated rows of vibrating probes while maintaining a fixed traverse distance (using the same starting and end points). They found that direction discrimination performance was better with shorter distances between rows (range 1.2 – 4.8mm). Furthermore, they found ceiling performance when 8 rows were activated, regardless of whether this was achieved by increasing traverse length or decreasing step distance. This is consistent with the receptor number hypothesis, as it is the amount of sensory information that is important for direction discrimination, rather than the particular spatial dimensions of the stimulus.

While the amount of sensory input in a motion stimulus is important for direction discrimination, it is not simply a matter of providing additional peripheral input; it must be of the right sort to improve discrimination. Additional peripheral recruitment that can potentially signal motion direction sometimes fails to produce an improvement in discrimination. For example, increasing the width of the stimulus along the axis orthogonal to the motion either has no effect (Drewing et al., 2005; Essick et al., 1992; Tan, Gray, Young, & Traylor, 2003), or in some cases, it even impairs direction discrimination (Essick, Rath, et al., 1996; Tan et al., 2003). This suggests that it is not simply the total amount of peripheral activation that determines direction sensitivity, but that additional stimulation along the axis of motion is needed for improvement in discrimination.

A similar observation has been made in vision, where increasing the size of high-contrast drifting gratings impairs direction discrimination (Tadin, Lappin, Gilroy, & Blake, 2003; Tadin & Lappin, 2005). This is thought to be due to the *centre-surround* receptive field structure of direction selective neurons in the middle temporal area (MT), an area of cortex associated with visual motion processing. These cells respond with excitation when stimulated in the centre of their receptive field, but response is inhibited when stimulation is applied to the region immediately surrounding the excitatory region (Barlow & Levick, 1965; Sterling & Wickelgren, 1969). When the stimulus size matches the excitatory region, it maximally stimulates these neurons, but when the size is increased, it stimulates both the excitatory and the inhibitory region, reducing the strength of the response, and with it the strength of the direction signal (Tadin et al., 2003). The effect of stimulus width on tactile direction discrimination suggests that centre-surround neurons may also be involved in tactile motion processing. While SI neurons have been reported with inhibitory regions, their receptive fields are not centre-surround (DiCarlo & Johnson, 2000; Gardner & Costanzo, 1980a), but centre-surround cells are found in the dorsal column nuclei (Bystrzycka, Nail, & Rowe, 1977; Gordon &

Paine, 1960), and the thalamus (Jänig, Spencer, & Younkin, 1979) of cats, and in small numbers in the monkey thalamus (Poggio & Mountcastle, 1963).

The effect of scanning speed on direction discrimination

Direction discrimination performance remains high over a wide variety of scanning speeds, approximately 10 – 300mms^{-1}, depending on the site and manner of stimulation (Dreyer, Duncan, Wong, & Whitsel, 1979; Dreyer et al., 1978; Essick & Whitsel, 1985a, 1985b; Essick, Afferica, et al., 1988; Essick, Rath, et al., 1996; Essick et al., 1991; Essick, Dolan, Turvey, Kelly, & Whitsel, 1990; Essick et al., 1992; Essick, Whitsel, Dolan, & Kelly, 1989; Eves & Novak, 1998; Gardner & Sklar, 1994; Whitsel et al., 1979). This range covers the range of functional scanning speeds (20-86mms^{-1}) spontaneously adopted during surface exploration (Connor, Hsiao, Phillips, & Johnson, 1990; Smith, Gosselin, & Houde, 2002; Yoshioka, Bensmaïa, Craig, & Hsiao, 2007). Because most of these studies measured critical traverse length for discriminating opposite directions of a brush stroked across the skin, this insensitivity to speed also constitutes insensitivity to changes in presentation duration, which is consistent with the receptor number hypothesis.

When judging a very slow or a very fast stimulus, direction discrimination performance declines, i.e. critical traverse length increases (Dreyer et al., 1979, 1978; Essick & Whitsel, 1985a, 1985b; Essick, Afferica, et al., 1988; Essick, Rath, et al., 1996; Essick et al., 1991, 1990, 1989; Gould et al., 1979; Whitsel et al., 1979). As the stimulus slows down, presentation duration increases, as does the time between stimulation of different receptors. Slow motion stimuli may be less effective at engaging motion processes, and instead be processed more like static stimuli, for which spatial resolution is poorer (Loomis & Collins, 1978; Weinstein, 1968). While most of the studies mentioned above used stimuli that provided both the successive positions and lateral stretch cues, there is also independent evidence for declines in direction discrimination for both cues. The successive positions cue is more poorly discriminated at both very high and low speeds, observed with an apparent motion stimulus that does not stretch the skin (Essick, Rath, et al., 1996); and lateral stretch of a probe glued to the skin is more easily discriminated when it is stretched at $10mms^{-1}$ than at $1mms^{-1}$ (Gould et al., 1979).

The decline in direction discrimination performance at very high speeds with successive positions cue may occur because the stimulus approaches the temporal resolution limits of the tactile system. If neighbouring receptors are stimulated very close together in time, the temporal order may not be preserved in the cortex, either due to variations in mechanoreceptor conduction velocities (Talbot et al., 1968) and the subsequent convergence of receptor inputs at the dorsal column nuclei (Jones, 2000), or because of temporal summation that occurs in direction selective SI neurons (Gardner et al., 1992). Stimulating for a longer duration and traversing a greater length of skin can compensate because receptors with greater receptive field separation will be stimulated with a greater temporal delay and bring the stimulus back within the temporal limits of the tactile motion system. This explanation is supported by the observation that more densely innervated areas have lower optimal speeds (Essick et al., 1991). As speed is increased on a densely innervated site, the temporal limits are reached sooner than they would be on a more sparsely innervated site because of the shorter time between activation of afferents with closer receptive fields.

This interpretation is also consistent with how speed interacts with traverse length in direction discrimination. While the optimal speed tends to not vary with traverse length (Dreyer et al., 1979, 1978; Essick et al., 1989), the range of effective speeds broadens with increasing traverse length so that good discrimination is maintained over a greater range of speeds (Essick et al., 1989; Whitsel et al., 1979). The same broadening of the effective speed range occurs when using a greater number of stimulation points in an apparent motion display, even when the traverse length is constant (Lakatos & Shepard, 1997). The greater number of receptors stimulated due to a greater traverse length (or additional stimulation points) compensate for less than ideal speeds.

1 .5 Perceived speed of tactile motion

Similar to perceived direction, both lateral skin stretch and successive positions cues can potentially contribute to perceived speed. The majority of previous research has used surfaces and objects that slide across the skin providing both stretch and successive positions cues. The contribution of stretch to speed perception has been largely ignored, but results of one study suggest that minimizing skin stretch results in a reduction in the perceived speed (Seizova-Cajic, Bergström, Karlsson, McIntyre, & Birznieks, 2013).

The physical motion of a natural surface or object sliding across the skin is defined by both the spatial and temporal properties of stimulation. The speed of an object such as a brush, is given by the stimulation duration and traverse length:

$$S = {}^{TL}/_{D}$$

Where S is the speed of the brush stroke; TL is the traverse length, or the distance that the brush travels across the skin; and D is the duration, or time it takes for the brush to move the traverse length. For these three features, only two can be manipulated independently at a time, and knowing the value of any two gives the value of the third.

Unlike an object that traverses the skin, when a surface is scanned across the skin, the motion is typically felt at the same region of skin throughout stimulation e.g. on the finger pad. Stimulation duration is also arbitrary, and unrelated to the speed or spatial features of the stimulus. Nevertheless, similar to an object traversing the skin, the motion of a scanned surface is defined by the relationship between the spatial and temporal properties of the stimulation. For a textured surface with periodic features such as ridges or bumps, the spatial period (SP) is the centre-to-centre distance between the features, measured parallel to the axis of motion. The relevant temporal parameter is the temporal frequency (TF), the frequency with which the spatial features of the surface cross a given skin location. Speed is then given by the following formula:

$$S = TF \times SP$$

Early studies of tactile speed perception used a brush stimulus stroked across the skin (Essick, Franzén, et al., 1996; Essick, Franzén, & Whitsel, 1988; Franzén, Thompson, Whitsel, & Young, 1984). They used a magnitude estimation method, asking participants to assign numbers on an arbitrary scale to the speed of motion that they felt. For a large range of speeds (5-2560mms^{-1}) and a variety of stimulation sites (index finger, dorsal forearm, face), participants' speed estimates increased monotonically with the actual speed of motion, fitting a power function (with exponent of 0.6). However, in these studies traverse length was fixed (or in some cases, duration was fixed), which means that speed judgments were confounded with duration (or traverse length). It is possible that participants were judging duration (or traverse length) and using that to infer speed.

Dépeault et al. (2008) conducted an experiment designed to evaluate the human ability to scale speed, free of confounds, and found that perceived speed is primarily determined by actual speed, rather than spatial or temporal features of the stimulation. Instead of a brush, they used textured surfaces with protruding bumps, and scanned the surfaces across participants' fingers. The surfaces were mounted on a rotating drum to create translational speeds of 33-110mms^{-1} at the skin surface. Importantly, they used different surfaces that varied in SP (2-8mm) in the direction of the scan, meaning that speed judgments could be analysed at a variety of combinations of SP and TF. They found that subjective speed judgments increased linearly with actual speeds. Further, the speed judgements were mostly independent of what surface was used (as well as SP, they also varied the feature density and periodicity of the surfaces), but there was a slight bias to perceive surfaces with a higher spatial period (8mm vs. 4.9mm and lower) as moving more slowly. This result shows that humans are able to judge the speed of motion across the skin and do not have to infer it from the temporal or spatial features of the stimulation.

It is not known how speed of motion across the skin is coded in the somatosensory system. While the firing rate of primary afferents increases with speed (Edin, Essick, Trulsson, & Olsson, 1995; Essick & Edin, 1995; Franzén et al., 1984; Goodwin & Morley, 1987b; LaMotte & Srinivasan, 1987a, 1987b), increasing contact force also increases firing rate (Darian-Smith, Davidson, & Johnson, 1980; Edin et al., 1995; Goodwin & Morley, 1987b), as does increasing TF (Darian-Smith & Oke, 1980; Morley & Goodwin, 1987). The firing rate of primary afferents provides an ambiguous signal with respect to these features, which must be decoded centrally.

Speed discrimination

Tasks that require judging the speed of motion across the skin tell us about the availability of this physical property to perception, and can reveal circumstances in which biases are introduced, such as the bias to perceive high SP surfaces as moving slightly slower than those with low SP (Dépeault et al., 2008). Tasks that require discriminating between surfaces moving at different speeds reveal the magnitude of the change in speed required for detection of a change, and this provides information about the precision of speed perception.

Early investigations of the capacity to discriminate between different speeds involved participants judging the relative speed of two successive presentations of a brush stroke. One such study investigated the respective capacity of human observers and individual SI neurons in monkeys to discriminate speed (Collins & Roppolo, 1980). Participants could correctly discriminate between brush strokes on the finger moving at 132 and 182mms^{-1} with a success rate of 80%. Of 37 SI neurons, 34 increased their activity monotonically with the speed of the moving brush, while for the remaining three neurons, response decreased with increasing speed. However, only four neurons were able to discriminate between different speeds with the same sensitivity as the human observers. On the other hand, SI must play a crucial role, as lesions to SI result in an inability to discriminate tactile motion speed (Zainos, Merchant, Hernández, Salinas, & Romo, 1997).

An early psychophysical study measured Weber fractions, the proportional increase in speed from a reference stimulus needed to reach a discrimination threshold. Essick, Franzén, et al. (1988) had participants judge a larger range of speeds (15-1400mms^{-1}) applied to the forearm. They reported Weber fractions between 0.20 and 0.24 for most of the speed range, with worse performance at speeds below 20mms^{-1}. Similar to the early speed scaling experiments described above, the brush stimuli in these experiments had a fixed traverse length, confounding speed with stimulation duration. Participants could have discriminated the stimuli based on their presentation duration.

Several studies have since used periodic textured surface stimuli to measure speed discrimination, avoiding the confound with presentation duration present in the brush stroke studies, and found results largely consistent with the studies using brushes (Basso et al., 2012; Damian, Ludersdorfer, Hernandez Arieta, Pfeifer, & Okamura, 2012;

Ricciardi et al., 2011; Salada et al., 2004). However, these studies did not vary the SP of their periodic surfaces, and so speed was confounded with TF. Dépeault et al. (2008), who disambiguated speed and TF for speed judgments by using surfaces with different SPs (described above), did not have their participants make direct speed discriminations. However, they did analyse the slope of the function relating perceived speed to actual speed, which is an indication of discrimination sensitivity. They found no evidence for any differences in slope due to the surfaces used, suggesting that participants do not rely on SP or TF when discriminating speed.

While speed discrimination appears to be invariant with respect to changes in SP, gross features of surface texture do appear to play a role in the discriminability of speed. Salada et al. (2004) found that when discriminating speeds from 80 or 140mms^{-1}, performance was better for a surface that had small bumps spaced 10mm apart (Weber fractions 0.09 – 0.11) than for a surface sand-blasted to create a homogenous rough surface (Weber fractions 0.10 – 0.25). Webster et al. (2005) used a lightly sanded plastic ball, and found discrimination performance similar to that with the sand-blasted surface used by Salada et al. (2004): to detect oscillations in speed from the base speed (100mms^{-1}), participants required the speed to oscillate between 70 and 130mms^{-1}, a difference of 0.3 of the baseline speed. Bensmaïa, Killebrew and Craig (2006) used a very dense tactile array to create an apparent motion stimulus, a sine wave grating pattern with 8mm SP, moving at 40mms^{-1}. Similar to Salada et al.'s bumpy surface with 10mm SP, this stimulus produced a high level of speed discrimination sensitivity (Weber fraction of 0.16). Finally, when Dépeault et al. (2008) had participants judge the speed of a smooth surface, the slopes of the function relating perceived speed to actual speed were about one third of those for textured surfaces, suggesting discrimination was worse for the smooth surface (although this condition may have been subject to adaptation effects as it was always tested last). These studies suggest that it is easier to discriminate the speed of surfaces with separable features than it is for smooth surfaces or surfaces with fine textures.

The ability to discriminate the speed of a surface may depend on that surface's provision of the successive positions cue. The superior speed discrimination observed with surfaces with separable bumps or ridges (Bensmaïa et al., 2006; Dépeault et al., 2008; Salada et al., 2004) compared to homogenous fine textures (Salada et al., 2004; R. J. Webster et al., 2005) or smooth surfaces (Dépeault et al., 2008) may be because the coarser features are more easily spatially resolved, providing a better successive positions cue. However, it could also be that the speed of lateral stretch is more robustly signalled as the elements of the coarse stimuli create more stick-slip events, repeatedly stretching and releasing the skin.

Discounting motion to preserve roughness constancy

The coding of speed in the tactile system plays an important role in surface perception. Although we shouldn't expect that speed coding as it relates to surface perception to necessarily have a direct correspondence to conscious perception of speed, the two are likely to share some neural mechanisms. Many researchers in tactile perception have been concerned with the question of how perceived roughness remains constant in the presence of motion when a surface is explored with the fingers, which usually varies in scanning speed. For periodic surfaces with ridges or raised dots, the main determinant of perceived roughness is the width of the gap between the features (which, added to feature width, gives SP), which scales with perceived roughness over the range 0.125-8.5mm (Cascio & Sathian, 2001; Kudoh, 1988; Lederman, 1974, 1983; Meftah, Belingard, & Chapman, 2000). Furthermore, perceived roughness is largely unaffected by scanning speeds between 10 and 250mms^{-1} (Katz, 1925, cited in Krueger, 1970; Katz, 1925, cited in Lederman, 1974; Lamb, 1983; Lederman, 1974, 1983; Meftah et al., 2000; Yoshioka, Craig, Beck, & Hsiao, 2011).

This phenomenon is known as *roughness constancy*. Roughness constancy functions within a similar range of speeds as direction discrimination (10-250mms^{-1} and 10-300mms^{-1}, respectively), and functions under ecologically valid scanning conditions. Perceived roughness varies with speed only at very high speeds (207-600mms^{-1}; Katz, 1925, cited in Lederman, 1974; Lederman 1974, 1983), and under other unusual conditions such as when passively scanning the surface with a probe (Yoshioka et al., 2011).

Motion across the skin facilitates perception of spatial features (Gould et al., 1979; Loomis & Collins, 1978; Morley et al., 1983; Weber, 1834/1996; Weinstein, 1968). In order take advantage of this facilitation while maintaining roughness constancy, scanning speed must be coded so that it can be discounted from ambiguous sensory inputs. Yoshioka et al. (2011) showed that when scanning a surface with the finger pads, there are two ways this can be achieved: 1) if proprioceptive information about arm movement is available, and 2) if the skin of the finger pad is directly stimulated with the translating motion. They found that perceived roughness was insensitive to scanning speed when the observers' arm moved, either actively or when moved by the experimenter, and whether surfaces were felt directly with the finger or indirectly via a rigid probe held in the hand so as to prevent translating motion. This demonstrates that proprioception provides adequate discounting of the motion cue to achieve roughness constancy.

When Yoshioka et al. (2011) passively scanned the surface across the finger (providing no proprioceptive information), perceived roughness was still reasonably robust to scanning speed (although roughness estimates did increase slightly with speed). But when a probe held by the fingers was used to passively scan the surface, roughness constancy disappeared and scanning speed was a major contributor to perceived roughness. Even without proprioceptive input, stimulation of the surface area of the finger provides sufficient successive positions cues to motion, allowing accurate computation of scanning speed, which is needed to achieve roughness constancy. When passively scanning with a probe, no spatial information is available to the observer (either via successive positions or stretch cues) who has to rely on the vibrations transmitted by the probe, which increase with speed.

The perceptual primitive

For stimulus features that depend on each other as with speed, TF and SP, the question arises whether percepts of these features also depend on each other or are computed independently. When investigating how any of speed, TF or SP is perceptually coded, there is a tendency, because of their mutually constraining nature, to try to explain the coding of the feature under investigation as being computed from or somehow based on the other two features. This presents a potential pitfall of simply deferring explanation of the sensory coding to a feature not currently under investigation. For example, Dépeault et al. (2008) suggested that speed is computed from TF and SP, but they did not offer an explanation of how TF and SP are themselves coded, nor did they provide any evidence that TF and SP are perceptual primitives and speed a second-order feature. Similarly, Tremblay et al. (1996) investigated SI neurons that coded surface texture independently of scanning speed, and when they also found neurons that coded speed independently of surface texture they argued that these speed sensitive neurons might be used to produce the speed invariance in the texture sensitive neurons, without considering how the speed sensitive neurons achieved their texture invariance.

Darian-Smith and Oke (1980) proposed an explanation of how SP is coded based on speed, but avoided problematic deferral of the explanation by explaining how speed could be the perceptual primitive. They suggested that the speed is computed based on the distance between successively stimulated receptive fields and the temporal delay between their stimulation. If the texture elements of the surface are sufficiently far apart and scanning speed is not too fast, then individual texture elements can be 'tracked' and the distance between them computed. For a periodic surface moving at a constant speed, multiple texture elements can be processed simultaneously providing redundancy in the computation.

1 .6 Adaptation

The experiments described in the following chapters all report on aftereffects of sensory adaptation, which are used to reveal features of speed and direction coding of tactile motion, as well as their interaction. The term 'sensory adaptation' can refer to two different but related phenomena: firstly a change in the perception of a sensory stimulus (the *test stimulus*) following exposure to some stimulus applied in a constant and sustained fashion (the *adapting stimulus*), and secondly a change in neural activity (at the level of single cells or populations), also following sustained exposure to an adapting stimulus. An example of perceptual adaptation is the visual motion aftereffect (here abbreviated 'vMAE'), sometimes referred to as the Waterfall Illusion, which was first described in detail by Purkinje (1820, 1825, cited in Mather, Verstraten, & Anstis, 1998) and Addams (1834). To produce this phenomenon, an observer views an adapting motion stimulus in one direction for a sustained period; the consequence is that subsequently viewed stationary test stimuli or direction-neutral dynamic test stimuli (e.g. flicker) appear to move in the opposite direction. The adaptation occurs during the sustained viewing of the adapting motion, and the effects of the adaptation are revealed in subsequent viewing of other (test) stimuli.

An early example of neural adaptation, related to the perceptual adaptation that produces the vMAE, is the observed reduction in responsiveness of direction selective retinal ganglion cells in the rabbit following exposure to motion in the cell's preferred direction (Barlow & Hill, 1963a, 1963b). These cells have a low resting discharge rate, and when exposed to visual motion in their preferred direction, initially respond with a high level of activity. Activity is sustained with continued exposure to motion (57s), but declines somewhat over time. At motion offset, the response drops to zero, below the resting discharge rate, and then slowly recovers.

Adaptation as a tool for investigating sensory systems

Sensory adaptation is both an interesting phenomenon and a useful tool for characterising the processes that relate sensory stimulation to perceptual phenomena. For example, observation of the vMAE prompted theories of the neural coding of perceived direction. Sutherland (1961) proposed that perceived speed is determined by the relative activity of direction selective neurons that prefer opposite directions. When neurons preferring leftward motion are stimulated, over time the response to leftward motion is attenuated. When a stationary stimulus in then viewed, the ratio of responses in neurons preferring rightward motion to neurons preferring leftward motion is higher than it was pre-adaptation, resulting in illusory motion to the right. This ratio model was later expanded in the distribution shift model (Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; Mather & Moulden, 1980), which states that perceived direction depends on the weighted average of activity in neurons preferring all directions. This development accounted for the observation that adaptation to a field of dots moving in one direction (e.g. 30°, up and to the right) resulted in a bias to perceive the test stimulus (actually moving 0°, directly to the right) as moving at an angle shifted away from the adapting stimulus (-10°, down and to the right).

Adaptation has also been used in the tactile domain to reveal how detection thresholds reflect the sensitivities of the fast adapting mechanoreceptors. Adaptation to vibration on the skin tends to elevate vibration detection thresholds such that higher amplitudes of vibration are required for detection after adaptation. For both mid-range (50-64Hz) and high frequency (125-500Hz) test stimuli, adapting stimuli with frequencies in the same range tend to produce the strongest threshold elevations (Harada & Griffin, 1991; Hollins, Goble, Whitsel, & Tommerdahl, 1990; Maeda & Griffin, 1993; Malchaire, Rodriguez Diaz, Piette, Gonçalves Amaral, & de Schaetzen, 1998; Wedell & Cummings, 1938). These two bands of vibration frequency correspond to the range of frequencies for which the FA1 (up to approx. 60-80Hz) and FA2 (approx. 60Hz and over) receptors are most sensitive (Johansson, Landström, & Lundström, 1982a; Mountcastle, LaMotte, & Carli, 1972). The correspondence between adaptation-induced changes in detection thresholds and peripheral neural responses was confirmed in a study simultaneously recording both perceptual and mechanoreceptor thresholds in humans, (Lundström & Johansson, 1986). Adapting to 20Hz vibration resulted in threshold elevation of FA1 units, but not FA2 units, and elevated perceptual thresholds when tested at 20Hz but not at 200Hz. Adapting to a high vibration frequency (200Hz) resulted in threshold elevation of both FA1 and FA2 units, and also of perceptual thresholds tested at either 20 or 200Hz. These studies demonstrate that adaptation is a powerful tool for characterising the mechanisms involved in sensory systems.

Functional accounts of adaptation

Adaptation is pervasive, occurring in multiple modalities with a wide range of stimuli. In laboratory experiments, it is easy to demonstrate how it can distort perception, causing illusory aftereffects and making judgments inaccurate, which may seem non-adaptive. However, a commonly proposed function for adaptation is that it optimises perceptual systems to detect changes in the environment and de-emphasise constant and pervasive features. Adaptation is thought to function as neural *gain control* to optimise the functional range of neural firing rates to best discriminate different intensities of a stimulus feature prevalent in the environment (Maravall, Petersen, Fairhall, Arabzadeh, & Diamond, 2007; Ohzawa, Sclar, & Freeman, 1982, 1985). Gain is defined as the ratio of the increase in neural activity to the increase in intensity of the eliciting stimulus. Because a neuron has upper and lower limits to its activity level, reducing gain can expand the range of stimulus intensity to which the neuron responds.

In this functional account of sensory adaptation, consistency of perceptual judgments about the absolute value of a physical quantity is compromised for the sake of maximising information transmission, which provides greater discrimination sensitivity (Brenner, Bialek, & de Ruyter van Steveninck, 2000; Wainwright, 1999). For example, adaptation to tactile vibration results in improved frequency and amplitude discrimination (Goble & Hollins, 1993, 1994). This can also result in repulsion effects in which the greater discrimination sensitivity caused by adaptation results in a bias for perceiving compared stimuli as more different than they were previously perceived. For example, adaptation can improve the speed discrimination of visual motion (Clifford & Wenderoth, 1999; Krekelberg, van Wezel, & Albright, 2006), and it also causes stimuli slower than the adapting speed to be perceived even slower, and in some cases, stimuli faster than it are perceived as even faster than before adaptation (Hietanen, Crowder, & Ibbotson, 2008).

However, improvements in discrimination do not always follow adaptation. Barlow, Macleod and van Meeteren (1976) found that following adaptation to visual gratings, there was no improvement in discrimination of spatial frequency, orientation or contrast. In other cases, discrimination declines for the adapting stimulus (De Valois, 1977) or improvements are seen for quite different stimuli (De Valois, 1977; Krekelberg et al., 2006). This prompted Gepshtein, Lesmes and Albright (2013) to propose a *system account* of sensory adaptation, contrasted with a *stimulus account*. They argue that adaptation effects should not be interpreted only with respect to the specific features of the adapting stimulus and the perceptual task, but in the larger context of other tasks that the perceptual system may be required to perform and other stimuli that may be quite different but nevertheless affected by the adaptation. The system responds to adaptation by optimising sensory tuning for a broad range of possible tasks within the new sensory context, rather than just the task demanded by the experimenter. Evidence for this is provided for visual contrast sensitivity, which shifted across a variety of spatial and temporal frequencies of drifting gratings in a way that shifted the whole contrast sensitivity function while preserving its overall shape, rather than just affecting stimuli with values close to the adapting stimuli (Gepshtein et al., 2013).

When little is known about the neural organisation of a sensory system, perceptual adaptation can be used as an exploratory tool. The effects of perceptual adaptation, and their generalisation and specificity, can identify the functional properties of neural subpopulations within the sensory system. For example, adaptation to the amount of arm extension required in an open-loop reaching task generalises from the adapted direction to other reaching directions (Bock, 1992). This suggests the existence of a common functional grouping of neurons representing multiple directions of reach. The fact that adaptation to visual motion results in a vMAE when using a static test stimulus reveals the broad engagement of the visual motion system. Adaptation may be more or less selective in the test stimuli that reveal its effects.

Aftereffects of tactile motion

Adaptation is used to invoke aftereffects in all of the experiments described in this thesis. The intention is to reveal features of the tactile motion system and the representation of both direction and speed of motion across the skin. The first of these aftereffects, used in experiments described in Chapters 2 and 3, is the tactile speed aftereffect (tSAE), in which perceived speed is reduced following sustained exposure to motion across the skin.

The tSAE is a large effect, and is easily induced, making it a valuable tool for studying speed perception. In the first report of the tSAE, Stöber (reported in Rausch, 1960) exposed one hand to four minutes of adaptation to motion of a textured celluloid strip moving at 217mms^{-1}, then had participants adjust the speed of another celluloid strip presented to the unadapted hand to match the perceived speed of the adapting stimulus. Perceived speed of the stimulus dropped 24% below unadapted levels. Stöber also found a tSAE using a second surface moving at the same speed (but with SP and TF varied four-fold), but the strength of the aftereffects were not compared.

The tSAE has received no attention since this first study, and its characteristics are largely unknown. There is a similar aftereffect in vision, in which prolonged viewing of a moving pattern results in apparent slowing of visual motion (Carlson, 1962; Clifford & Langley, 1996; Clifford & Wenderoth, 1999; Clymer, 1973; Goldstein, 1957; Hietanen et al., 2008; Rapoport, 1964; Smith & Edgar, 1994; Smith, 1985; Stocker & Simoncelli, 2009; Thompson, 1981). Some studies reported that this reduction in perceived speed is greater when the adapting and test stimuli move in the same direction compared to when they move in opposite directions (Rapoport, 1964; Smith & Edgar, 1994; Thompson, 1981). At least one study found the speed reduction was similar regardless of direction, and that the aftereffect can also be induced by adaptation to directionless flicker (Clifford

& Wenderoth, 1999). Stocker and Simoncelli (2009) proposed a model for speed adaptation in vision to resolve these apparently conflicting observations. They suggested two separate adaptation mechanisms, producing two 'signature' patterns of results, one directional and one non-directional component. This model not only explained the apparently conflicting psychophysical results, but is also supported by evidence of known neurophysiological processes underlying visual motion processing. Non-directional neural populations in the lateral geniculate nucleus, and direction-selective populations found in V1 or MT provide plausible sites for the two separate mechanisms proposed (Stocker & Simoncelli, 2009).

In the experiments described in Chapter 2, the tSAE was tested for direction sensitivity, i.e. whether the strength of the tSAE (the amount by which perceived speed is reduced following adaptation) is different when the adapting and test stimuli move in the same direction in comparison to when they move in opposite directions. The neural mechanisms encoding tactile motion are not nearly as well understood as those encoding visual motion, and the existing neurophysiological evidence suggests no strong hypotheses about the direction sensitivity of the tSAE.

In Chapter 3, the strength of the tSAE was tested for a range of adapting and test speed combinations. In general for sensory systems, the strength of the aftereffect seems to reflect the degree of adaptation in the relevant neural population (Lundström & Johansson, 1986), and the degree of neural adaptation depends on the amount of excitation evoked in those neurons by the adapting stimulus (Barlow & Hill, 1963a; Bensmaïa, Leung, Hsiao, & Johnson, 2005; Leung, Bensmaïa, Hsiao, & Johnson, 2005; Lundström & Johansson, 1986). By observing the variations in strength of the tSAE, inferences can be made about how speed is coded in the somatosensory system. For example, if the strength of the tSAE increased monotonically with adapting speed, that would indicate an intensive code for speed – with higher speeds represented by greater activity in the neurons that underlie speed perception. Alternatively, if the strongest tSAE were evoked when the adapting and test speeds were similar to each other, then that would indicate speed tuning, with sub-populations of speed sensitive neurons preferring different ranges of speeds.

The second tactile aftereffect investigated in this thesis is the tactile motion aftereffect (tMAE) – the tactile equivalent of the vMAE, in which adapting to motion causes subsequently viewed stationary or flickering stimuli to appear to move in the opposite direction. In early attempts to elicit a tactile motion aftereffect (tMAE), investigators found it difficult. These researchers had expected to find a consistent and robust negative (opposite direction) aftereffect, similar to what is observed with visual motion adaptation, in which the adaptation reveals processes encoding direction of motion. Even when successful, it was reported as often in the same direction as the adapting motion as it was in the opposite (expected) direction (Hazlewood, 1971; Lerner & Craig, 2002; Planetta & Servos, 2008; Thalman, 1922; Wohlgemuth, 1911). The observed unreliable and directionally inconsistent tMAE elicited with stationary test stimuli, which I will refer to as the static tMAE, is difficult to interpret.

The static tactile motion aftereffect

In Wohlgemuth's (1911) famous monograph on the visual motion aftereffect, he reports an attempt to find its tactile equivalent. The experiment is not well described but he stimulated the forearm with a band of knotted silk for 1-3 minutes. The stimulus was either removed from the arm or remained in contact. No aftereffect was observed. Thalman (1922) conducted a much more thorough investigation, conducting ten experiments using different materials to create different patterns of stimulation, and testing different axes of motion relative to the limb. He also tested both the forearm and the calf. He recorded only counts of a *negative* aftereffect, without mention of any motion aftereffects in unexpected directions. However, the manuscript implies other perceptual phenomena occurred apart from the reported negative aftereffect, so we cannot rule out the possibility that non-negative aftereffects occurred in some cases.

Across all experiments, Thalman (1922) recorded 224 instances of a negative tMAE out of a possible 1080 (21%). The tMAE was most reliably obtained under the following conditions: adaptation was applied for 30, 60 or 120s to the shaved underside of the forearm using coarsely corrugated muslin mounted on a continuous track, which moved along the arm from wrist to elbow at a very fast speed of 1090mms^{-1} (good results were also achieved with 390mms^{-1}). After the motion stopped, contact was maintained with the stationary stimulus. Under these circumstances, a negative tMAE was reported on 81% of trials. A major concern with Thalman's (1922) result is that he used only 4 participants, and used the same participants in all ten experiments. Thalman himself was one of the participants, and only two of the others were naïve to the purpose of the study. The instructions did not mention the expected aftereffect, but it is not unlikely that over the course of the extensive study some demand characteristics may have biased even the naïve participants' responses.

Later studies investigating the tMAE using a similar method did not approach Thalman's (1922) 81% rate. For example, Hazlewood (1971) reported only 10 instances of any tMAE out of a possible 100, and 4 of those were in the positive (unexpected) direction. Like Thalman (1922), Hazlewood (1971) conducted a series of experiments. She tested several sites including forearm, fingertips, palm and hand using a corrugated band of matchsticks glued to foam rubber moving at 750mms^{-1} for 120s. In contrast to Thalman (1922), Hazlewood (1971) used different groups of 10-40 of participants for each experiment. Her paradigm was not remarkably different to Thalman's (1922) and she attributes the different results to the small number of participants in the former study and the influence of the expectation of an aftereffect. Hazlewood (1971) concludes: "The tactile motion aftereffect, if it occurs at all, is very slight and requires conditions markedly different from those causing the visual motion aftereffect".

Hollins and Favorov (1994) reported a higher 73% rate of aftereffect incidence in one experiment and 98% in another, but this included both positive and negative aftereffects because they found individual differences in the direction of the aftereffect reported. They used a smooth surface with ridges made of mounting tape affixed at regular intervals to create a square wave pattern, mounted on rotating cylinders that produced surface motion at 280mms^{-1}. In contrast to Thalman's (1922) results, Hollins and Favorov (1994) found that there was no difference between a stationary test stimulus and no test stimulus (the hand in the air), for either the incidence or subjective strength of the aftereffect. This discrepancy might be due to the fact that Hollins and Favorov (1994) had participants actively raise their hands in both conditions (it was returned to the surface for the stationary test condition), whereas Thalman (1922) moved the surface away from the arm. The active motion in Hollins and Favorov's (1994) experiment could have disrupted the tMAE for both test stimulus conditions. As well as recording the incidence rate of the aftereffect, Hollins and Favorov (1994) also tested its duration and subjective vividness, and found that these increased with the duration of adaptation from 30 to 180 seconds.

Lerner and Craig (2002) replicated the conditions of Hollins and Favorov's (1994) experiment, closely matching the apparatus and procedural details, except that they tested many more participants (50 instead of 5). In contrast to Hollins and Favorov (1994), and also Thalman (1922), they found that only 47% of trials resulted in a tMAE in which any motion was felt along the axis of the adapting motion (in either direction or alternating directions). Lerner and Craig (2002) also ran a similar protocol with an Optacon, a tactile array producing apparent motion with vibrating rods. During the test period, participants held their hand in the air. Similar rates of the tMAE were reported with the Optacon and the surface. With both types of stimuli, both positive and negative direction tMAEs were observed, with the surface producing more positive aftereffects than negative. The participants also reported various other types of motion (e.g. orthogonal to the axis of adapting motion) during the test periods. In a second experiment using different hand positions and configurations on the surface, only 38% of trials resulted in either a positive or a negative tMAE.

Planetta and Servos (2008) proposed that the discrepancy in observed rates of the tMAE between Hollins and Favorov's (1994) study and Lerner and Craig's (2002) study might be due to the fact that in the latter study the thumb was adapted in addition to the other fingers. Planetta and Servos (2008) used a moderately large sample of 24 and a similar stimulus to that used by both Hollins and Favorov (1994) and Lerner and Craig (2002), a smooth square wave surface moving at 280mms^{-1}, and a similar procedure in which participants returned their hand to the stationary drum after it stopped. They did not find any evidence that the presence of the thumb or the palm, in addition to the fingers, influenced the rate of report, vividness or duration of the tMAE. A tMAE was reported on 45% of trials with similar numbers in the positive and negative direction. In a second experiment, they varied the speed of the adapting stimulus (from 150 to 350mms^{-1}) and found that frequency, duration and vividness of the tMAE all increased monotonically with increases in speed. For frequency data, they included reports of perceived motion of any nature (positive, negative and “other”) during the test period. For duration and vividness data, they included only trials on which a tMAE (positive or negative) occurred.

The dynamic tactile motion aftereffect

Only recently has an experimental paradigm been identified for eliciting a reliable and robust *negative* tMAE. Watanabe, Hayashi, Kajimoto, Tachi and Nishida (2007) had observers feel the tips of three fixed pins made of piano wire, which were vibrated to stimulate different points on the skin surface. By vibrating successive positions on the skin, Watanabe et al. (2007) created tactile apparent motion. Crucially, their test stimulus, which they used to check for the tMAE following adaptation to apparent motion, was *dynamic* – the piano wires were vibrated at different temporal offsets and they found a bias to perceive motion in the direction opposite to the adapting stimulus.

Using a dynamic test stimulus may have allowed Watanabe et al (2007) to activate some of the same neural populations that were affected by adaptation. A model similar to the distribution shift model, used to explain the vMAE, may explain the dynamic tMAE: the direction selective neurons each 'vote' for their preferred direction, and the weight of the neural response over the population gives the perceived direction. In order for a negative aftereffect to be revealed, the test stimulus must engage the adapted direction selective neural population. This means that for a static test stimulus to produce a reliable negative aftereffect, the direction selective neurons must have a resting discharge response greater than zero so that the adaptation can suppress the resting rate below its normal level – a static test stimulus would not excite motion sensitive cells very well, and thus would not reveal a change in the weighted population coding of direction.

In SI, very few (7% according to one study, Costanzo & Gardner, 1980) of direction selective cells are the required sort of cells (sometimes referred to as 'opponent'), with a high resting discharge rate inhibited by motion in the anti-preferred direction (Costanzo & Gardner, 1980; Hyvärinen & Poranen, 1978). This might explain why no reliable negative tMAE is observed with a static test stimulus. Alternatively, it is possible that a negative tMAE is not observed with a static test stimulus because of a neural gating mechanism that filters out input from direction-selective neurons in the absence of other evidence that the stimulus is dynamic. Either way, a dynamic test stimulus would be able to excite the mostly non-opponent direction selective neurons in SI, revealing a population change in direction coding, resulting in a negative aftereffect.

It is challenging to interpret the mixed results of studies on the static tMAE because it does not easily fit into the neural framework described above. While the same neural pathways are affected as in the dynamic tMAE because the adapting stimulus is the same, it is unclear why a stationary test stimulus elicits heterogeneous illusory motion sensations. One possibility is that the stationary stimulus provides weak and inconsistent stimulation of the adapted sensory processes, producing variable and weak sensory percepts that are sensitive to the interpretations of the observer. This is supported by the evidence that in some studies the static tMAE was more consistently reported when the skin was in contact with the surface for the test period than when contact was broken (Hollins & Favorov, 1994; Thalman, 1922), suggesting that the impoverished stimulation of a stationary surface is more likely to result in illusory sensations than no stimulation at all. In addition, the studies that found the highest rates of the static tMAE (Hollins & Favorov, 1994; Thalman, 1922) used a small number of observers (4 - 5) participating in a large number of trials, whereas the studies that found lower incidence of the tMAE (Hazlewood, 1971; Lerner & Craig, 2002; Planetta & Servos, 2008, 2010), used a larger number of participants (17 – 100) who participated in relatively few trials. This suggests that knowledge and experience of the paradigm may develop more focused attention to minor sensations in the observer, resulting in an increased likelihood of noticing and reporting motion aftereffects.

In Chapter 4, the strength of the dynamic tMAE is tested for its sensitivity to adapting speed, similar to the test in Chapter 3 of the tSAE's sensitivity to adapting speed. In this case, observing differences in the strength of the tMAE due to adapting speed provides information about how speed is coded in the population of direction selective neurons that underlie perceived direction of tactile motion. A monotonic increase in the strength of the tMAE with increasing adapting speed would indicate an intensive coding of speed in the direction selective neurons, whereas if the strongest tMAE were produced with adapting speeds similar to the speed of the test stimulus, this would indicate speed tuning of direction selective neurons, with different preferred speeds similar to the preferred directions.

1 .7 Aims

The aim of this thesis is to conduct research that leads to a better understanding of how tactile speed and direction of motion are coded. The experimental approach is to use behavioural adaptation, and thus the immediate conclusions relate to features of adaptation processes of the tactile motion system. Specifically, the experiments use two tactile motion aftereffects, the tSAE and the tMAE, in which adaptation induced within the tactile motion system alters perception of motion. The four points below specify how adaptation was used to achieve four research aims.

1) The effect of adapting direction relative to test direction on the strength of the tSAE was tested. The aim was to determine whether the amount of speed reduction caused by the adaptation was direction selective, a property that, if present, would indicate velocity (speed and direction) coding at the neural site of adaptation.

2) The effect of adapting speed, and its relationship to test speed, on the strength of the tSAE was tested. The aim was to determine how speed is coded in the neural site of

the adaptation that influences perceived speed, and to distinguish between (a) *speed tuning* of the tSAE, in which a match between the adapting and test speeds produces the strongest aftereffect, and (b) an *intensive speed code* for the tSAE, in which the strength of the aftereffect increases monotonically with the adapting speed.

3) The speed of the adapting stimulus was disambiguated from other features of the motion stimulation, the temporal frequency and spatial period. The aim was to determine which of these motion features influenced the strength of the tSAE, which would reveal the properties of the underlying neural channels.

4) The effect of adapting speed, and its relationship to test speed, on the strength of the tMAE was tested. The aim was to determine how speed is coded in the neural site of the adaptation that influences perceived direction, and to distinguish between (a) speed tuning of the tMAE and (b) an intensive speed code for the tMAE.

Chapter 2: Direction sensitivity of the tactile speed aftereffect

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2 .1 Introduction

Exploratory movement of the fingers across a surface is crucial for determining the physical properties of that surface and when humans discriminate different surfaces based on their roughness, performance is better when there is relative motion between the skin and the surface (Gibson, 1962; Morley et al., 1983). Furthermore, the speed of such motion can vary without affecting performance (Meftah et al., 2000). One explanation for this is that the speed is accounted for in the neural computation of surface features (Chapman, 1994; DiCarlo & Johnson, 1999; Lederman, 1983). Little is known about how the speed of a moving surface is perceived, and this is crucial for understanding functional mechanisms of tactile perception.

We use an adaptation paradigm to study perceived speed of a moving surface, and its relationship with direction of motion. Adaptation can serve as a powerful tool to investigate the mechanisms of sensory coding of a feature of interest (see, e.g., Blakemore & Sutton, 1969; Clifford & Rhodes, 2005; Webster, 2011). For a long time, researchers used a simple psychophysical paradigm involving exposure to a moving surface (adaptation) followed by exposure to a stationary surface to test for an illusory motion aftereffect. They expected to find a tactile equivalent of the visual motion aftereffect (MAE; see Wohlgemuth, 1911) in which the stationary test stimulus appears to move in the opposite direction to the previously adapting motion. While motion aftereffects were found, they were often inconsistent in their perceived direction, i.e., there was no reproducible *negative* (opposite direction) motion aftereffect when using the above, stationary-test paradigm (Hazlewood, 1971; Hollins & Favorov, 1994; Lerner & Craig, 2002; Planetta & Servos, 2008, 2010; Thalman, 1922; Wohlgemuth, 1911).

More recently, studies using dynamic test stimuli (achieved with vibrating pin arrays) rather than stationary surfaces at test have found a reliable negative tactile motion aftereffect or "tMAE" (Konkle, Wang, Hayward, & Moore, 2009; Kuroki, Watanabe, Mabuchi, Tachi, & Nishida, 2011; Watanabe et al., 2007). This result shows that tactile motion mechanisms adapt, and is consistent with theories of motion coding, originally proposed in vision, in which the percept is determined by the difference between the activity in neurons that code opposite directions of motion. When one group of cells adapt, the ratio shifts in favour of the non-adapted cells, influencing subsequent perception of a neutral stimulus (e.g., Barlow & Hill, 1963; Sutherland, 1961). In contrast to vision, a study of direction-sensitive cells in the primary somatosensory cortex (SI) Costanzo and Gardner (1980) found 93% were non-opponent. Opponent cells have a high resting discharge rate and get excited by one (broad) direction of motion and inhibited by another - properties that could, in principle, create tMAE in a *static* test stimulus. Non-opponent neurons that comprise a majority in SI would not respond as well to a static stimulus, but any dynamic test stimulus (a test stimulus involving changing stimulation of the skin over time including motion or vibration) able to excite them should reveal a population change in direction coding due to adaptation.

Speed, which is a feature of surface motion to which humans are perceptually sensitive (Dépeault et al., 2008), could in principle be coded in the same neural channels that code direction. If so, then adaptation to motion in one direction should affect perceived speed for that direction but not necessarily for the opposite. Stöber (reported in Rausch, 1960) found a 24% drop in perceived speed following 4 minutes of adaptation to motion of a textured celluloid strip. We label this effect the "tactile speed aftereffect" (tSAE; our preliminary findings were reported in a conference presentation, McIntyre, Seizova-Cajic, Holcombe, & Birznieks, 2010). Another recent conference poster (Tomassini, Gori, Burr, Sandini, & Morrone, 2010) also reported the tSAE. However, whether tactile speed adaptation is direction-specific has not been tested. This is the question we address.

In the standard adaptation paradigm we use, prolonged exposure to the adapting stimulus is followed by a test stimulus. Perception of the test stimulus after this adaptation is compared to the perception of it without prior adaptation. It is assumed that a) in the course of adaptation, some neurons in the sensory system respond; and b) the greater their response, the greater the adaptation in those neurons. Thus the largest aftereffects should occur if perception of the test stimulus relies on the *same mechanisms* as those adapted, habituated or fatigued during adaptation (Thompson, 1998). Because we are testing for a *speed* aftereffect, our test stimulus is necessarily dynamic (in this case a moving surface) and should excite direction-sensitive cortical neurons, similar to previous studies that successfully reported a consistent *direction* aftereffect (Konkle et al., 2009; Watanabe et al., 2007). This is an optimal stimulus for detecting any influence of direction on the tSAE.

We use a psychophysical method of constant stimuli to test whether the tSAE is direction sensitive. Rotating drums with textured surfaces created the motion our participants felt with their fingers. The use of a natural surface that stretches the skin distinguishes our study from many others (Bice, 1969; Burtt, 1917; Harrar, Winter, & Harris, 2008; Kirman, 1974; Konkle et al., 2009; Pei et al., 2008; Rinker & Craig, 1994; Sherrick & Rogers, 1966; Watanabe et al., 2007). A natural surface provides two cues to motion direction. The first is present in most studies and involves displacement across the skin, which stimulates the skin at successive locations. In the second cue, present in our study, friction also pulls the skin in the direction of motion, causing lateral skin stretch.

We found a substantial reduction in perceived speed following adaptation, but no evidence of direction sensitivity, with similar levels of adaptation regardless of the direction of the adapting motion. This result was strengthened by the results of a second experiment in which we used bilateral adaptation to isolate adapting motion direction as the only feature that differed between conditions. Here also, no effect of direction was found. To confirm that the adapting stimuli used in our psychophysical paradigm resulted in adaptation in sensory afferents, we measured activity in the primary afferents in two of our subjects, using microneurography, during exposure to the rotating drum. It is known that vibrotactile adaptation reduces the response of tactile afferents (Bensmaïa et al., 2005; Lundström & Johansson, 1986), and although prolonged motion is likely to have a similar effect, this has not been established.

2 .2 Materials and Methods

Participants

Nine participants volunteered, six naïve observers and three authors (2 left-handed). Written informed consent was obtained and the Human Research Ethics Committee of the University of Sydney approved the study, which was conducted according to the principles expressed in the Declaration of Helsinki.

Apparatus

A hard rubber surface was attached to two cylindrical drums. The surface was textured with ridges 1mm high and 10mm wide, and troughs 12mm wide. The ridges were spaced at regular intervals with a centre-to-centre distance (spatial period) of 22mm. The surface had clearly separated ridges that provided rich cues to movement as they successive stimulated the skin. The surface was covered (Figure 2.1B) with ladies' stocking fabric (98% nylon, 2% elastine) to reduce friction with the fingers while the drums were in motion (without the covering, prolonged exposure to the moving drum was uncomfortable). The circumference of the drums was 338mm, and they were rotated by a stepper motor (Lineartec MOT-122 High Torque Hybrid Stepping Motor) with a step size of 1.8 degrees controlled by LabView software (National Instruments, USA). At all speeds used (see Procedure section, below), motion felt smooth and no vibration was detected from the stepper motor. Depending on the speed, there were between 8 and 72 steps of the motor per second.

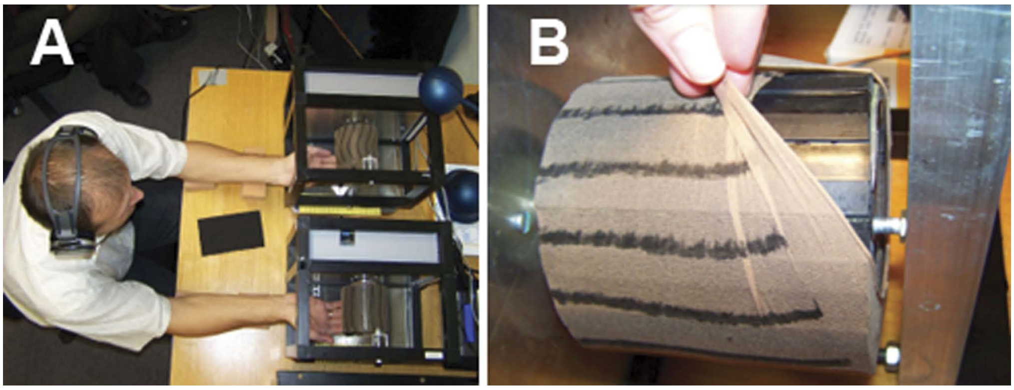

Figure 2.1. The apparatus. A: Observers judged the relative speed of two different moving drums. (The subject of the photograph has given written informed consent to publication of their photograph.) B: One of the drums used to create tactile motion. Here, the stocking is pulled back to reveal the ridged rubber surface underneath.

Procedure

Perceived surface speed was measured with a two-alternative forced-choice procedure involving two rotating drums. Participants rested their arms on foam cushions and gently touched the two drums (one with each hand) from underneath (Figure 2.1A). They were instructed to touch the drum with only the distal segments of their index, middle and ring fingers. Pigment powder on the drums resulted in marking of the areas of skin the drum contacted, and inspection of the fingers after the experiment allowed the experimenter to check that participants followed the instructions regarding finger contact area with the drums. Participants placed their fingers on the surface at the start of each run while the drums were stationary and stayed in this position for the duration of the run. Participants were instructed to close their eyes to avoid visual cues to the motion of the drums. White noise delivered through headphones masked any auditory cues.

In the test phase (preceded by an adaptation phase in some experimental conditions), both drums moved simultaneously and in the same direction for one second. Participants were asked to compare the speeds of the two drums, saying, “left” or “right” to indicate which one moved faster, and the experimenter recorded each response using a button box. The two stimuli to be compared were presented simultaneously with synchronous onset and offset. No participant ever reported that one stimulus was felt to last longer than another, and this perceived simultaneity suggests that relative duration was not used to make the judgment. One hand, the reference hand, was presented with the standard stimulus, which was the same speed on every trial. This is also the hand that was adapted in the adaptation conditions. The other hand, the comparison hand, was presented with comparison stimuli of a variety of speeds (14 – 122mms^{-1}). For three of the participants the right hand was the reference hand and the left was the comparison hand; for the remaining participants the reverse was true. Using the method of constant stimuli, we estimated the point of subjective equality (PSE) between the speed felt on the reference (adapted) hand and the comparison hand. The PSE indicates the perceived speed of the standard stimulus. The speed of the standard and adapting stimuli was 81mms^{-1}, a speed well within the functional range used in active surface exploration (Smith et al., 2002).

The metal frame of the drums rested on electronic scales, which measured normal (upward) contact force that participants applied to the drums with their fingers. Participants made no contact with any other part of the apparatus or the scales. Auditory tones delivered through headphones indicated to participants when they pressed too hard (with a force greater than 100gm-wgt) or too softly (less than 10gm-wgt) and they were asked to keep within this range throughout the experiment.

2 .3 Experiment 1

The goal of Experiment 1 was to determine whether the tSAE is direction sensitive – whether the relative direction of the adapting motion has an effect on the perceived speed of the test stimulus. Participants adapted to sustained tactile motion in different directions, then judged the speed of a subsequent tactile motion stimulus that was either the same or the opposite direction as the previously exposed adapting stimulus.

Design and Procedure

Experiment 1 comprised three conditions: two adaptation conditions and a baseline condition (Figure 2.2A). The adaptation conditions differed in the relative direction of the adapting stimulus motion. In the Same Direction condition, the adapting stimulus moved in the same direction as the standard and comparison stimuli (distal to proximal for three of the participants and vice versa for the remaining six). In the Opposite Direction condition, it moved in the opposite direction. During the adaptation phase, the reference hand was exposed to 30 seconds of motion (the adapting stimulus) immediately before the speed judgments began, a duration which is similar to that used in previous adaptation experiments (Hollins & Favorov, 1994; Thalman, 1922), and which piloting found to produce an aftereffect. During the test phase, the adaptation conditions also included 5 seconds of "top-up" adaptation following each left/right judgment. This stimulus sequence is illustrated in Figure 2.2B. In the Baseline condition, no adaptation preceded the speed judgments, and there was no top-up period during the test phase.

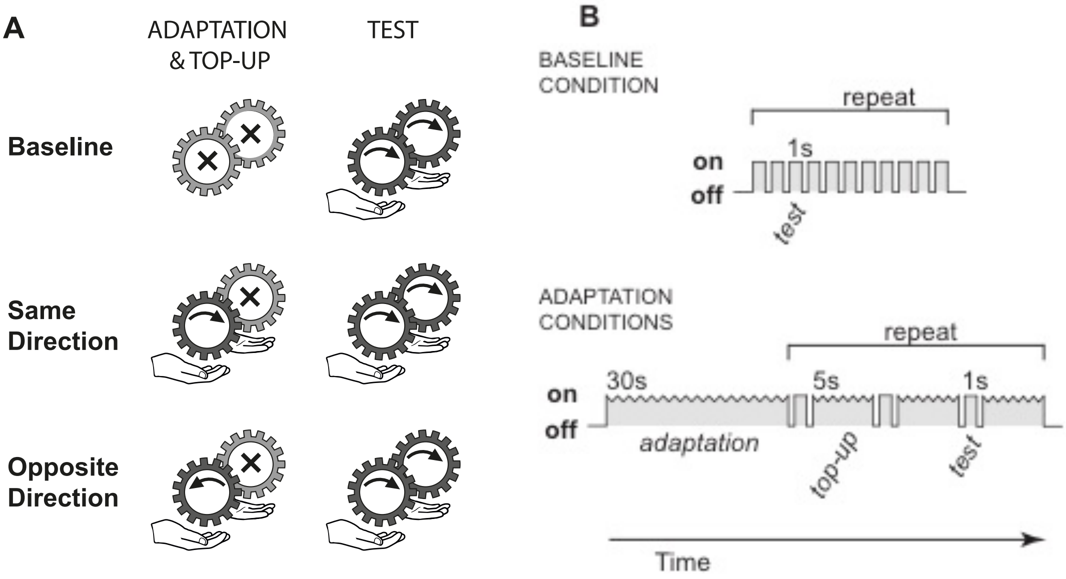

Figure 2.2. Design of Experiment 1. A: The three experimental conditions in Experiment 1. B: The stimulus sequence in the two adaptation conditions of Experiment 1.

All participants completed the three experimental sessions (one for each condition), with the first session preceded by a short practice to familiarise participants with the task. Each session consisted of three runs, separated by two-minute rest breaks. Each session comprised 162 judgements of 9 comparison speeds (18 judgements per comparison speed). To minimise lingering adaptation effects, all sessions were preceded by a break of at least one hour following any adaptation session conducted earlier that day.

The following factors varied across participants: (1) which hand was presented with the test stimulus (left vs. right), (2) the direction of the test and comparison stimuli (proximal vs. distal), (3) the order of the two adaptation conditions (same direction first vs. opposite direction first). The nine participants were assigned values of these three factors in a pseudo-random fashion.

Neurophysiology

To confirm that there was adaptation at the periphery, we include microneurographic recordings obtained in two participants (SM and TSC). We recorded from primary afferents during tactile motion to document the adaptation. We obtained one single-unit recording of a type 1 fast adapting unit (FA1) and one multi-unit recording. The multi-unit recording was made while one hand was stimulated in a fashion similar to the reference (adapted) hand in the Same Direction condition of the psychophysics protocol described above. The comparison hand was not stimulated, and the participant made no responses. The single-unit recording was made from the adapted hand during an altered version of the psychophysics protocol for the Opposite Direction condition in which there were 12 presentations (instead of 18) for each comparison speed. For both the multi-unit and single-unit recordings, the fingers did not touch the stimulus until immediately prior to the start of adaptation.

The median nerve was located at the wrist by palpation and electrical stimulation via a surface probe. A tungsten microelectrode (Frederick Haer & Co. Inc., Brunswick, ME, USA) was then inserted percutaneously and guided towards the median nerve by weak electrical stimulation through the electrode tip. Once in the nerve, multiunit recordings were obtained by positioning the electrode within the fascicle innervating mechanoreceptors in the fingertip skin. Fine adjustments of electrode position were guided by auditory feedback of the neural activity associated with mechanical stimulation to the fingertip skin applied by the electrophysiologist (author IB).

Neural activity was amplified (gain 1 x10^4) and band-pass filtered at 0.3–2.0 kHz, 50Hz notch (Neuro Amp EX, ADInstruments, Bella Vista, Australia). All electrophysiological data were recorded and analysed on a computer-based data acquisition system LabChart 7/PowerLab (ADInstruments). Single nerve impulses (spikes) were identified by template matching and counted using the Spike Histogram module. For the multi-unit recording, no attempt was made to separate or identify individual afferents.

The participants provided informed written consent to the procedure, which was approved by the human ethics committee of the University of New South Wales and conformed to the Declaration of Helsinki.

2 .4 Experiment 2

In Experiment 1 the receptors of the adapted hand were stimulated to a greater extent overall than the non-adapted hand, and participants occasionally commented that the moving stimuli evoked different sensations in the two hands. Conceivably, this difference may have impaired comparison of the speeds felt by the two hands, obscuring any effect of direction. In Experiment 2, we eliminated all differences in stimulation between the hands except for the direction of the adapting motion. We adapted both hands, one in each direction, and measured the resulting speed adaptation using one hand as the reference and the other as comparison.

The methods were the same as for Experiment 1, except as noted below. In all three conditions illustrated in Figure 2.3, both the reference and the standard hand were adapted with 30 seconds of continuous motion in the adaptation phase, plus the 5 seconds "top-up" adaptation following each left/right judgment during the test phase. As in Experiment 1, the test phase immediately followed the adaptation phase. The conditions of Experiment 2 differed in the direction of adaptation that was applied to the two hands. In two conditions, the adapting stimulus applied to one hand was in the opposite direction to the adapting stimulus applied to the other hand. In one of these, called the Same Direction condition, the adaptation applied to the reference hand was the same direction as that of the stimuli presented during the test phase (to both hands). In the other, Opposite Direction condition, the adaptation applied to the reference hand was in the opposite direction to the stimuli presented during the test phase. In a third condition, Baseline, the two adapting stimuli applied to the two hands were both in the same direction.

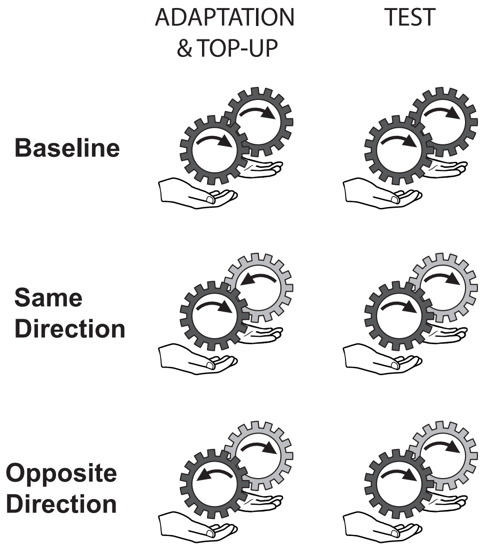

Figure 2.3. Design of Experiment 2. The three experimental conditions of Experiment 2.

All participants completed three experimental sessions (one for each condition). The second and third sessions followed a break of at least one hour to minimise carry-over of adaptation from the previous session. The order of the conditions was randomly determined.

Unlike in Experiment 1, the PSE in Experiment 2 is not necessarily expected to be different in Baseline compared to the other two conditions because both hands were adapted. Differences should only appear if direction influenced speed adaptation.

Table 2.1 gives the predicted outcomes of Experiment 2 given the various possible effects of direction of adaptation on perceived speed.

Table 2.1. Possible outcomes of Experiment 2. The first possibility is that matching the direction of the adapting and test stimuli leads to greater adaptation of perceived speed (first row). If this is the case, then the Opposite Direction condition should produce the highest PSE (smallest tSAE) and the Same Direction condition should produce the lowest PSE (greatest tSAE). This is because in the Same Direction condition, the direction of motion for the reference hand is matched at adaptation and test, whereas in the Opposite Direction condition, the motion for the reference hand at adaptation and test are in opposite directions. The second possibility is that the greatest adaptation occurs with an adapting stimulus moving in the opposite direction to the test (second row). In this case the Same Direction condition should produce the highest PSE (smallest tSAE) and the Opposite Direction condition should produce the lowest PSE (greatest tSAE). The third possibility is that the tSAE is insensitive to direction, with the adapting stimulus creating similar levels of adaptation regardless of its direction relative to test (third row). In this case, we would not expect to see any consistent differences across conditions.

Effect of Adaptation	PSE by Condition
Matched Direction > Opposite Direction	Opposite Direction > Baseline > Same Direction
Opposite Direction > Matched Direction	Same Direction > Baseline > Opposite Direction
Matched Direction = Opposite Direction	no differences across conditions

2 .5 Experiment 3

Because of previously reported difficulties eliciting a negative tMAE with moving surfaces like ours (Hazlewood, 1971; Hollins & Favorov, 1994; Lerner & Craig, 2002; Planetta & Servos, 2008, 2010; Thalman, 1922; Wohlgemuth, 1911), a reviewer questioned the capacity of these surfaces to evoke a clear enough perception of direction to ensure it provides a good test for the presence of a direction-sensitive tSAE. Experiment 3 shows that the moving surfaces we used produce a clear direction percept.

Participants

Six participants volunteered, three naïve observers and three authors (2 left-handed). Written informed consent was obtained and the Human Research Ethics Committee of the University of Sydney approved the study, which was conducted according to the principles expressed in the Declaration of Helsinki.

Procedure

Using the same apparatus as in Experiments 1 and 2, participants felt the moving surface for four minutes with the index and middle fingers of their right hand. Direction of motion was distal. Participants responded to the stimulus by continuously reporting the perceived direction of motion by pressing one of three buttons: 1) distal, if the stimulus appeared to move away from their body, 2) proximal if it appeared to move towards their body, or 3) unclear, if they could not judge the direction of motion. Participants were instructed to continuously monitor their perception and press the appropriate button as soon as the direction of motion appeared to change. They were instructed to respond every few seconds even if perceived direction did not change. Participants were told that sometimes people experience illusory perceptions of motion and that they should report what they felt, rather than what they thought the stimulus was actually like. Participants were also warned that their perception might change so rapidly that their button presses could not keep up. If they experienced this, they were to report all perceived directions even if their responses lagged behind. To test for the presence of a tMAE, participants also continued reporting the perceived direction for three seconds after the drum stopped moving. Three speeds were tested, 27, 54 and 108mms^{-1}, in sessions separated by breaks of at least 2 minutes.

Data Analysis

For the psychophysical data in Experiments 1 and 2, the proportion of responses for which the comparison stimulus was judged faster was calculated for each comparison speed. Using the statistical software R (R Development Core Team, 2010) with the 'modelfree' package (Marin-Franch, Zychaluk, & Foster, 2010), the data for each participant for each condition were fitted by logistic regression function. The resulting psychometric function provided the point of subjective equality (PSE), the speed for which participants were equally likely to say that the comparison was faster or slower than the standard. The PSE indicates the perceived speed of the standard stimulus. The slope of the function provides a measure of discrimination sensitivity.

For the microneurography data, the stimulus event time – that is, the timing of spikes relative to the temporal period of the ridges – was estimated via ad-hoc observation of the spike data. For each period of motion - 30s adaptation, 1s test, 5s top-up - the stimulus was manually re-aligned with the spike train to account for slight variations in acceleration and deceleration time at the onset and offset of drum motion.

For the direction judgement data collected in Experiment 3, perceptual state was interpolated at 1s intervals from button presses, then the proportion of each perceptual state (veridical direction, opposite direction, unclear) was calculated for 10s bins.

Figures 2.4 – 2.6 and 2.8 – 2.11 were generated using the R package "ggplot2" (Wickham, 2009). Data and statistical scripts are available at The Sydney eScholarship Repository (http://ses.library.usyd.edu.au/handle/2123/8648).

2 .6 Results

Experiment 1

Perceived Speed

The results of Experiment 1 revealed a substantial tSAE in all participants – adaptation reduced perceived speed. Compared to Baseline, adapting the hand decreased perceived speed by an average of 30%. Psychometric functions are shown in Figure 2.4. The direction of the effect is the same for all nine participants: the curves for the Same Direction and Opposite Direction adaptation conditions are shifted to the left of the curve for the Baseline condition, indicating that perceived speed in the adaptation conditions was lower.

The mean PSE across participants is shown in Figure 2.5. When adapted in the same direction as the test, the mean PSE was reduced 23mms^{-1} (SD = 11) from Baseline; following adaptation in the opposite direction, the mean reduction in PSE was 26mms^{-1} (SD = 9). A repeated measures ANOVA shows a significant effect of condition ($F_{2,16}$ = 49.20, p < .001). Post-hoc contrasts revealed a significant difference between mean Baseline PSE and those in the two adaptation conditions (p < .001). The direction of the adapting stimulus relative to the test stimulus did not matter; the PSEs of the two adaptation conditions did not significantly differ (mean difference = 3mm/s, p = .09).

The slope of the psychometric function is a measure of discrimination sensitivity. There were no significant differences in slope between the conditions, (Baseline mean slope = 0.021, SD = 0.007; Same Direction mean slope = 0.023, SD = 0.006; Opposite Direction mean slope = 0.027, SD = 0.006), the difference was not significant ($F_{2,16}$ = 2.91, p = .08). This stands in contrast to the subjective experience of participants, several of whom spontaneously reported that the ridges of the moving drum felt less clear after prolonged exposure. Following adaptation runs, they reported some "numbness" when touching surfaces and objects, which faded over time. However, this subjective numbness did not influence speed discrimination performance.

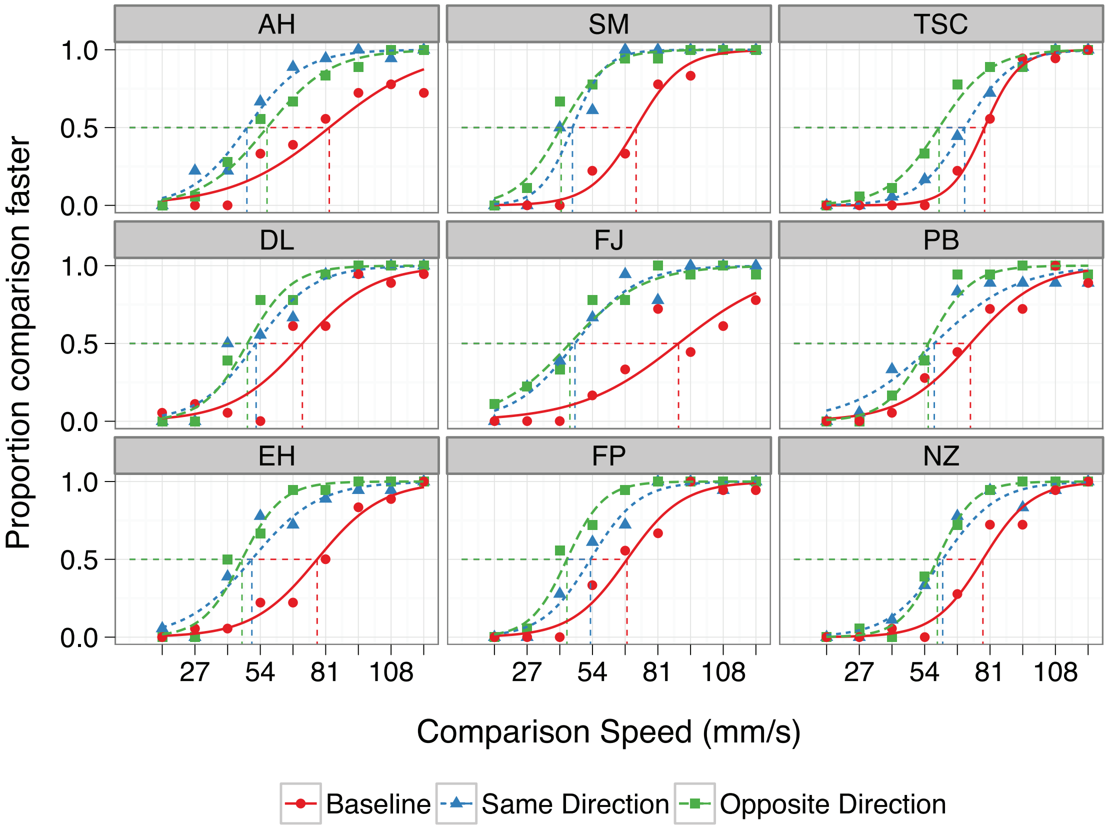

Figure 2.4. Individual psychometric functions for three experimental conditions, Experiment 1. The actual speed of the standard stimulus was always 81mms^{-1}. Comparison speed is on the abscissa. The ordinate gives the proportion of responses in which the comparison stimulus was judged faster than the test stimulus. The three experimental conditions are: no adaptation (circles), adaptation in the same direction as the test speed (triangles), and adaptation in the opposite direction to the test speed (squares). The lines are the fitted logistic regression curves. Also shown are the PSEs given by the mean of the fitted logistic function. PSEs in the baseline condition were higher in all participants (perceived speed faster) than PSEs in the adaptation conditions.

Contact Force

The contact force data show that the participants successfully exerted similar contact force on both drums across all conditions, and indicate that changes in contact force over the course of the experiment cannot account for any adaptation effects. Figure 2.6A shows the normal (upward) contact force that was applied by one representative participant (DL) during the Same Direction adaptation session. The session comprises three runs (depicted in three panels), each starting with 30s adaptation, followed by fifty-four 1s comparisons and fifty-four 5s top-ups. Figure 2.6B gives the mean normal contact force across all subjects and conditions.

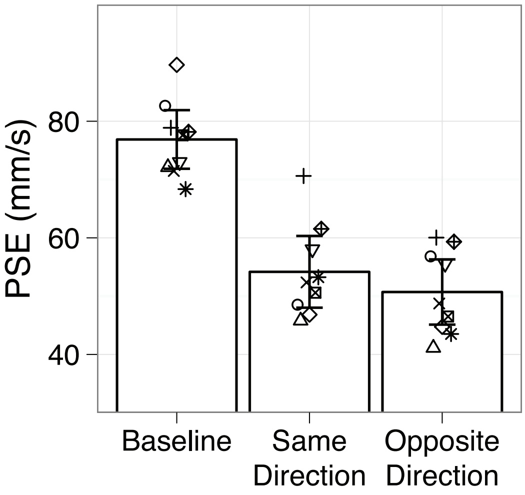

Figure 2.5. Mean PSE (bars) across participants as a function of experimental condition, Experiment 1. Error bars represent 95% confidence intervals of the mean PSE. The symbols indicate the PSE for each participant.

The overall mean contact force was 52gm-wgt (SD = 13) applied by the reference hand, and 56gm-wgt (SD = 13) applied by the comparison hand. The mean contact force applied by the two hands for the Baseline, Same Direction and Opposite Direction conditions was 54 (13), 54 (14) and 54gm-wgt (14) respectively. A repeated measures ANOVA revealed no significant main effect of hand ($F_{1,8} = 3.36$, p = .10) nor condition

($F_{2,16} = 0.01$, $p = .99$), nor was there a significant interaction effect between hand and condition ($F_{2,16} = 1.03$ $p = .38$).

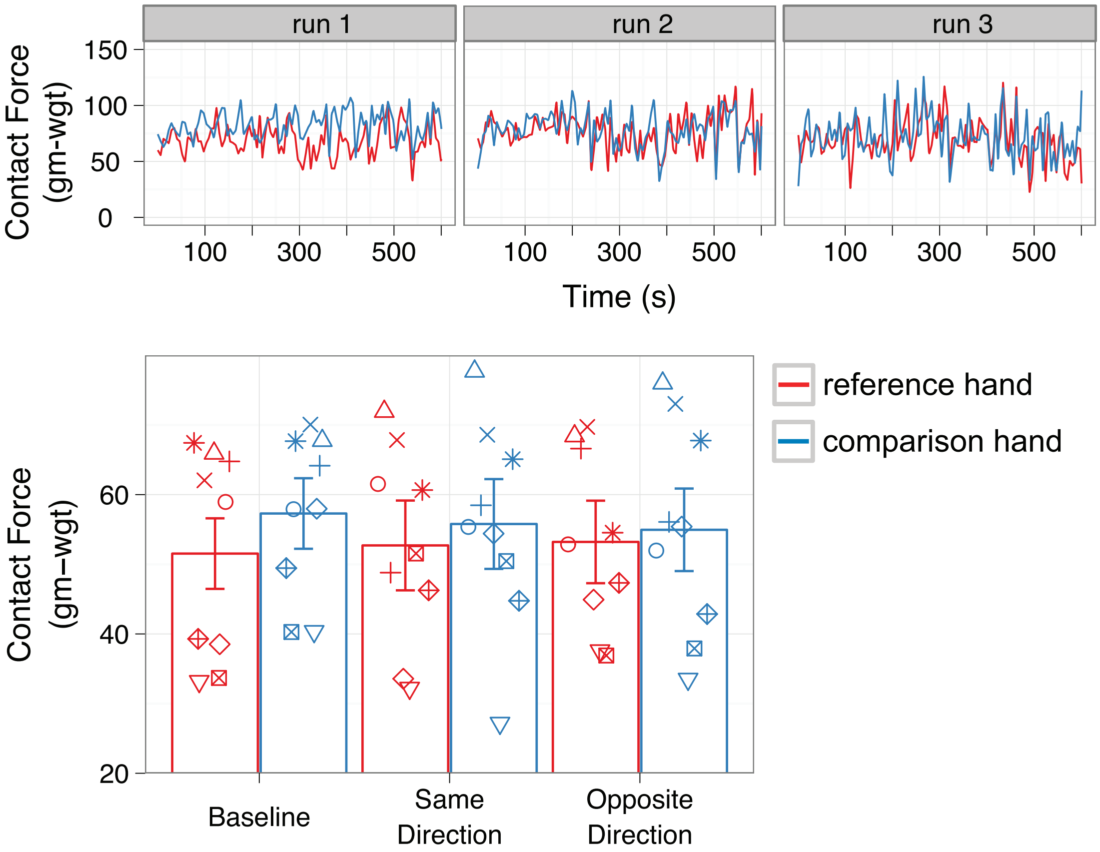

Figure 2.6. Contact Force data. A: Contact force over time for the reference (black) and comparison (white) hands for one representative participant (DL) in the Same Direction condition. The session consisted of three successive runs, represented by one panel each. B: Mean contact force for the reference and comparison hands for each condition. Error bars on each pair of bars within the same condition are identical and represent 95% CI of their difference scores (comparison – reference).

Neurophysiological data

It was expected that peripheral afferents would show reduced activity following exposure to sustained motion stimulation. Our microneurographic recordings illustrate this adaptation. Both the multiunit recording and the single FA1 recording showed a decrease in unit activity over time in response to prolonged stimulation, indicating that significant primary afferent adaptation took place. After 30s adaptation to the 81mms^{-1} adapting motion, the multi-unit recording had decreased to 57% of its initial level of 33.4 impulses per second (ips; see Figure 2.7). For the single-unit (FA1) recordings, activity was recorded during two runs of the stimulus protocol used in the Opposite Direction condition (see Materials and Methods section for details), and the recording was successful for run 2 only (there was a two-minute rest between the runs). During run 2, the firing rate of the FA1 was initially 6.8ips during the adaptation phase and continued at 8.3ips for the next 30s of top-up adaptation. In the last 30s of top-ups, after approximately 4 minutes of adapting motion, the firing rate had reduced to 3.4ips, 50% of its initial level.

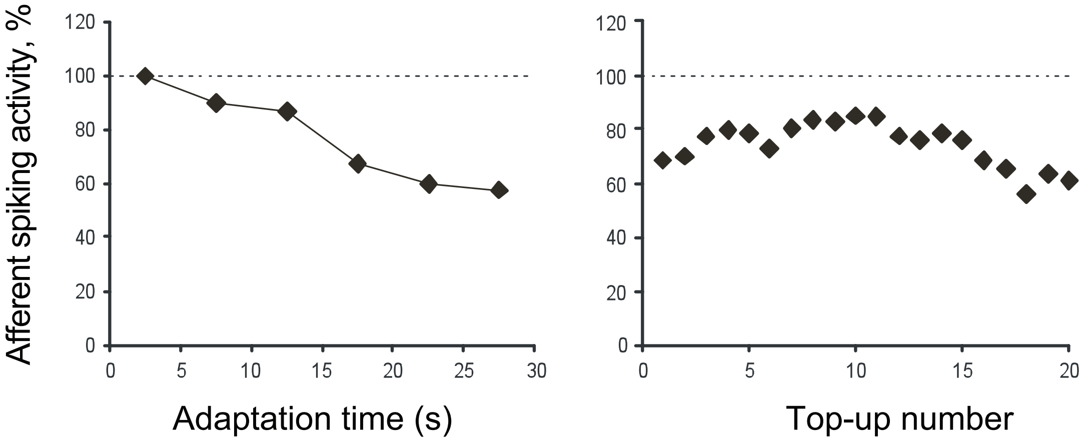

Figure 2.7. Multiunit recording of neural activity in primary afferents exposed to prolonged tactile motion. A. Relative changes in the spiking activity during 30s long adaptation phase. Data averaged over 5s time bins. B. Level of spiking activity during twenty 5s long top-up periods in the test phase, relative to the same baseline as in A.

For a more detailed picture of how adaptation affected the response of the FA1 unit, we examined the temporal profile of its response at key stages of run 2. Figure 2.8 is a post stimulus spike histogram, showing the timing of the spikes within a temporal window equal to the period of the surface profile (278ms). The three key stages of run 2 shown are 1) the 30s adaptation period (continuous proximal motion) at the start of the run; 2) the first six top-ups (30s proximal motion stimulation time) immediately following adaptation; and 3) the last six top-ups (30s proximal motion stimulation time) at the end of the run. Over 4 minutes of motion stimulation occurred between the first six and the last six top-up periods.

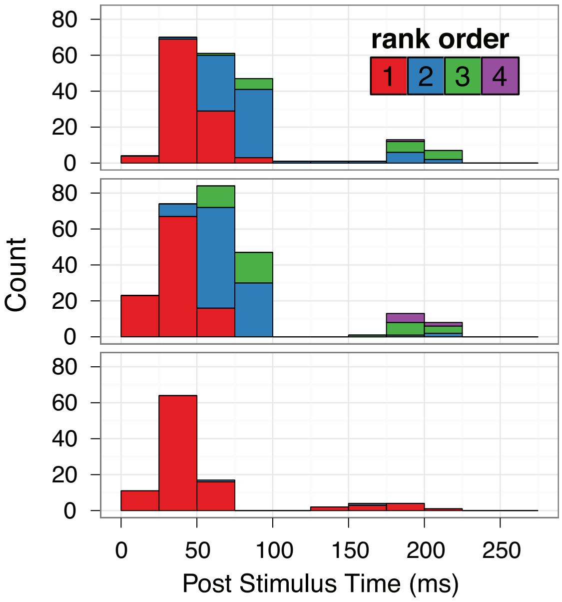

Figure 2.8. Frequency histograms showing the timing of spikes relative to surface ridges (278ms temporal period). The stimulus event time was recovered via ad-hoc observation of the spike data. Three key stages of run 2 are shown: 1) Top panel: the 30s adaptation period; 2) middle panel: the first five top-ups; and 3) bottom panel: the last five top-ups. Shades give the rank order of the spikes after the onset of a given ridge.

The top panel of Figure 2.8 shows the adaptation period of run 2. Nearly every time (98%) a ridge moved over its receptive field, the afferent responded faithfully, with the first spike precisely phase-locked to the ridge movement. These initial spikes were often followed by a few more: multiple spikes were evoked by a ridge for 76% of the 107 ridge presentations during this period. A similar pattern is also present in the middle panel, which shows the first six top-up periods following adaptation. Again, the afferent responded to nearly all (98%) of the 108 ridge presentations, and 89% of these generated multiple spikes. A pattern consistent with adaptation is evident in the bottom panel, which shows the last six top-up periods of the run. Here, 84% of the 108 ridges evoked a spike that was precisely time-locked to the ridge onset, while only two ridge presentations (1.9%) evoked multiple spikes.

The results indicate that the steps of the motor driving the surface rotation did not cause vibration that stimulated primary afferents. For the adapting and standard speed of 80mms^{-1}, the motor stepped approx. 50 times per second, whereas the ridges of the surface passed over the skin about 4 times per second. The single unit recording was precisely phase-locked to the timing of the ridges (see Figure 2.8), indicating that the ridges rather than the steps of the motor drove the neural response. The maximum firing rate of the two recordings (33.4ips for the multi-unit recording, 6.8ips for the single-unit) never approached the frequency of the motor steps (50Hz). Therefore, if the stepper motor generated any vibration, it was below the threshold of primary afferents from which we recorded.

Because we applied the Opposite Direction stimulus protocol, in which different directions of test and top-up periods alternated, we were able to determine the FA1 unit's direction preference. We did this by comparing its response during the 1s test periods, in which the drum moved in a distal direction, with its response in the first 1s of the 5s top-up periods, when it moved in a proximal direction. We used the first six top-up and test periods, before the unit had shown a substantial reduction in response due to adaptation. During this period the FA1 displayed a preference for proximal motion, responding at a rate of 9.3ips, compared to 4.2ips for distal motion.

Experiment 2

The results of Experiment 2 revealed no significant differences between conditions – the effect of adaptation did not significantly depend on its direction relative to the test. Figure 2.9 shows the psychometric functions for the three conditions for each observer. The response curves for the same direction and opposite direction conditions are not shifted in any consistent direction relative to baseline. The non-significant shifts that are sometimes visible are usually small, with considerable overlap of the response curves for the different conditions.

The PSEs across participants are given in Figure 2.10. The mean PSE was 78mms^{-1} (SD = 8) in Baseline, 79 (SD = 11) in the Same Direction condition and 72 (SD = 9) in the Opposite Direction condition. These small differences were not statistically significant according to a repeated measures ANOVA ($F_{2,16} = 1.42$, $p = .27$).

We also examined whether discrimination sensitivity was affected by adaptation direction, using slope of the logistic regression as an index of discrimination sensitivity. There was a trend for a slightly steeper slope in the Baseline condition, although the effect of condition did not reach significance with a repeated measures ANOVA ($F_{2,16} = 3.62$, $p = 0.05$). The mean slope was 0.031 (SD = 0.008) in Baseline, 0.025 (0.006) in the Same Direction condition and 0.029 (0.007) in the Opposite Direction condition.

Experiment 3

Out of three possible responses regarding direction of motion in this experiment - veridical, reverse and unclear – the most frequent direction perceived was veridical throughout the 4 minutes of the run. Figure 2.11 shows the mean probability of each response for 6 participants. The mean probability of the veridical response averaged across runs was .77, .70 and .68 for the 27, 54 and 108mms^{-1} speeds, respectively. The mean probabilities of the veridical response within the first 30s – equivalent to the duration of our adaptation period in Experiments 1 and 2 – was even higher: .86, .84 and .79 for the 27, 54 and 108mms^{-1} speeds, respectively.

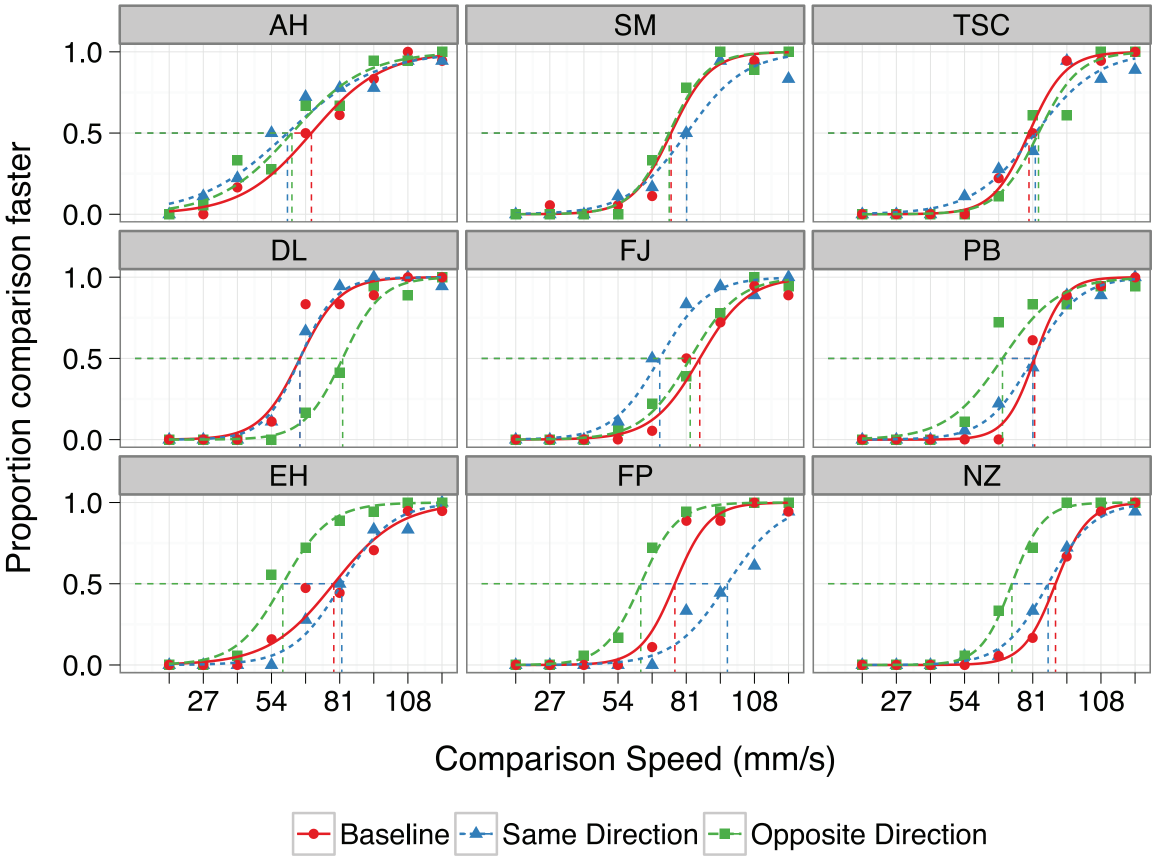

Figure 2.9. Individual psychometric functions for three experimental conditions, Experiment 2. Format the same as in **Figure 2.4**. Data are plotted for three adaptation conditions: baseline (circles), in which both hands received adaptation in the same direction; same direction (triangles), in which the reference hand was adapted in the same direction as test, and the comparison hand was adapted in the opposite direction; and opposite direction (squares), in which the reference hand was adapted in the opposite direction to test, and the comparison hand was adapted in the same direction.

After the drum stopped, participants continued reporting the perceived direction of the stationary surface for three seconds. Five of the six participants reported an aftereffect on at least one trial (TSC never experienced an aftereffect). Overall, a negative tMAE (illusory motion perceived in the opposite direction to the adapting stimulus) was reported in 19 of the 70 trials (27%), and a positive tMAE (in the same direction as the adapting stimulus) was reported in 4 of the 70 trials (6%). This result is consistent with previous studies that have found a low incidence of the tMAE, and that it occurs in both positive and negative directions (Hazlewood, 1971; Hollins & Favorov, 1994; Lerner & Craig, 2002; Planetta & Servos, 2008, 2010; Thalman, 1922; Wohlgemuth, 1911).

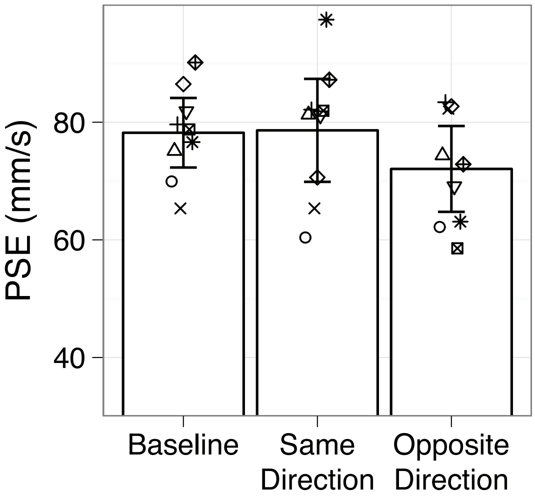

Figure 2.10. Mean PSE (bars) across participants as a function of adaptation condition, Experiment 2. Error bars represent 95% confidence intervals of the mean. The symbols indicate the PSE obtained for each participant.

2 .7 Discussion

We found that adapting to a surface moving across the skin reduces its perceived speed, an effect we labelled the tactile speed aftereffect (tSAE). This is the first known replication of this effect since it was reported in 1960 (Stöber, reported in Rausch, 1960). We also report, for the first time, that this effect is *not* direction sensitive. Experiment 1 showed that the perceived speed of the test stimulus decreases by approximately one third and does not depend on whether the adapting stimulus moved in the same or the opposite direction as the test. This insensitivity to direction was confirmed in Experiment 2 in which bilateral adaptation to motion in different directions revealed no perceptual differences. Experiment 3 demonstrated that the direction of the motion of our stimulus is clearly perceived most of the time, even during prolonged stimulation, indicating that this stimulus engages directional processes. This combined with the fact that we used a dynamic test stimulus to engage the same processes during both adaptation and test phases indicates that our stimulus is suitable for testing direction sensitivity of motion adaptation.

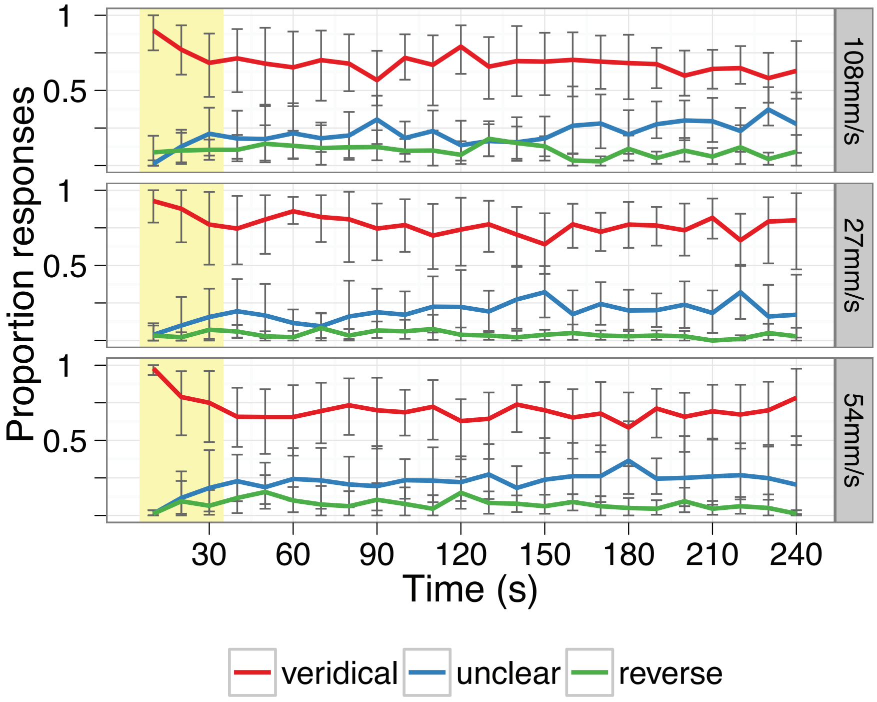

Figure 2.11. Perceived direction of the moving surface over time. The proportion of time each response was given is plotted over a four-minute period. Data are averaged over 10s time bins. Error bars give the bootstrapped 95% confidence interval of the mean.

Our participants were asked to judge speed, but it is possible that their speed judgments were based on stimulus features other than the speed. One candidate is temporal frequency (TF), or the number of prominent ridges on our surface (see Figure 2.1B) stimulating the skin per unit of time. This was confounded with speed because we always used the same surface (22mm spatial period), and with increased speed, more ridges would have touched the fingertip in the same time period (3.7Hz for the standard stimulus, 0.6 – 5.5Hz for the comparison stimuli). This confound could in principle explain our findings if our participants relied on the TF of the ridges, and if perceived TF is susceptible to adaptation. We think it is unlikely that our participants based their judgments on TF, primarily because people are able to judge the speed of the moving surface independently of its TF (Dépeault et al., 2008). If relying on TF offered some advantage, it might be a preferred strategy, but it is not obvious what advantage it would have offered to our participants.

It is also unlikely that adaptation of perceived temporal frequency can explain our results. Our microneurography data from the present study suggest that information about the TF of the stimulus was preserved following adaptation. Adaptation to the duration of the interval between successive ridges hitting the skin could also have occurred (274ms for the standard stimulus, 183 – 1644ms for the comparison stimuli). Tactile interval durations are subject to adaptation, making them appear shorter (Watanabe, Amemiya, Nishida, & Johnston, 2010). However, if this occurred in our experiment perceived speed should increase, which is the opposite of what we observed.

Furthermore, preliminary results of another study in our laboratory, in which we completely dissociated speed from either TF or interval duration by using a number of different speeds and surfaces, suggest strongly that speed rather than TF or duration explains the adaptation effects, and this in turn supports our proposal that tSAE is based on speed judgments, rather than on judgments of other features. This preliminary result also suggests that the adaptation responsible for the shift in speed judgments occurs in neural channels encoding speed itself, rather than in those encoding the temporal frequency of the stimulus that feed into the speed channels.

Our results show *no* effect of direction on speed adaptation (regardless of whether the adapting motion direction was distal or proximal, the decrease in perceived speed of the test stimulus was very similar). One could argue that the result is due to a ceiling effect. If too much adaptation occurred, it would drive all primary afferents and other stimulated neurons into an equally unresponsive state, despite our intention to adapt units preferring one direction more than those preferring the opposite direction. But this scenario is unlikely. Neurophysiological studies on adaptation to vibration (Bensmaïa et al., 2005; Leung et al., 2005) show that adaptation to a non-preferred stimulus will cause a primary afferent unit to reduce its response rate until it reaches a stable level of adaptation. However, a preferred vibration frequency or amplitude is able to create an even stronger adaptation. Because primary afferents are also sensitive to direction (Birznieks et al., 2010, 2001; Edin et al., 1995; Goodwin & Morley, 1987a; Wheat et al., 2010), a preferred direction of motion should also create stronger adaptation than a non-preferred direction, even after prolonged adaptation.

Since direction of motion was of no consequence to the size of the tSAE, it follows that *peripheral adaptation is not the cause of the reduction in perceived speed*. The level of adaptation in peripheral units caused by the rotating drum would vary depending on their direction preference and movement direction. An example of such a unit, preferring proximal over distal motion, is provided in our microneurography data. If adaptation of primary afferents were responsible for the tSAE, one would expect the effect to be stronger in the direction of the adapting stimulus, which is not what we found. The lack of direction sensitivity thus indicates that the adaptation that reduces perceived speed occurs centrally. A possible central mechanism that is robust to peripheral firing rates is one based on sequential activation of afferents with receptive fields positioned along the trajectory of the moving stimulus (Darian-Smith & Oke, 1980; Essick, 1998). Speed could be estimated from the distance between successive positions and the time between stimulation (Darian-Smith & Oke, 1980).

The absence of direction sensitivity of the tSAE also suggests that *speed is coded separately from direction*, i.e., in different neurons. With joint coding, where single neurons show a preference for both a particular stimulus speed and direction, we would expect a reduced response to the adapted combination of speed and direction, which we did not observe. An exception to this would be a 'gain control' mechanism, similar to that observed in the visual motion system of flies (Harris, O'Carroll, & Laughlin, 2000), in which activation of direction sensitive neurons transfers adaptation to units tuned to all directions. In touch, neurophysiological evidence is mixed. In support of joint coding, a subset of direction selective neurons in areas 3b and 1 show a stronger direction preference with increased speed (Pei et al., 2010; Ruiz et al., 1995). Romo and colleagues found neurons in the supplementary motor area involved in a tactile speed discrimination task, but they did not test for direction sensitivity. Support for separate coding is found in clinical evidence. Essick and colleagues (Essick, Franzén, et al., 1996) described patients with cortical damage whose capacity to discriminate the direction of tactile motion was either eliminated or severely impaired, while capacity to judge speed was preserved (Essick, Franzén, et al., 1996). A similar though less pronounced dissociation was also reported in patients with dorsal column damage (Wall & Noordenbos, 1977).

The tSAE is a perceptual aftereffect of adaptation to tactile motion. A reliable aftereffect also occurs for perception of motion direction (Konkle et al., 2009; Kuroki et al., 2011; Watanabe et al., 2007). The use of a *dynamic* test stimulus is a characteristic of our speed adaptation study that is shared with "successful" tMAE studies that found a consistent negative aftereffect in perceived direction. Watanabe and colleagues, authors of the first tMAE study that used a dynamic test (Watanabe et al., 2007), emphasised the importance of a good match between the adapting and the test stimuli (pp 578, 581), contrasting their experimental design with earlier studies that used a stationary test stimulus and failed to observe a reliable tMAE (Hollins & Favorov, 1994; Lerner & Craig, 2002; Thalman, 1922). Stöber's early investigation of the tSAE (reported in Rausch, 1960) also shares this characteristic - the test stimulus was in motion (i.e., dynamic) – and similar to what we found, reported a robust and large aftereffect. In summary, the use of a stationary test produces no reliable aftereffects in touch, but the use of a dynamic one does. This contrasts with vision where both stationary and dynamic tests result in robust directional aftereffects (for review, see Mather, Pavan, Campana, & Casco, 2008). The full implications of the difference in response to a stationary test stimulus between vision and touch are not yet clear, but there is no doubt that tactile motion mechanisms also adapt, affecting both perceived direction and speed. Further, we can rule out the possibility that surface motion across the skin is not a good stimulus to study aftereffects. Our Experiment 3 shows that motion direction of a surface moving across the skin is clearly perceived most of the time, even after minutes of continuous stimulation.

In conclusion, our results are consistent with other tactile adaptation studies that relied on a dynamic – rather than stationary - test stimulus for robust aftereffects. We documented that the tactile speed aftereffect (tSAE) was similar in size regardless of whether the direction of the adapting and test stimuli match. Our results suggest that speed-encoding processes are robust to reductions in the firing rates of primary afferents, and thus that non-directional adaptation of central mechanisms is likely to be responsible for the tSAE.

Chapter 3: The effect of adapting speed on the tactile speed aftereffect

3 .1 Introduction

The tactile speed aftereffect (tSAE) is the illusory slowing of movement across the skin following a period of adaptation to tactile motion (Stöber, reported in Rausch, 1960; McIntyre et al., 2012, Chapter 2). The previous chapter presented evidence that the tSAE is not direction sensitive, that is, the amount of illusory slowing does not require the adapting motion to be in the same direction as the motion stimulus used to test for the aftereffect; adaptation in the opposite direction resulted in a tSAE of similar strength. It was argued that the tSAE was a result of adaptation occurring in the central nervous system. It could not be attributed to the amount of reduced firing observed in primary afferents, because unlike the tSAE, they are sensitive to direction.

Little is known about neural or perceptual speed coding, and characterising adaptation effects such as the tSAE allows inferences to be made about the perceptual processes that form its basis. In this chapter, the tSAE is further characterised by testing whether the strength of the adaptation varies with adapting speed. In general, the strength of the aftereffect reflects the degree of adaptation in the relevant neural population (Lundström & Johansson, 1986), and the degree of neural adaptation depends on the amount of excitation evoked in those neurons by the adapting stimulus (Barlow & Hill, 1963a; Harris et al., 2000).

One possibility is that the strength of the tSAE is based on neurons that increase their firing rate with increasing speed of motion across the receptive field. If such an intensive code were present, we would expect the strength of the tSAE to increase with greater adapting speeds. Another possibility is that the neurons that encode speed have a variety of preferred speeds. That is, some neurons might fire maximally for slow speeds and others fire maximally for fast speeds. If this were the case, we would expect to see speed *tuning*[1] of the tSAE – that is, we would expect the strength of the tSAE to require a certain degree of correspondence between the speeds of the adapting and test stimuli.

Neurophysiological evidence seems to favour the intensive code account. A handful of studies have recorded neurons in the primary somatosensory area (SI) of primates that are sensitive to speed of motion. Collins and Roppolo (1980) reported that the mean response of 34 out of 37 recorded SI neurons increased monotonically with the speed of a moving brush, while for the remaining 3 neurons, response decreased with increasing speed. Tremblay, Ageranioti-Bélanger and Chapman (1996) also reported that some SI neurons increased their firing rate with increases in the speed of a surface scanned across the skin. However, there is some doubt about whether these neurons form the basis of speed perception – Collins and Roppolo (1980) found that most individual units could not discriminate speed as well as human observers of the same stimuli, and Tremblay et al. (1996) did not compare neural responses with perceived speed.

Neither of those studies tested whether the speed sensitive neurons were direction selective, but several other studies have reported direction selective SI neurons that showed greater activity in their preferred direction when speed was increased (Pei et al., 2010; Ruiz et al., 1995; Whitsel, Dreyer, & Hollins, 1978; Whitsel et al., 1972), raising the possibility that speed and direction might be jointly coded in these neurons. Although the tSAE isn't direction specific (McIntyre et al., 2012, Chapter 2), speed could still be coded in direction selective neurons if adaptation generalises across different directions.

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[1] Note that while both neural codes proposed here are based on the firing rate of neurons, and in this sense could be thought of as 'intensive', they are named for the effect that the *stimulus* has on the firing rates of neurons. That is, an 'intensive code' refers to the case where a more intense (faster) stimulus evokes a stronger response, whereas 'speed tuning' refers to the case where different speeds evoke the strongest response in different neurons.

This might occur via a neural gain control mechanism similar to what has been reported in direction selective neurons in the visual motion system of flies (Harris et al., 2000).

Evidence from another perceptual aftereffect also suggests that increasing the adapting speed might produce a stronger tSAE. The static tactile motion aftereffect (static tMAE) occurs when adaptation to a moving surface induces illusory motion of a subsequently felt stationary surface. Planetta and Servos (2008) found that the tMAE occurred more frequently, lasted longer, and was rated as more vivid when the speed of the adapting stimulus was increased over a range of 150-350mms^{-1}. The adaptation phase in their tMAE protocol is the same as in the protocol for inducing the tSAE presented in this chapter, and as such, they activate the same neural populations. It may therefore be expected that perceived speed during the test phase will show a similar effect of the adapting speed. On the other hand, it is possible that separate neural channels underlie the different perceptual tasks (judging direction or judging speed), with each affected differently by the same adapting stimulus.

The aim of Experiment 4, presented in this chapter, was to distinguish between an intensive code of speed, which predicts the tSAE will increase monotonically with adapting speed, and speed tuning, which predicts the tSAE will be greatest when the adapting and test speeds are matched. The protocol for inducing the tSAE involved using different *test* speeds to determine whether they are differentially affected by the adapting speed. The tSAE was induced for a variety of test speeds using an adapting stimulus that was faster than the test, and the strength of the tSAE was compared to that obtained when the adapting and test speeds were matched.

Another aspect of tactile speed coding that is addressed in this chapter is how speed relates to the temporal and spatial features of a surface moving across the skin. A ridged, periodic grating that is scanned across the stationary fingers at a given speed, perpendicular to the axis of the ridges, results in the ridges crossing a given skin location with a particular frequency. This is characterised by the following formula:

$$TF = {}^{Speed}/_{SP}$$

Where TF is the temporal frequency of the ridges crossing the skin, Speed is the scanning speed and SP is the spatial period: the centre-to-centre distance between the ridges in the direction of scanning. For these three features, only two can be manipulated independently at a time, and knowing the value of any two gives the value of the third. While human speed judgments depend primarily on the physical speed of the stimulus, they can also be influenced by changes to the SP of the surface (Dépeault et al., 2008). It is possible that SP and TF are perceptual 'primitives', with speed being computed from them at a later stage in the tactile motion processing system. If perceived speed is computed from sensed SP and TF, it is possible that the tSAE varies in strength due to changes in adapting SP or TF, rather than adapting speed.

Much of the evidence supplied above in support of the hypothesis that increasing adapting speed will increase the strength of the tSAE is also consistent with a hypothesis that increases in adapting TF will cause a stronger tSAE. In the static tMAE study reporting an effect of adapting speed (Planetta & Servos, 2008), the same surface was always used, meaning that increases in speed were also increases in TF. Several of the studies reporting SI neurons responding to changes in speed used a point stimulus (e.g. a brush; Collins & Roppolo, 1980; Dreyer, Hollins, & Whitsel, 1978; Pei, Hsiao, Craig, & Bensmaïa, 2010; Whitsel et al., 1972). Point stimuli cannot be described in terms of SP and TF in the same way as periodic surfaces, but their speed is confounded with either traverse length or duration of stimulation. These studies held traverse length constant, so higher speeds were associated with shorter durations, again confounding speed with the temporal features of stimulation. The one exception was Tremblay et al. (1996), who varied surface roughness as well as speed. They found some neurons that increased firing for increases in either surface roughness or speed. However, others responded to speed but not roughness or pressure, indicating that speed is coded independently of TF in at least some neurons.

The goal of Experiment 5, presented in this chapter, was to test whether the tSAE was based on changes induced in speed coding, or changes in temporal frequency coding. Stöber (reported in Rausch, 1960) found a tSAE when using either of two different surfaces moving at the same speed (SP and TF varied four-fold). However, the strength of the aftereffects was not compared. In Experiment 5, the effect of adapting speed was disambiguated from other features of the motion stimulation, such as the distance between the ridges of the surface (spatial period), and the frequency with which the ridges pass across the skin (temporal frequency).

Experiment 4 compared adaptation with motion faster than the test speed to adaptation with motion matched to the test speed, for a variety of test speeds. This was to test between 1) speed tuning, in which the tSAE is strongest when the adapting and test speeds are matched, and 2) an intensive speed code, in which the tSAE is strongest when the adapting speed is faster than the test speed. Experiment 5 tested whether the effect of adapting speed was due to induced changes in speed coding or temporal frequency coding, by adapting with a variety of periodic surfaces with different spatial periods.

3 .2 Experiment 4

Method

Participants

Six participants volunteered - three naïve observers, the author and the two co-investigators (thesis supervisors). Two participants were left-handed. Written informed consent was obtained and the Human Research Ethics Committee of the University of Sydney approved the study.

Apparatus

The same apparatus, including drums and rubber surfaces, was used as in Chapter 2.

Design

Four different test speeds were used: 30, 81, 143 and 242mms^{-1}. For each test speed, participants were adapted in two adapting conditions, 'faster' (242mms^{-1}) and 'matched', in which the adapting speed was the same as the test speed (for the 242mms^{-1} test speed, there was only one adapting speed, labelled 'matched'). This was to test whether the tSAE was stronger when the adapting speed was faster, as predicted by intensive speed coding, or when the adapting and test speeds were matched, as predicted by speed tuning. There was also a 'no adaptation' condition, in which perceived speed was measured for each of the test speeds without any prior adaptation, and was used as a baseline. Both adaptation and test stimuli were always in the same direction, proximal-to-distal. Two participants (SM and TSC) were tested in an additional adapting condition, 'slower' (30 mms^{-1}).

Procedure

The procedure is illustrated in Figure 3.1. Similar to the experiments described in Chapter 2, experimental sessions for adaptation conditions began with a 30s adaptation phase, in which the reference finger was exposed to motion (the adapting stimulus). This was followed by the test phase, in which the speed was judged. The adaptation conditions also included 5 seconds of "top-up" adaptation following each left/right judgment. In the No Adaptation condition, no adaptation preceded the speed judgments, and there was no top-up period during the test phase.

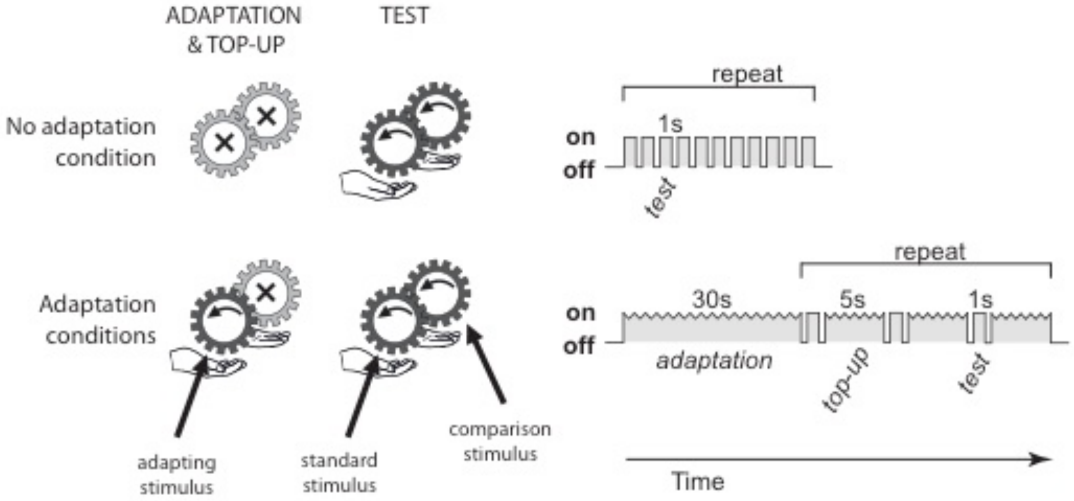

Figure 3.1. Procedure for Experiment 4. Illustration of the stimuli presented during adaptation, top-up and test. The adaptation conditions presented the adapting stimulus to the right index finger during the initial 30s adaptation period and also in the 5s top-up periods between tests. During the test phase, the standard stimulus was presented to the adapted right index finger and a comparison stimulus was presented to the unadapted left index finger. The Baseline (no adaptation) condition had only the test phase.

Participants were instructed to touch the drums with only the distal segment of the index finger. To ensure that consistent pressure was maintained on the finger, only one finger was used. All stimuli moved in a proximal-to-distal direction. The adapted right finger was always presented with the standard stimulus, which was the same speed on every trial. The left finger was presented with comparison stimuli of a variety of speeds. The speeds used were equally spaced on a logarithmic scale. Similar to the experiments described in Chapter 2, white noise was delivered through headphones to mask the sound of the rotating drums. Auditory tones indicated to participants when they pressed too hard (with a force greater than 40gm-wgt) or too softly (less than 10gm-wgt) and they were asked to keep within this range throughout the experiment.

All participants completed eleven experimental sessions, one for each adapt-test speed combination, including the ‘no adaptation’ condition for each test speed. These sessions were distributed across multiple days. In each session, participants made 20 judgements for each of 7 comparison speeds in each of the 11 conditions, for a total of 1540 trials over the course of the experiment. Each session consisted of two runs separated by a 2-minute break. Both runs began with the 30s adaptation phase.

Results

A clear tSAE was evident in almost all cases, with adaptation causing a reduction in perceived speed of the test stimulus. Figure 3.2 shows the psychometric functions for each participant at each combination of adapting and test speeds. Logistic regression functions were fitted to the responses as a function of log comparison speed. The 50% point on the curve gives the Point of Subjective Equality (PSE): the comparison speed that the participant is equally likely to say is faster or slower than the standard speed. This is an indicator of the perceived speed of the test stimulus. There is a visible trend such that the darker the curve (indicating a faster adapting speed), the further it is to the left (indicating a slower perceived speed). That is, the greater the adapting speed, the stronger the adaptation effect.

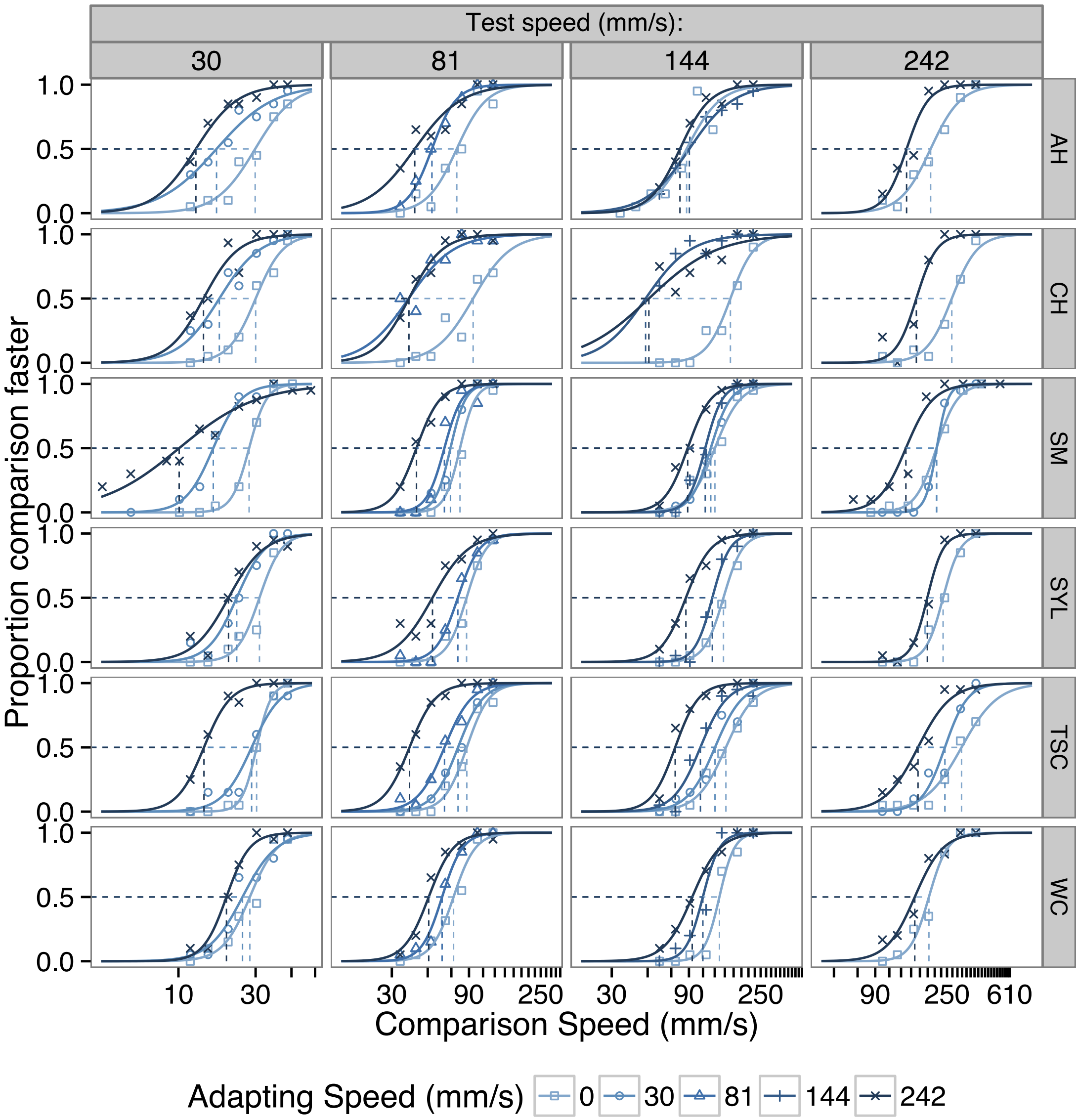

Figure 3.2. Individual psychometric functions for each combination of adapting and test speeds. Different test speeds are shown in columns, and different adapting speeds are represented within each panel as separate lines, with darker lines for higher speeds. On the ordinate is the proportion of trials that the participant judged the comparison speed to be faster than the standard (equal to the test speed). On the abscissa is the comparison speed, on a log scale. Both raw data and fitted logistic regression functions are shown. Dotted lines give the Point of Subjective Equality (PSE) for each curve.

In order to compare the strength of the tSAE across different test speeds, the proportional change in PSE from baseline was calculated for each adapting and test speed combination (Figure 3.3). When the adapting and test speeds were matched, the PSE was reduced by a mean (± 95% confidence interval) of 28 ± 9% from baseline. This is consistent with the 30% reduction observed in Experiment 1 (Chapter 2). When the adapting speed was faster (242mms^{-1}) than the test speed (30-144mms^{-1}), the PSE was reduced by 44 ± 9% from baseline. This was significantly greater than the reduction when adapting and test stimuli were matched ($t_{40} = 3.3$, $p = .002$)[2]. For the two participants that were tested with an adapting speed slower (30mms^{-1}) than the test speed (81-242mms^{-1}), the PSE was reduced by a mere 11 ± 8% from baseline. This suggests that the faster the adapting speed, the greater the tSAE.

The group data seem to suggest that the proportional change in PSE depends not only on the adapting speed but also on the test speed, and that the relationship between the speeds of the adapting and test stimuli may be important. This is in contrast to the possibility that the adapting speed alone determines the proportional change in PSE, with faster adapting speeds producing a greater proportional change. While the experimental conditions were defined by the relative speeds of the adapting and test stimuli ('faster', 'matched', 'slower'), it can be tested whether this definition was justified by examining just the cases in which the adapting speed was 242mms^{-1}, for a variety of test speeds (Figure 3.3, *right*). When adapting speed was fixed at 242mms^{-1}, there was a significant linear trend such that increases in the test speed were associated with a decrease in the strength of the tSAE ($F_{1,2} = 171$, $p = .006$, $R^2 = .99$). Increasing the test speed from 30mms^{-1} up to the speed matching the adapting stimulus (242mms^{-1}) was

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[2] Excluding the matched condition in which both adapting and test speeds were 242mms^{-1} allowed for a paired t-test to be conducted (with each pair having the same test speed and participant). This also revealed that adaptation with a faster speed produced a significantly greater reduction in perceived speed compared to adaptation with a matched speed ($t_{17} = 6.9$, $p < .001$, mean difference = 18 ± 6%).

associated with a decrease of .17 in the magnitude of the proportional change in PSE induced by the adaptation.

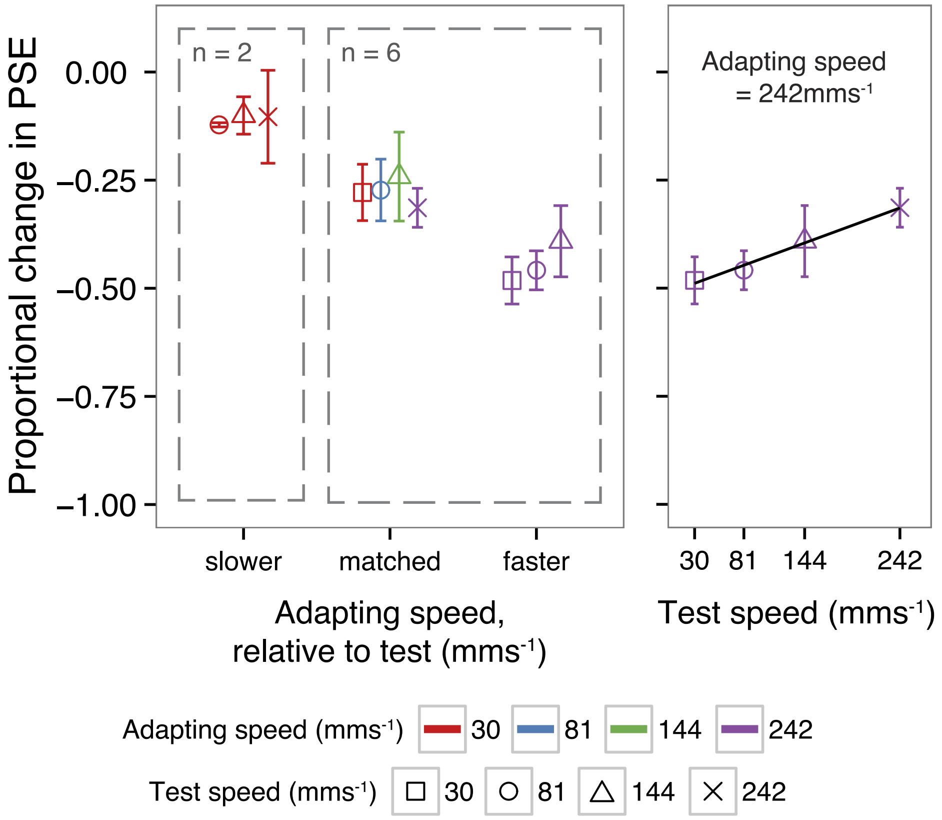

Figure 3.3. Proportional change in PSE for different adapting and test speed combinations. Error bars are 95% confidence intervals of the mean. *Left:* Mean proportional change in PSE is shown for each test speed following 'slower' (SM and TSC only), 'matched' and 'faster' adaptation conditions. The negative scale means that lower values indicate a greater proportional decrease in perceived speed. *Right:* A subset of the data (with adapting speed equal to 242mms^{-1}) is re-plotted showing mean proportional change in PSE as a function of test speed. A fitted linear regression line is shown.

A limitation of this experiment is that the same surface was used at all speeds, with the same spacing between the ridges on the surface. This means that an increase in speed was always accompanied by an increase in the frequency with which the ridges crossed the skin. For this reason, the stronger tSAE might have been due to the higher temporal frequency (TF) of the ridges, rather than to the higher speed of the surface. Experiment 5 addressed this confound, independently testing the influence of speed and TF on the strength of the tSAE, using surfaces with different textures.

3 .3 Experiment 5

Method

Participants

Six participants volunteered - four naïve observers, the author, and one co-investigator (thesis supervisor). Two were left-handed. Written informed consent was obtained and the Human Research Ethics Committee of the University of Sydney approved the study.

Design

The same apparatus was used as before, but with new, laser-cut rubber surfaces mounted on the rotating drums. In this experiment, a single test stimulus was used in all conditions. This was a surface with a spatial period (ridge-to-ridge distance) of 6mm that moved at 40mms^{-1}, resulting in the ridges crossing the skin at a temporal frequency of 6.7 Hz.

Several adapting stimuli were used. They were chosen to disambiguate the following three stimulus features, to determine which of them influence the strength of the tSAE, as observed in Experiment 4: 1) speed, 2) temporal frequency (TF) and 3) spatial period (SP). Given any two of these features, the third can be calculated (speed = SP x TF), meaning that at any one time, only two of the variables can be varied independently. Three adapting surfaces were used (SP = 3, 6 and 12mm), and they moved at three speeds (20, 40 and 81mms^{-1}) to produce three different TFs (3.4, 6.7 and 13.4Hz). These combinations are listed in Table 3.1. Any given value of speed occurs with at least two different combinations of SP and TF (e.g. 20mms^{-1} occurs with 3mm, 6.7Hz and also with 6mm, 3.4Hz). This is true for all three features and allows the comparison of equivalent adaptation with respect to any one feature, while the other features vary. This design allows independent evaluation of the contributions of each of the three stimulus features.

Table 3.1. The combinations of adapting surfaces, adapting speeds and adapting temporal frequencies used in the experiment. The 7 combinations chosen produced three levels of each feature, with each level of a given feature combined with at least two levels of each other feature. Note that the "middle" adapting stimulus (SP = 6; Speed = 40mm/s; TF= 6.7Hz) is identical to the test stimulus.

Spatial Period (mm)	Speed (mms^{-1})	Temporal Frequency (Hz)
3	20	6.7
3	40	13.4
6	20	3.4
6	**40**	**6.7**
6	81	13.4
12	40	3.4
12	81	6.7

Procedure

The procedure was the same as in Experiment 4, except that the experimental design required participants to repeatedly switch the reference finger between the adapting and standard stimulus surfaces for the adapting/top-up and test periods, respectively (see Figure 3.1). To facilitate this, different textures were mounted on each half of the drum (Figure 3.4). On one half of each surface was the standard stimulus texture (SP = 6mm), and on the other half was the adapting stimulus texture (SP = 3, 6 or 12mm). All of the textures had ridges 1mm wide, with the gaps between ridges varying to produce different spatial periods.

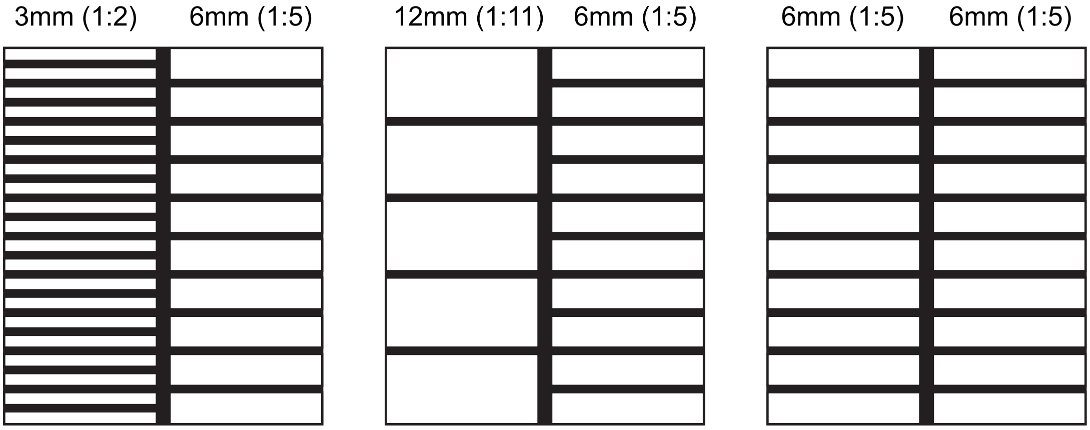

Figure 3.4. The surfaces used in the experiment. Three drums were mounted with each of the surfaces shown. A fourth drum was used for the comparison stimuli, mounted with the third surface (6mm-6mm; while this surface had the same texture on both halves, the participants were not told of this beforehand, and they switched their finger between the two halves as with the other surfaces – see text). Between runs, the drums were swapped according to the adaptation condition. The spatial periods are given above each texture, with the ratio of ridge to gap width in brackets.

A plexiglass plate with two apertures guided participants where to switch the reference finger between the adapting texture (felt during the adaptation and top-up phases), and the standard texture (felt during the test phase). This is illustrated in Figure 3.5. The comparison finger also switched between apertures at the same time as the reference finger. Although the comparison finger was presented with the same stimulus (the 6mm texture) during the adapting and test periods, and the comparison drum moved only during the test phase; the switch was nevertheless required in order to equate the action of the two fingers.

The comparison stimuli had constant SP but varied in speed, with values around the standard stimulus. The pause between the top-up and test periods was 3s, giving participants time to switch their finger between textures on the drum before the surface started moving again. As in previous experiments, white noise was delivered through headphones to mask the sound of the rotating drums, and auditory tones indicated to participants when they pressed too hard (with a force greater than 40gm-wgt). However, because switching between apertures meant that participants had to lift the finger off the drum completely, there was no tone to indicate that they pressed too softly, as it would have been unhelpfully triggered on every switch.

All participants completed 8 experimental sessions, one for each of the 7 Adapting stimuli, plus the No Adaptation condition. These sessions were distributed across multiple days. The experiment was preceded by a brief practice to familiarise participants with the task. In each session, participants made 20 judgements for each of 6 comparison speeds, for a total of 960 trials over the course of the experiment. Each session consisted of four runs (two for the No Adaptation condition) separated by a 2-minute break. Each run for an adaptation condition began with the 30s adaptation phase.

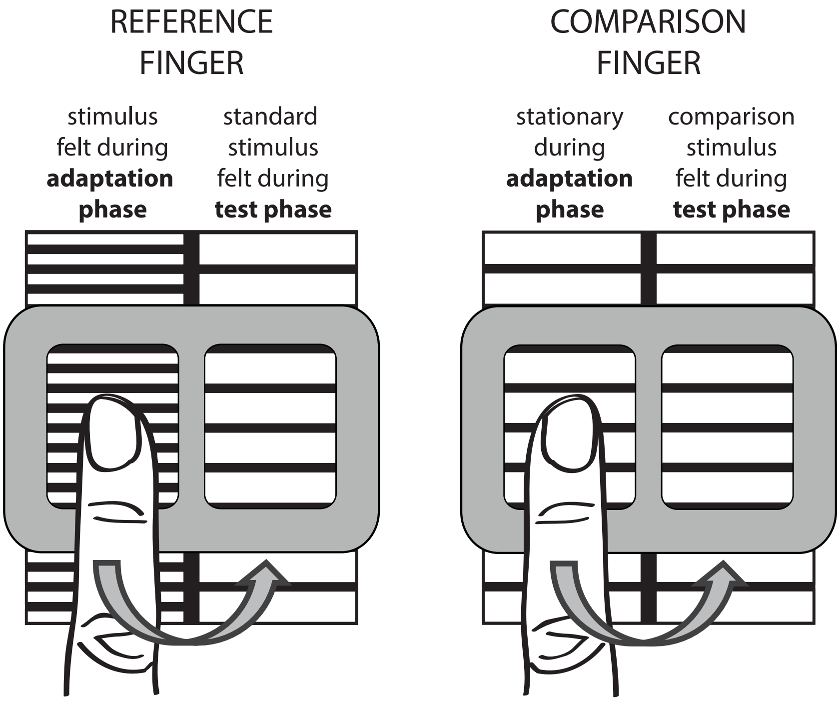

Figure 3.5. Switching the finger between textures on the drum. During a run, participants switched the reference finger between the adapting texture (in this example, SP = 3mm) and the standard texture (SP = 6mm), guided by the aperture frame (grey). The comparison finger also switched apertures, but the same stimulus was presented through both apertures (SP = 6mm). The pauses between top-up and test stimuli indicated to the participant that it was time to switch to the other aperture. The fingers are shown in position for the adaptation (and top-up) phase, in which the reference finger felt a moving surface, while the comparison finger felt a stationary surface. The arrows indicate to where the fingers switched for the test phase, in which both surfaces moved and participants judged which was faster.

Results

As expected, a tSAE was observed, with adaptation to motion resulting in a decrease in perceived speed of the test stimulus. Consistent with Experiment 4, the strength of the adaptation also appeared to increase with adapting speed. Figure 3.6 shows the psychometric functions for all adaptation conditions. The top row shows data for the no adaptation condition, with the next three rows showing data for increasing adapting speeds. The PSEs, indicated by the vertical lines, tend to be shifted further to the left as adapting speed increases, but tend to cluster where adapting speed is equal but the TF and SP vary. This suggests that the adapting speed predominantly determines the strength of the tSAE.

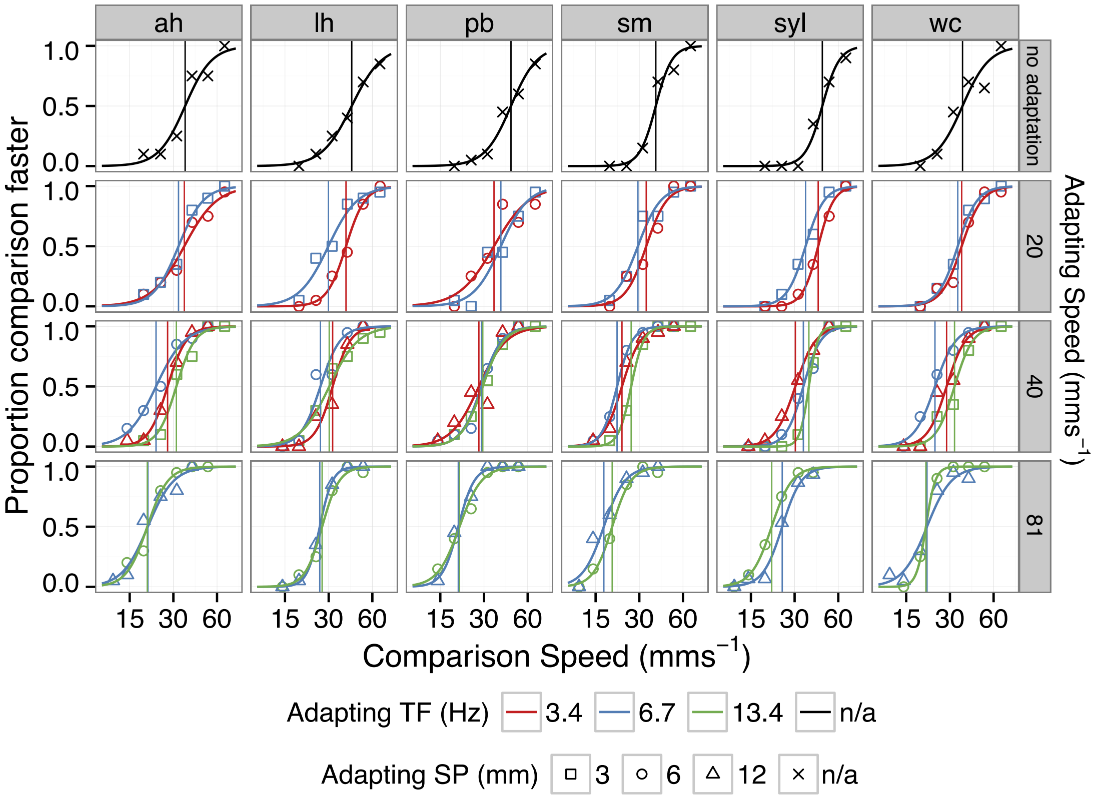

Figure 3.6. Psychometric functions for all adaptation conditions. Plotted on the ordinate is the proportion of speed judgments for which the participant judged the comparison speed faster than the standard. This is plotted as a function of the comparison speed on a log-scale. (Standard stimulus: 40mms^{-1} speed; 6mm SP; 6Hz TF). Raw data are shown, and curves are fitted logistic regression functions. The top row shows the baseline results in which speed judgments were made without any preceding adaptation. The bottom three rows give the psychometric functions following adaptation at 20, 40 and 81mms^{-1}. Adapting TF is indicated by colour, and the adapting spatial period is indicated by shape of the points. Vertical lines give the PSE for each condition, and can be compared across rows within a column (for the same participant).

To more closely examine the influence of adapting speed, temporal frequency and spatial period, independently of the other features, PSE was plotted in six different configurations: Figure 3.7 has three pairs of plots, with each pair holding one of the three features constant (e.g. Figure 3.7A and B hold adapting SP constant), and each in the pair plotted as a function of each of the other two features (e.g. Figure 3.7A plotted as a function of adapting TF, Figure 3.7B plotted as a function of adapting speed). Adapting speed appears to influence PSE such that greater adapting speeds produce a greater reduction in perceived speed, and this is true when either adapting SP or adapting TF is held constant (Figure 3.7B and D, respectively). When adapting SP is held constant, adapting TF also appears to influence PSE (Figure 3.7A). However, in this plot, increases in TF are accompanied by increases in speed for each SP and when adapting speed is instead held constant (Figure 3.7F), this apparent effect of adapting TF disappears. The same applies to the apparent effect of adapting SP in Figure 3.7C when comparing it to Figure 3.7E. Finally, in both plots showing PSE as a function of adapting speed (Figure 3.7B and D), the three lines are nearly overlapping, showing that adapting SP and TF contribute very little to the variations in PSE, and adapting speed is the primary determinant of tSAE strength.

Combining data across different values of TF and SP, when the adapting speed was 20mms^{-1}, PSE was reduced by a mean of 14 ± 10% from baseline. When the adapting speed was 40mms^{-1} (same as the test speed), PSE was reduced by 31 ± 10% from baseline. When the adapting speed was 81mms^{-1}, PSE was reduced by 48 ± 7%. These results are consistent with those observed in Experiment 1 (Chapter 2) and Experiment 4.

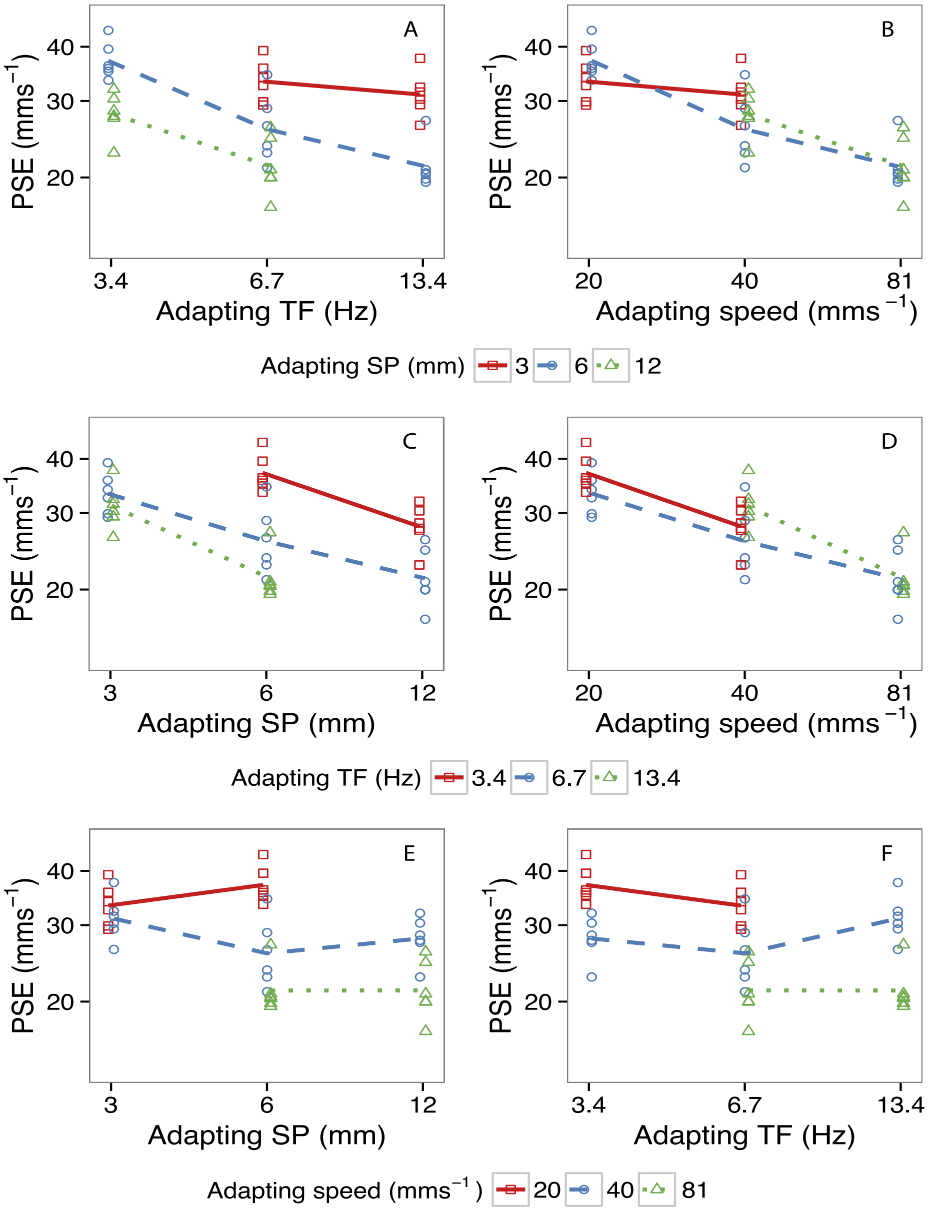

Figure 3.7. Point of Subjective Equality (PSE) plotted for different stimulus features. The adapting stimulus has three important features (speed, TF and SP), but they are not independent (S = SP x TF). PSE has been re-plotted in six different ways to reveal its relationship to each of the three stimulus features. In each of the three pairs of plots, one feature has been held constant and the PSE plotted as a function of the other two on a log-log scale. Plots *A* and *B* have adapting SP held constant at 3, 6 and 12mm (separate lines). In the same format, plots *C* and *D* have adapting TF held constant, and plots *E* and *F* have adapting speed held constant. Separate data points are plotted for each participant, and lines indicate the group means.

Linear regression analyses were used to model each participant's data separately for each of the adapting stimulus features as a predictor of PSE. Both the predictor and the PSE were log transformed. The results are shown in The slopes of the psychometric functions are an indication of speed discrimination sensitivity. Adaptation did not significantly change the slopes ($F_{7,35} = 1.4$, $p = .229$), suggesting that speed discrimination sensitivity was unaffected by adaptation. This is consistent with what was found in Experiment 1 (Chapter 2).

3 .4 Discussion

The results show a clear tSAE, with perceived speed being reduced by between 11 and 48% below baseline when tested following adaptation to a variety of motion stimuli. Both experiments found that when the adapting and test speeds are matched, perceived speed is reduced by about 30%, and this is also consistent with the results of Experiment 1 (Chapter 2). Experiment 4 expanded this result by showing that this was true for a range of speeds (30 – 242mms^{-1}).

Table 3.2. Adapting speed was a significant predictor of PSE for 5 of 6 participants, while neither adapting SP nor TF were significant predictors of PSE for any participant. The significant adapting speed models accounted for 78-97% of the variance in PSE, whereas the non-significant SP and TF models accounted for only 1-35% and 12-37% of the variance in PSE, respectively. The fits for the adapting speed model are illustrated in Figure 3.8. In order to test whether adapting speed was the sole predictor of PSE, separate models were tested with the addition of either adapting SP or adapting TF as predictors of PSE. In no case, did either adapting SP or adapting TF significantly increase the explained variance beyond adapting speed alone (not shown).

The slopes of the psychometric functions are an indication of speed discrimination sensitivity. Adaptation did not significantly change the slopes ($F_{7,35} = 1.4$, $p = .229$), suggesting that speed discrimination sensitivity was unaffected by adaptation. This is consistent with what was found in Experiment 1 (Chapter 2).

3 .5 Discussion

The results show a clear tSAE, with perceived speed being reduced by between 11 and 48% below baseline when tested following adaptation to a variety of motion stimuli. Both experiments found that when the adapting and test speeds are matched, perceived speed is reduced by about 30%, and this is also consistent with the results of Experiment 1 (Chapter 2). Experiment 4 expanded this result by showing that this was true for a range of speeds (30 – 242mms^{-1}).

Table 3.2. Linear regression models for each adapting stimulus feature. The regression model takes the form ln(PSE) = a + b*ln(Predictor).

Participant	Predictor	$F_{1,5}$	p-value	R squared	sig.
AH	Speed	24.6	0.004	0.83	*
AH	SP	2.0	0.220	0.28	
AH	TF	0.8	0.400	0.14	
LH	Speed	5.5	0.070	0.52	
LH	SP	0.1	0.802	0.01	
LH	TF	2.9	0.150	0.37	
PB	Speed	161.7	0.000	0.97	*

PB	SP	2.7	0.161	0.35	
PB	TF	0.9	0.385	0.15	
SM	Speed	32.7	0.002	0.87	*
SM	SP	2.7	0.161	0.35	
SM	TF	0.6	0.457	0.12	
SYL	Speed	18.0	0.008	0.78	*
SYL	SP	1.4	0.291	0.22	
SYL	TF	1.1	0.351	0.17	
WC	Speed	26.3	0.004	0.84	*
WC	SP	2.0	0.218	0.28	
WC	TF	0.9	0.396	0.15	

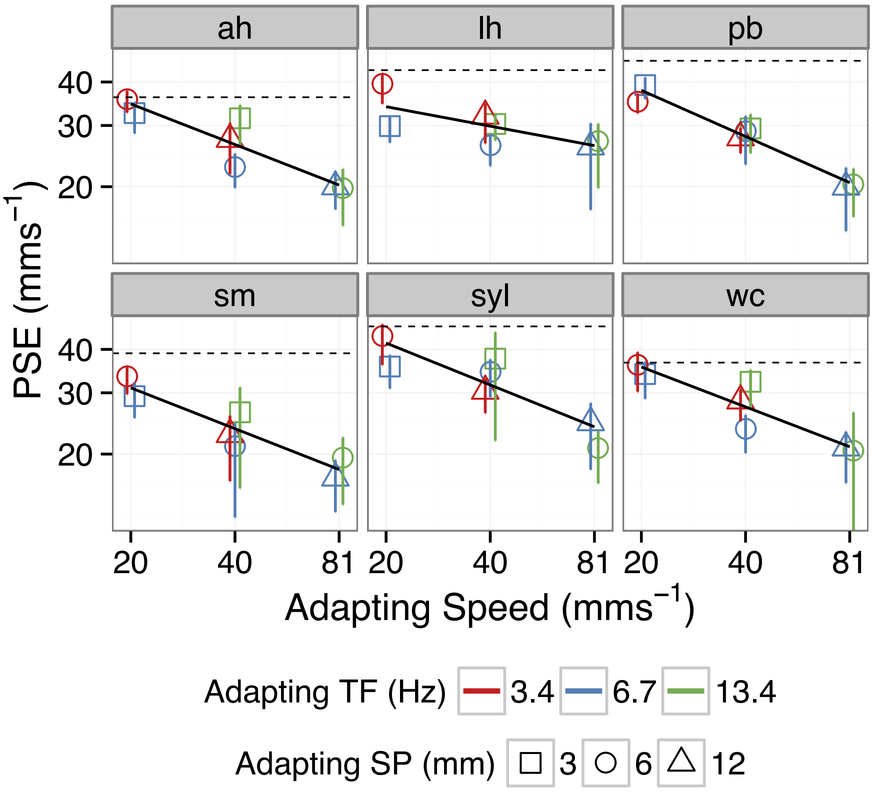

Figure 3.8. Linear regression line for each subject, with adapting speed as the predictor of PSE. PSE is plotted as a function of adapting speed on a log-log scale for different participants. Error bars are the 95% bootstrapped confidence intervals (2000 samples). The dotted lines indicate the baseline PSE found with no adaptation.

The first aim of this chapter was to distinguish between an intensive code for speed and speed tuning in the tactile motion system, by testing whether the tSAE is stronger when a) the adapting and test speeds match, or b) when the adapting speed is faster than the test. The results favour an intensive code for speed in which perceived speed is based on the amount of neural activity in the relevant population. It was found that faster adapting speeds were associated with greater reductions in perceived speed. In all but 2 cases of a possible 18, the faster adapting stimulus produced a stronger tSAE than the adapting stimulus that matched the speed of the test; and the slower adapting speed produced a weaker tSAE than the matched adapting stimulus in all 6 cases. The results also showed that it is not just the speed of the adapting stimulus that affects the proportional change in PSE induced by the adaptation, but that the test speed also plays a role. For a given adapting speed (242mms^{-1}), the strongest aftereffect was seen with the slowest test speed (30mms^{-1}), and decreased linearly as the test speed approached the adapting speed.

The second aim of this chapter was to determine whether variations in the strength of the tSAE are due to changes in the speed of the adapting stimulus, the spatial period of the adapting surface, or the temporal frequency with which the ridges of the adapting surface cross the skin. This would provide evidence of whether speed coding in the tactile motion system is based on a computation of TF and SP. Experiment 5 showed that the tSAE depends primarily on the adapting speed, with no significant influence of adapting TF or adapting SP. This suggests that the adaptation occurs in neural populations that code for speed, and not in neurons that code for TF or SP.

This contrasts somewhat with previous findings that perceived speed, while primarily determined by actual speed, is also influenced by SP (Dépeault et al., 2008). In that study, participants were asked to scale the speed of surfaces with a variety of SPs using magnitude estimation. The speed judgments depended primarily on the actual speed of the stimuli (accounting for 75-82% of the variance), but there was a slight bias to perceive the surface with the highest SP (8mm) as moving slower than surfaces with lower SP (accounting for 14-19% of the variance). Similar parameters were used in Experiment 5 reported here as in Dépeault et al.'s study, for both speed (20-81mms^{-1} and 33-110mms^{-1}, respectively) and SP (3-12mm and 2-8mm, respectively), so it is not obvious why SP would influence speed judgments, but not the strength of adaptation. Nevertheless, in both studies, speed was the primary determinant of the reported effect.

Dépeault et al. (2008) suggest that the effect of SP on speed scaling that they observed indicates that perceived speed depends on the spatial and temporal cues in the stimulus (for their stimuli, the SP and TF). However, support can also be found in their data for speed coding independent of SP and TF. At the very highest speeds there was a slight decline in the slope of the function relating speed estimates to actual speed. This change in slope occurred at the same speed for the three different surfaces (see their Figure 4), but at different TFs (see their Figure 7). Like the results reported here, this aspect of Dépeault et al.'s data is inconsistent with the conclusion that perceived speed is derived from perceived TF and SP, and suggests instead a relationship between perceived and actual speed that is not mediated by other features. However, if speed were coded unambiguously in the nervous system, then one would expect perceived speed to be uninfluenced by SP (or TF). It is possible that the bias observed at higher SPs serves a function in surface exploration, and is added to the unbiased speed code at a later stage. When a sparsely textured surface is felt, a faster scanning speed may improve perception of the surface features, and a slower perceived speed might prompt the observer to speed up.

Furthermore, it is not clear how the SP and TF of moving surfaces are themselves coded, nor has the case yet been made for which features are most easily available to the nervous system or perception (perceptual 'primitives'). In fact, several researchers have proposed that perceived roughness (which is a perceptual correlate of SP) and representations of roughness in the nervous system rely on prior access to unambiguous speed coding. 'Roughness constancy' is observed when perceptual judgments about the roughness of surfaces are robust to changes in scanning speed (Katz, 1925 cited in Lederman, 1974; Lederman, 1974, 1983; Lamb, 1983; Meftah et al., 2000, Yoshioka et al., 2011). While proprioceptive input is used when available (Yoshioka et al.), roughness constancy persists even when the hand does not move and the surface is varied in speed (Katz, 1925 cited in Lederman, 1974; Lederman, 1974, 1983; Lamb, 1983; Meftah et al., 2000, Yoshioka et al., 2011), suggesting that speed cues used to produce roughness constancy can be gleaned from the relative motion between the surface and the skin.

Support for speed as the perceptual primitive is provided by a plausible model of neural speed coding in which speed is calculated from the distance and time between successively stimulated primary afferents whose receptive fields lie along the path of the surface motion (Darian-Smith & Oke, 1980). Once speed is determined it is then used to compute the spatial period of the surface. Tremblay et al. (1996) suggested a similar sequence – that SI neurons sensitive to changes in speed but not surface roughness might be used to produce an unambiguous representation of roughness in the cortex. Darian-Smith and Oke's (1980) model of speed coding relies on a *labelled line* account of spatial coding in the nervous system in which information about the spatial organisation of the receptive fields of different afferents is available i.e. each afferent is 'labelled' with its location. Evidence for labelled line spatial coding comes from studies showing that electrical stimulation of both peripheral (Ochoa & Torebjörk, 1983) and cortical (Penfield & Boldrey, 1937) tactile neurons produce localised subjective sensations, with participants able to consistently locate the site of sensation on the skin. This account of speed coding also requires precise timing of spike events across different primary afferents. This is evident in the neural responses of fast adapting primary afferents whose action potentials are precisely phase locked to the cycle of vibration (Johansson et al., 1982b; Johnson, 1974; Talbot et al., 1968), and to the timing of surface features that cross the receptive field (Darian-Smith & Oke, 1980; McIntyre, Holcombe, Birznieks, & Seizova-Cajic, 2012; Morley & Goodwin, 1987).

Two cues to tactile motion were present in the stimuli used: 1) the stimulation of successive positions on the skin along the path of the motion, and 2) lateral skin stretch. This chapter did not examine the relative contributions of each of these cues to perceived speed or the strength of adaption, but either or both could have played a role. While it is clear that there are differences in the successive positions cue that vary with speed (the time between stimulation of two points is shorter for a faster speed), the stretch cue may also vary with speed, and this may have contributed to the observed effect of adapting speed on the strength of the adaptation.

The results presented here provide evidence that the tSAE varies in strength with the adapting speed, and an intensive speed code is favoured over a speed tuning model because of the observation that higher adapting speeds produce a stronger tSAE than adapting speeds that match the speed of the test stimulus. The adaptation that causes the tSAE occurs in neurons that code the speed of the stimulus, independent of the spatial period of the surface or the temporal frequency of the ridges traversing the skin.

Chapter 4: The effect of adapting speed on the tactile motion aftereffect

4 .1 Introduction

Early investigations of tactile adaptation sought to find a tactile correlate of the visual motion aftereffect (here called 'vMAE'), a robust illusion in which adapting to motion in the visual field produces a subsequent perception of motion in the opposite direction when viewing a static or flickering test stimulus (Addams, 1834; Levinson & Sekuler, 1976; Mather, 1980; Purkinje, 1820, 1825, cited in Mather, Verstraten, & Anstis, 1998; Wohlgemuth, 1911). These early studies searched for a tactile equivalent of this illusion (a 'tactile motion aftereffect' or 'tMAE') by adapting to surface motion across the skin and testing for aftereffects with a static surface (Hazlewood, 1971; Hollins & Favorov, 1994; Lerner & Craig, 2002; Planetta & Servos, 2008; Thalman, 1922; Wohlgemuth, 1911). However, they typically found only a weak or unreliable aftereffect, with the illusory motion perceived in multiple directions. This raised questions about the extent to which motion processing mechanisms are similar in touch and vision.

Only recently has an experimental paradigm been identified for eliciting a reliable tMAE (Konkle et al., 2009; Watanabe et al., 2007). Watanabe et al. (2007) had observers feel the tips of three fixed pins made of piano wire, which were vibrated to stimulate different points on the skin surface. By vibrating successive positions on the skin, Watanabe et al. created tactile apparent motion. Their test stimulus, which they used to check for the tMAE following adaptation to apparent motion, was *dynamic* – the piano wires were vibrated at different temporal offsets. The result was a bias to perceive motion in the opposite direction to the adapting stimulus, a *negative* aftereffect. This dynamic tMAE produces illusory motion that is both reliable and consistent in its direction.

The choice of a dynamic test stimulus was likely a critical factor in reliably eliciting a motion aftereffect. Theories of visual motion coding proposed to explain the vMAE claim that perceived direction is determined by relative neural activity coding different directions of motion, and exposure to sustained motion in one direction will selectively adapt neurons preferring that direction (Levinson & Sekuler, 1976; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Sutherland, 1961). According to one such model, the distribution shift model, when the test stimulus is viewed, the weighted average of neural responses signal the direction opposite the adapting motion. This model can explain MAEs (visual or tactile) when the test stimulus is dynamic, but if the test stimulus is stationary it also requires that the relevant neurons have a resting firing rate above zero. Otherwise, unadapted neurons will not respond any more to the stationary test stimulus than adapted neurons (Mather, 1980).

Unlike the visual cortices, the primary somatosensory cortex (SI) has very few direction selective neurons with a high resting discharge rate (Costanzo & Gardner, 1980; Hyvärinen & Poranen, 1978). In one study (Costanzo & Gardner, 1980), only 7% of motion sensitive neurons were described as ‘opponent’ – direction selective cells with a high resting discharge rate that increase their activity in response to motion in one direction across the receptive field (the preferred direction), and reduce their activity in response to motion in another direction (the anti-preferred direction). Because the majority of neurons in SI are non-opponent, a dynamic test stimulus may be required to excite them and reveal a change in the weighted average direction signal due to adaptation.

In the experiments presented in this chapter, the optimal conditions for producing the dynamic tMAE are investigated in order to reveal potential underlying neural mechanisms. This approach has been used in vision, resulting in the finding that the dynamic vMAE depends on the speed of the adapting motion (Ashida & Osaka, 1995), and this effect depends on the flicker rate of the test stimulus (Alais, Verstraten, & Burr, 2005). Fast adapting speeds produced the strongest vMAEs (measured by duration) with quickly flickering tests, while slower adapting speeds produced the strongest vMAEs with test stimuli that flickered more slowly (Alais et al., 2005). This result, in which a degree of correspondence between the adapting and test stimuli yielded the strongest aftereffect, is called *tuning*. In this example, the tuning suggests at least two neural channels of visual motion processing, one sensitive to (and optimally adapted by) high speeds and another sensitive to slow speeds.

In the experiments described here, the strength of the tMAE was tested for its sensitivity to adapting speed. The goal was to determine whether the neurons that code direction of tactile motion show speed tuning, similar to visual neural populations that code direction of visual motion revealed by the speed tuning of the vMAE (Alais et al., 2005), or if an alternate coding of speed is present, such as an *intensive speed code*, in which the neurons increase their firing with increasing speed.

Evidence for an intensive speed code was reported for perceived speed of tactile motion in another tactile aftereffect, the tactile speed aftereffect (tSAE), in which perceived speed decreases following adaptation to motion (Experiments 4 and 5, Chapter 3). The tSAE was shown to depend on the speed of the adapting stimulus such that greater adapting speeds produced stronger aftereffects. The adaptation stimuli for both the tSAE and the tMAE are similar (although in the experiments reported here, an apparent motion stimulus is used instead of a natural surface), and are likely to affect common neural populations. It is possible that direction is jointly coded in the same neurons that code speed, in which case one would expect the tMAE to be sensitive to speed in the same way, showing an intensive code rather than tuning. Indeed, there are direction selective neurons in SI with firing rates that increase monotonically with speed (Pei et al., 2010; Ruiz et al., 1995; Whitsel et al., 1978, 1972).

On the other hand, the tMAE reveals selective adaptation of a given direction, whereas the tSAE does not. Experiments 1 and 2 (Chapter 2) tested for direction sensitivity of the tSAE and found no evidence for it, that is, the strength of the tSAE was similar regardless of wether the adapting stimulus matched the direction of the test, or was in the opposite direction. This result raises the possibility that speed and direction of tactile motion may not be jointly coded in the same neurons.

Comparing the sensitivity of these two aftereffects (the tSAE and the tMAE) to adapting speed can help to reveal the shared and diverging neural pathways for coding speed and for coding direction of tactile motion. In order to test the tMAE for an intensive code, multiple adapting speeds were used, and in order to test for speed tuning, these were combined with different test speeds. To best elicit the tMAE, a dynamic test stimulus was used, one with no net objective direction signal. It was composed of interleaved local motion in two directions simultaneously – in the same, and the opposite direction to the adapting motion. When referring to ‘speed’ of the test stimulus, this means the speed of these motion components. Figure 4.1 shows the predicted results for intensive speed coding, for speed tuning, and for a combined model in which both intensive coding and speed tuning mechanisms are present.

4 .2 Method

Participants

Volunteers were recruited from three groups: inexperienced naïve students, colleagues experienced in psychophysical observation but naïve to the hypotheses of the study, and investigators. Participants provided informed written consent, which was approved by the human ethics committee of the University of New South Wales and conformed to the Declaration of Helsinki. Inexperienced students were compensated for their time at a rate of AU$20 per hour.

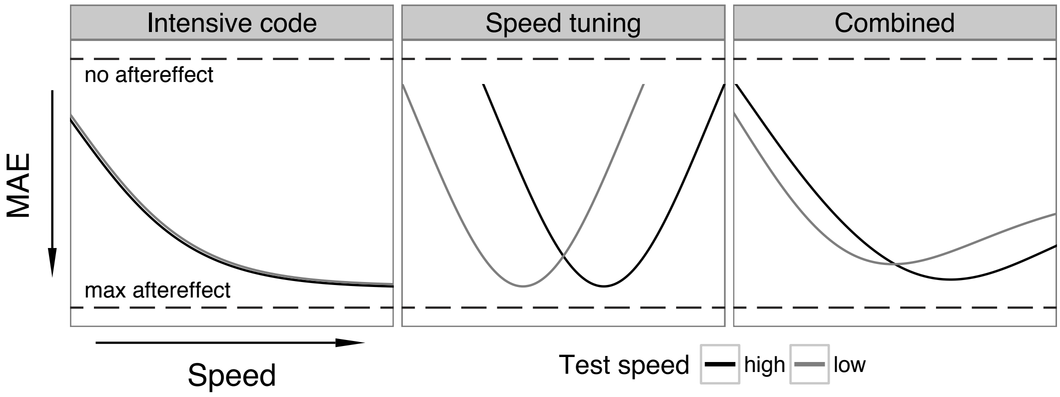

Figure 4.1. Three possible outcomes of the experiment, showing the predicted results of an intensive speed code, speed tuning, or both. MAE plotted as a function of adapting speed, on arbitrary scales. The MAE is given a negative direction, with lower values indicating a stronger aftereffect, to reflect a negative MAE in the direction opposite to the adapting motion. Both high (black lines) and low (grey lines) test speeds are shown. *Left:* An intensive speed code results in an aftereffect that increases its strength monotonically with increasing adapting speed, and is the same for both test speeds. *Middle:* Speed tuning results in the strongest aftereffect occurring when there is a correspondence between the speeds of the adapting and test stimuli, the low test speed produces its strongest aftereffect at a lower speed than does the high test speed. *Right:* Intensive speed coding and speed tuning may be present at different stages of tactile motion processing, and both affected by adaptation. In this case, the aftereffect would reflect both mechanisms.

Nine volunteers participated in Experiment 6, but two were excluded because the recorded responses were not as frequent as required, resulting in subsampling of their perceptual states (see Data Analysis). The remaining 7 participants included 5 naïve, the author (SM) and one co-investigator (thesis supervisor AH). Nine volunteers also participated in Experiment 7, including 7 naïve, the author and one co-investigator (thesis supervisor TSC). Three volunteers participated in both experiments (PG, WC and author SM).

Apparatus

Stimulation was applied using the tactile array of an Optacon device (Telesensory Systems Inc., Palo Alto, CA). The tactile array consists of 144 thin rods (250 μ m contact area) arranged with 6 columns and 24 rows. Rows are spaced 1.18 mm apart and columns 2.29 mm apart (point-to-point). The total area of the array is 27.2 x 11.4 mm. The rods moved vertically to indent the skin, and caused no lateral skin stretch. Each protraction of a rod has a fixed temporal profile with a protraction time of 2ms. The speed and amplitude of the protraction are independent of the frequency of activation (maximum 230Hz). The maximum amplitude is 65µm (Bliss, 1967), although this is likely to vary with exact positioning relative to the skin.

Participants rested their right arm on a table, supported by a cushion with their hand held palm-up, and the tactile array was lowered to apply stimulation to the distal two segments of the participant's right index finger. The index finger was prevented from moving by sticking it to a finger support using Blu-Tack (Bostik, Paris-La Défense, France) in Experiment 6 and Play-Doh (Hasbro Inc., Rhode Island, US) in Experiment 7. The Optacon was mounted onto one end of a cantilever. A counterweight on the other end of the arm was adjusted to control the normal force applied by the tactile array and its casing. This was maintained at approximately 30gm-wgt, measured from a height of 10cm, which was approximately level with where the participants' fingers were positioned. This setting was determined to be comfortable and provide reasonable contact with the rods, while avoiding problematic damping of the vibration.

Participants wore earplugs and headphones through which white noise played to mask the sound of the vibrating rods. The stimulus was not visible to participants, so no visual cues were available. Participants responded by pressing buttons with the left hand.

Stimuli

The adapting motion stimulus was created by activating rods in successive positions of the tactile array in a proximal-to-distal direction or vice versa. The test stimulus was identical to the motion stimulus except that odd columns moved in one direction (randomly determined for each trial) and even columns in the other. This created a balanced stimulus with equal motion signals in each direction.

Rather than present a moving "bar" stimulus like some previous studies using apparent motion (Essick, Rath, et al., 1996; Gardner & Sklar, 1994), the activated columns were phase-offset so that the spatial area of activation was not too narrow (clumped) at any given time. There were two reasons to avoid this clumping: first, so that the stimulus could be continuously loop for the desired duration without providing any strong apparent motion cues opposite to the intended direction. If a bar stimulus had been used, its reappearance on the opposite side, after reaching the edge of the array, would have provided a strong cue for apparent motion in the opposite direction. With our phase-shifted arrangement, the majority of columns signalling motion in the intended direction presumably overwhelmed any opposite-direction signal due to the reappearance of any one stream (See Figure 4.2).

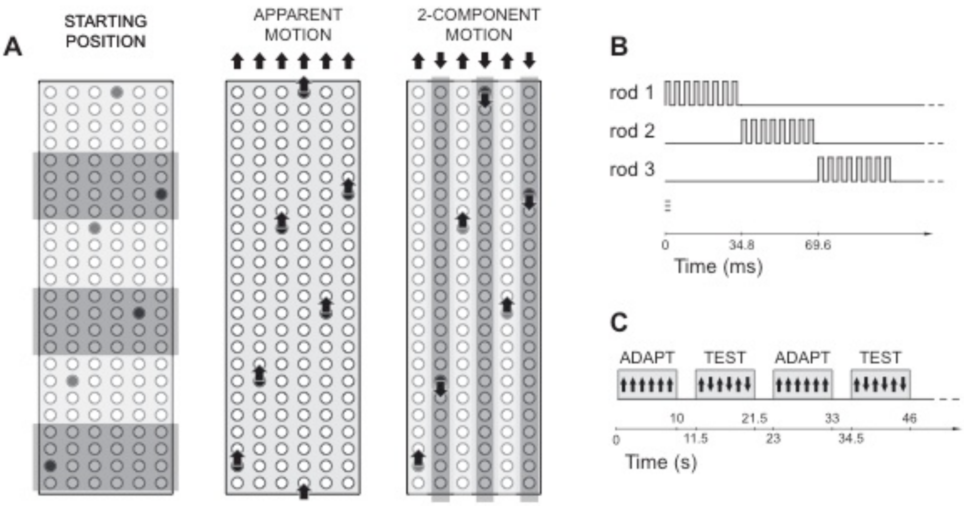

Figure 4.2. Grid representation of the Optacon and the activation patterns used. A: The Optacon array is represented with a circle for each rod. A filled circle indicates an activated (vibrating) rod. *Left: Example starting position of the motion stimulus.* The Optacon was divided into six 4-row sections. In the starting position, a rod from a different column was activated in each of these sections, randomly determined. The specific row within each section to be activated was also randomly determined. *Middle: The motion stimulus.* Rods in each column were successively activated to produce apparent motion. The arrows indicate the rods to be activated in the next step of the stimulus sequence. When activation reached the edge of the array, it started again at the other edge (in the example shown here, this is about to happen in column 4). *Right: The test stimulus.* As in the motion stimulus, rods in each column were successively activated, but here, half the columns stepped in one direction and the other half stepped in the other direction. B: The first three rods in a column to be activated are shown, in the temporal sequence used to produce motion at 34mms^{-1}. C: The stimulus sequence in Experiment 6. Each run consisted of 10 seconds continuous presentation of the adapting stimulus followed by 10 seconds of the two-component test stimulus. For each condition, this sequence was presented ten times, with 1.5s breaks separating the adapting and test stimuli.

The second reason for using phase-shifted streams of motion was so that the adapting motion and ambiguous test stimuli would be qualitatively more similar. Because the test stimulus included simultaneous motion in opposite directions, the streams could not all move in phase, and a bar stimulus would have been broken. Phase-shifting the streams for both motion and test stimuli meant they were more difficult to distinguish.

The starting position was randomly determined for each column, creating independent streams of motion (Figure 4.2A), which all moved at the same speed. The spacing of these motion streams was constrained thus: the length of the array was divided into equal sections, one for each column used (six in Experiment 6, four in Experiment 7), and each column's starting position fell into a different section. Repeatedly activating the adjacent rods (within a column) in sequence created apparent motion (Figure 4.2B).

The speed of motion is determined by the temporal delay between activating one rod and the next. The inter-stimulus onset interval (ISOI) is defined as the time interval between the onset of one stimulus (vibrating the rod) and the onset of the next (Figure 4.2B). While the frequency of the apparent motion steps varied with speed, (e.g. the 68mms^{-1} motion stepped twice as often, 57 steps/sec. as the 34mms^{-1} motion with 27 steps/sec), the vibration frequency at a given location was always the same (230Hz), and therefore is unlikely to have interfered with the experimental manipulation. Furthermore, the perceptual features of apparent motion have been shown to be similar regardless of whether vibration, point stimuli or electrocutaneous stimulation is used (Hill & Bliss, 1968; Sherrick & Rogers, 1966), and also similar to motion of real surfaces (Bensmaïa et al., 2006; Essick, Rath, et al., 1996; Lerner & Craig, 2002). Additionally, over the whole run, the amount of stimulation (number of protractions) at a given skin location was always the same. The range of speeds used in Experiments 6 and 7 were chosen based on pilot data that found these speeds produced a compelling apparent motion illusion, for which the direction could be reliably discriminated. The upper end of the speed range was limited by the temporal resolution with which the device could be driven.

4 .3 Experiment 6

The aim of this experiment was to distinguish between speed tuning and an intensive code for speed in the mechanisms underlying perceived direction of tactile motion. The strength of the tMAE was measured following adaptation to motion at a variety of speeds. Speed tuning predicts that the strongest aftereffect will be observed when the speed of the adapting and test stimuli correspond, whereas an intensive code predicts that the strength of the aftereffect will increase monotonically with increasing adapting speed. Five adapting speeds (23, 34, 45, 68, 136mms^{-1}) and two test speeds (34, 68mms^{-1}) were used, and adapted in both distal and proximal directions with each speed. To produce these speeds, the ISOI was varied (52.2, 34.8, 26.1, 17.4, 8.7ms), which also determined the step frequency (19, 29, 38, 57, 115 steps/sec). In addition, the perceived direction of the two test stimuli was tested without adaptation. If the tMAE were speed tuned, one would expect to find the that the strongest effect observed with the 34mms^{-1} test stimulus to be achieved when the adapting stimulus also moved at 34mms^{-1}, and that the strongest effect observed with the 68mms^{-1} test stimulus to be achieved when the adapting stimulus also moved at 68mms^{-1}. If instead, the tMAE has an intensive code for speed, one would expect the strength of the effect to increase with adapting speeds from 23 to 136mms^{-1} regardless of test speed.

Procedure

Each adapt-test stimulus combination was tested in a separate session (lasting 5 minutes), with at least one hour between sessions to allow time for recovery. This prolonged recovery time was designed to avoid the influence of each adapt-test stimulus on responses to the subsequent tests. Within each run, the adapting stimulus was presented for 10s, followed by the test stimulus for 10s and this sequence was presented ten times, with 1.5s breaks between stimuli (see Figure 4.2C). In the sessions that measured perception of the test stimuli without adaptation, participants felt the inactive array (no vibrating rods) in the periods in which the adapting stimulus was normally presented. The order in which the sessions were presented was randomised for each participant.

Because of individual differences in finger shape and size, it could not be ensured that all rods had equally good contact with the skin. This was a concern for the test stimulus where equally strong motion signals in both the distal and proximal directions were desired. To avoid any uneven contact incidentally resulting in a stronger stimulation of motion in one direction compared to the other, after every two seconds of stimulation with the test stimulus, the direction of each column switched to the reverse. This meant that over the course of a 10s test period, any given column would spend the same amount of time moving proximally and distally.

Participants responded to the stimulus by continuously reporting the perceived direction of motion by pressing one of three buttons: 1) ‘distal’, if the stimulus appeared to move away from their body, 2) ‘proximal’ if it appeared to move towards their body, or 3) ‘unclear’ if they could not judge the direction of motion. Continuous responses were used rather than single responses to each stimulus in order to capture any changes in the percept during its presentation. The ‘unclear’ option was important for testing whether the adapting motion stimulus produced a clear motion percept. It also allowed for the possibility that participants might perceive the test stimulus accurately, with neither direction dominant. Several previous studies that investigated the static tMAE and found inconsistent results used an open-ended question about how the test stimulus was perceived. In contrast, studies that investigated the dynamic tMAE and found a consistent negative aftereffect used forced-choice tasks. The inclusion of an 'unclear' response option was important for testing whether the question posed to participants played any role in the discrepancy, and also whether the aftereffect was a compelling motion percept.

Naïve participants were not aware of the nature of the adapting and test stimuli, and were instructed to continuously monitor their perception and press the appropriate button as soon as the direction of motion appeared to change. Additionally, if the perceived direction remained the same for long periods, they were instructed to press the same button again, making a response at least every 2 seconds. Based on observations made during piloting, participants were also warned that their perception might change so rapidly that their button presses could not keep up. If they experienced this, participants were instructed to report everything that they felt, in order, and not to worry if their responses lagged slightly behind.

Data Analysis

The dynamics of perceived direction throughout the presentation of each adapting and test stimulus were considered. At the stimulus onset, before any buttons were pressed, the perceptual state was unknown. Because of this, the first percept was considered to begin with the first button press. Responses in the 1.5s break between stimuli were considered to reflect the perceptual state at the end of the last stimulus. Perceptual state was interpolated at 0.1s intervals from button presses, such that the perceptual state at any given time was taken as that corresponding to the most recent button pressed (although button presses were usually much less frequent than this resolution suggests, it was necessary to avoid losing information about some rapid perceptual switches from one state to another, then back to the first). The proportion of the duration out of the total response time spent in each perceptual state (distal, proximal, unclear) was then calculated for each stimulus presentation. The Direction Index (DI) was then calculated from the three perceptual states as a single measure of the perceptual direction bias, according to Equation 1:

Equation 1

$$\boldsymbol{DI = \frac{dur(dist) - dur(prox)}{dur(dist) + dur(prox) + dur(uncl)}}$$

Where *dur(dist)* is the duration for which distal motion was perceived, *dur(prox)* is the duration for which proximal motion was perceived, and *dur(uncl)* is the duration for which the stimulus was perceived as unclear. Note that the denominator is the total duration for which any response was given, and excludes the time for which the observer had not yet responded. Therefore Equation 1 is identical to:

Equation 2

$$\boldsymbol{DI = p(dist) - p(prox)}$$

Where *p(dist)* is the proportion of time for which distal motion was perceived, and *p(prox)* is the proportion of time for which proximal motion was perceived. DI varies between -1 and 1, with 1 indicating the strongest possible bias to perceive distal motion, and -1 indicating the strongest possible bias to perceive proximal motion. A DI of 0 indicates a neutral percept in which there was equal bias to perceive distal or proximal motion.

Trials in which 4s or more elapsed with no response for a given stimulus were eliminated. Two participants were excluded from data analysis because on more than five per cent of trials insufficient button presses were recorded. Data are reported for the remaining seven participants.

The first button press for a stimulus had a median latency from the stimulus onset of 1.1s (interquartile range: 0.7 – 1.5s). Given this observed response latency at onset, our decision to treat responses in the 1.5s break period as reflecting perception of the tail end of the previous stimulus was reasonable.

Results

Effect of adaptation

There was a clear effect of adaptation in which the test stimulus was usually perceived to move in the opposite direction to the preceding adapting motion. Figure 4.3 shows the DI of the test stimulus following each adapting stimulus for each participant. Most of the points in the left-hand side of the panel for each participant (proximal adaptation) fall in the top half of the graph, indicating a distal motion aftereffect, while most of the points in the right-hand side of the panel (distal adaptation) fall in the bottom half of the graph, indicating a proximal motion aftereffect.

For several participants (AH, SM, SYL, WC), the DI of the aftereffect was close to or at ceiling for several adapting speeds (Figure 4.3), indicating that the tMAE was so strong in these cases that the participants almost always felt motion in the direction opposite to the adapting speed throughout the entire 10s test period. The conditions of this experiment were therefore very well suited to producing a tMAE. In testing for variations in the strength of the aftereffect, the individual differences in the aftereffect following adaptation in different directions had to be accounted for. This is visible in Figure 4.3; for example, for participant WC, the aftereffect was at ceiling following adaptation in the proximal direction, but was weaker following distal adaptation, indicating a 'distal' response bias (WC also had a bias to respond 'distal' to the test stimulus when it did not follow adaptation – see section below for further discussion).

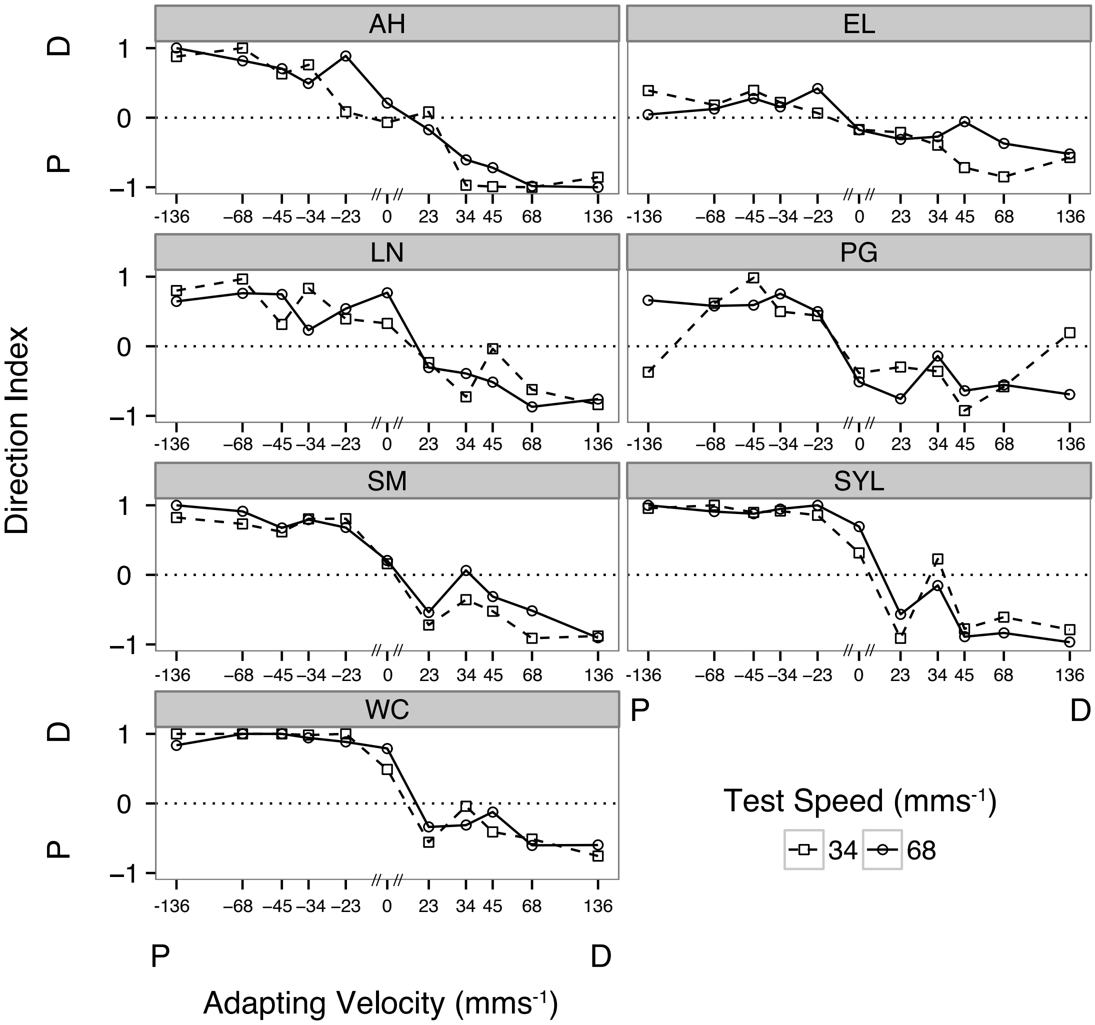

Figure 4.3. Individual data showing perceived direction of the two-component test stimulus following adaptation, Experiment 6. In most cases, the perceived direction of the test stimulus is the opposite of the preceding adapting motion. The Direction Index (DI, see text for its calculation) is shown on the ordinate, with positive values indicating perceived direction was distal, negative values indicating perceived direction was proximal, and a value of 0 indicating a neutral percept. The adapting speed is shown on the abscissa on a log scale, with negative values indicating adaptation in the proximal direction and positive values indicating adaptation in the distal direction. The two test speeds are shown as separate lines: 34mms^{-1} (dashed lines with squares) and 68mms^{-1} (solid lines with circles).

In order to account for any directional biases present, the data from adaptation to both directions were combined, and a *DI difference score* was computed. That is, the DI following proximal adaptation was subtracted from the DI following distal adaptation for each combination of adapting and test speeds. The DI difference score indicates the overall strength of the aftereffect: a score of 0 indicates no effect of the direction of the adapting stimulus on the perceived direction of the test stimulus. A negative value (minimum = -2) indicates an aftereffect in the expected direction (opposite to the adapting motion), and a positive value (maximum = 2) indicates an aftereffect in the unexpected direction (same as the adapting motion).

The median DI difference score for the test stimulus was -1.25 (on a scale -2 to +2; 95% confidence interval: -1.38, - 1.27), which was significantly less than 0 (Wilcoxon signed rank test, W = 8, $p < .001$), indicating that overall, the aftereffect was in the direction opposite to the adapting stimulus, as expected. A repeated-measures ANOVA was carried out with two factors: test speed and adapting speed. Because the DI difference score is bounded between -2 and 2, it is inappropriate for linear modelling. To address this, the DI difference score was transformed to span negative infinity to positive infinity by first rescaling it to vary between 0 and 1, and then applying the logit transformation (inverse of the logistic). This transformed variable was then used as the dependent variable in statistical analyses reported below. However, untransformed DI difference scores are reported for ease of interpretation. There was a significant main effect of adapting speed ($F_{4,24} = 3.7$, $p = .017$, $\eta^2 = .38$), but there was no significant main effect for test speed ($F_{1,6} = 0.1$, $p = .736$, $\eta^2 = .02$), nor was there a significant interaction between adapting speed and test speed ($F_{4,24} = 1.7$, $p = .187$, $\eta^2 = .22$).

The relationship between the DI difference score and adapting speed is shown in Figure 4.4. There is no evidence in the pattern of the data for speed tuning of the tMAE. That is, the strongest aftereffect does not appear to depend on the test speed. However, the strength of the tMAE appears to increase with adapting speed. A linear contrast was conducted on the transformed DI difference score to test this effect, with contrast weights reflecting the spacing of the log of the adapting speeds used in the experiment. The contrast was significant ($F_{1,6}$ = 7.4, p = .035, η^2 = .55), indicating a positive relationship between adapting speed and the strength of the aftereffect. This effect did not significantly interact with test speed ($F_{1,6}$ = 2.7, p = .154, η^2 = .31).

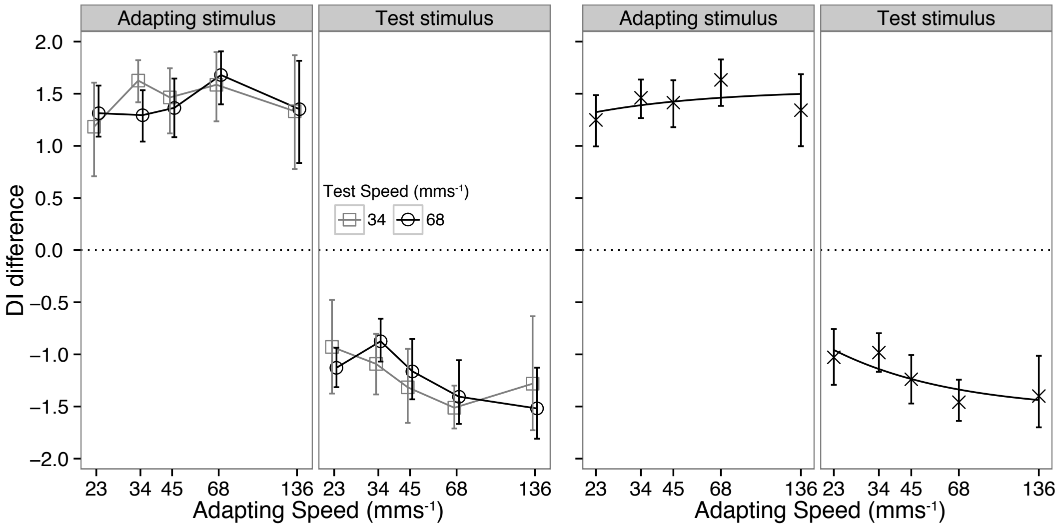

Figure 4.4. Group data showing perceived direction of both the adapting and test stimuli, Experiment 6. The abscissa gives the adapting speed on a log scale. The DI difference score given on the ordinate is an indicator of the directional bias, with a value of 2 being the maximum aftereffect in the direction opposite to the adapting stimulus (see text). For the test stimulus, DI difference indicates the strength of the tMAE, with lower values indicating a stronger aftereffect. *Left:* The mean DI difference scores are plotted separately for each test speed, 34mms^{-1} (grey) and 68mms^{-1} (black). *Right:* Data are averaged across the two test speeds, and the lines show the predicted values from the linear contrast of the transformed DI difference score (see text). Error bars are 95% bootstrapped confidence intervals.

The effect of adapting speed on the strength of the tMAE was evaluated for each participant by applying linear regression to the logit-transformed DI difference scores for the test stimuli (Figure 4.5). For four of the seven participants, the regression was significant with a negative slope indicating that stronger aftereffects were associated with greater speeds, consistent with the group data. Only one participant had a (non-significant) positive slope.

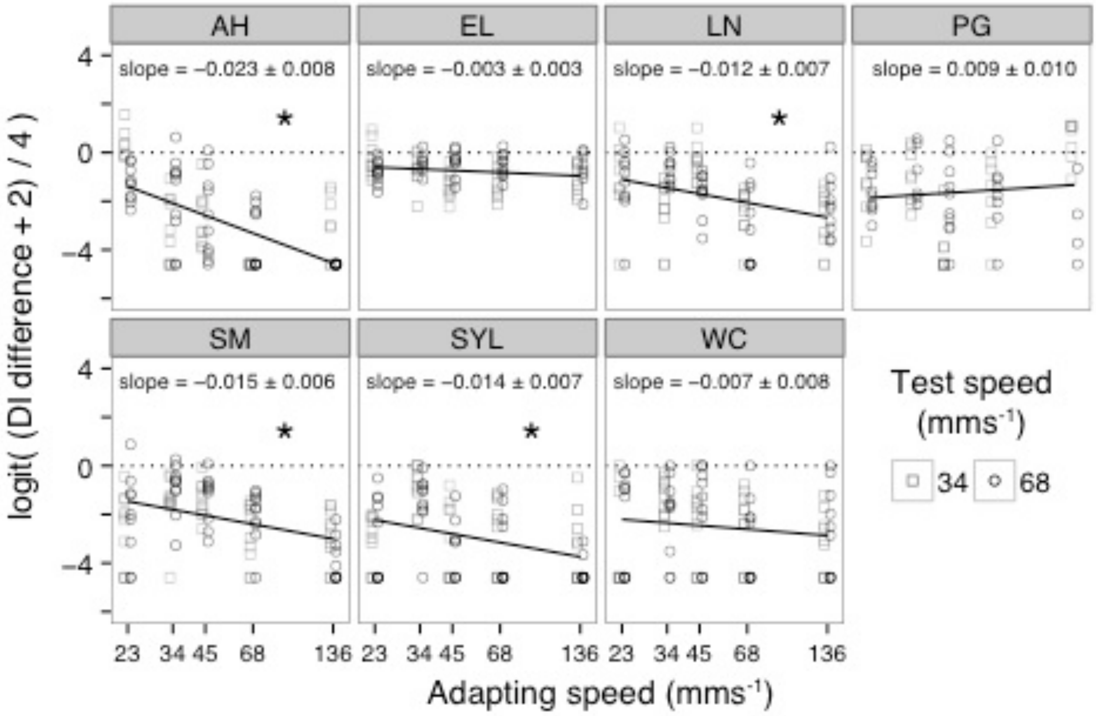

Figure 4.5 The effect of adapting speed on the transformed DI difference scores for the test stimuli, for each participant. Data are shown for each of the ten test periods for each adapt-test speed combination. Semi-transparent plotting has been used so that overlapping data points appear darker. Black lines indicate the regression lines. The slope of the regression line and 95% confidence intervals are given, and asterisks indicate a significant fit ($p < .05$). For the significant fits, the regression models accounted for 11 – 25% of the variance.

Strength of adaptation over time

Because a blocked procedure was used in which each adapting and test speed combination was presented ten times in a row, it was possible to test for any cumulative effects of adaptation duration on the strength of the aftereffect. Figure 4.6 shows the DI difference score for the test stimulus following adaptation by order of presentation (collapsed over adapting and test speed combinations). There was no significant effect of test number on the transformed DI difference score ($F_{9,54} = 0.7$, $p = .697$). Separate analyses for each adapting speed similarly did not reach significance.

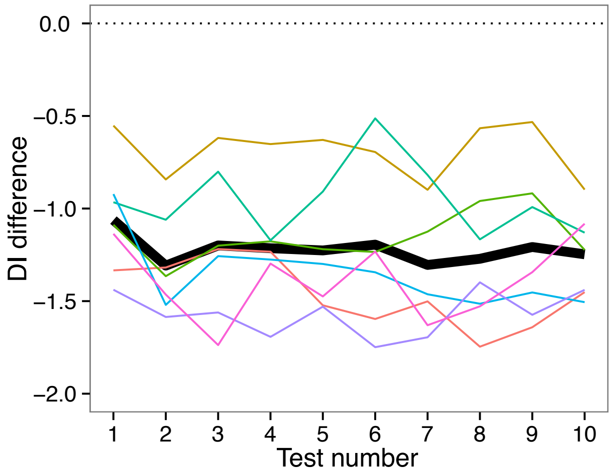

Figure 4.6. The strength of the tactile motion aftereffect over time. The abscissa gives the test number: each successive test followed an additional 10s adaptation to the same stimulus. The DI difference score given on the ordinate is an indicator of the strength of the tMAE, with lower values indicating a stronger tMAE (see text). Coloured lines show the strength of the aftereffect for different participants, and the heavy black line is the group mean.

When only the first test period was considered and the analyses repeated, the results were similar to when the full data set was used, with the same pattern of significant results being observed. Examining the data at a smaller scale, visual inspection of responses did not suggest any particular temporal patterns within the 10s test periods.

Perception of the two-component test stimulus without adaptation

The proportion of time for which the two-component test stimulus was perceived as moving distal, proximal or was unclear is shown in Figure 4.7 for each participant. Three participants (LN, SYL, WC) showed a greater tendency to respond ‘distal’, suggesting that for these participants, the distal component of the test stimulus was stronger than the proximal component. One participant (PG) showed a greater tendency to respond 'proximal'. These biases are unlikely to be due to systematic differences in how different rods contacted the skin because the direction of motion presented at any given skin location varied from trial to trial. The data suggest there may be individual differences in the amount of directional bias present in tactile motion perception.

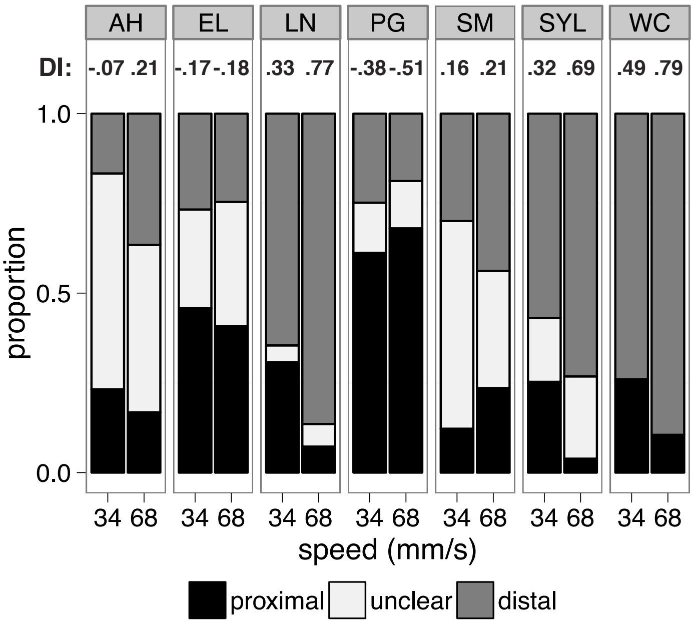

Figure 4.7. Proportion of responses 'distal', 'proximal' and 'unclear' to the neutral, two-component test stimulus. Responses are shown for both speeds of movement for each participant. The calculated DI is shown above the plot, with positive values indicating a primarily distal percept, negative values indicating a primarily proximal percept and values close to 0 indicating a relatively neutral percept (these DI data are also plotted in **Figure 4.3**, at adapting speed = 0).

Perception of the adapting stimuli

The adapting stimuli were apparent motion stimuli with a single unambiguous direction signal (proximal or distal), and it was expected that perceived direction would be at least as clear as it was for the aftereffects perceived with the two-component test stimuli. Subjective reports indicated that this was the case, with unambiguous motion stimuli seeming difficult to distinguish from two-component test stimuli when experiencing an aftereffect (the DI scores for the adapting stimuli are shown in Appendix A, Figure A.1). The median DI difference score for the adapting stimuli was 1.46 (95% confidence interval: 1.33, 1.59), which was significantly greater than 0 (Wilcoxon signed rank test, W = 2485, $p < .001$), the positive sign indicating perceived motion in the correct direction. Compared to the strength of the aftereffect, the strength of the direction percept for the adapting motion was significantly greater (median DI difference = 1.25, paired Wilcoxon signed rank test, W = 1937, $p < .001$). A repeated measures ANOVA indicated that the strength of the direction percept was not significantly affected by speed ($F_{1,6} = 1.9$, $p = .218$). This means that the variations in the strength of the aftereffect due to speed were not caused by variations in the directional discriminability of the adapting stimulus.

Unclear responses

Participants rarely perceived the adapting stimuli (which signalled motion in one direction) as unclear, with the mean proportion at which the adapting stimuli were labelled unclear being 0.16. The two-component test stimulus, with no preceding adaptation, was perceived as unclear at a higher rate of 0.24. However, the two authors (AH and SM) perceived the two-component test stimulus as unclear more often than other participants (at rates of 0.53 and 0.45 respectively), and this may have been due to their knowledge of the stimulus. When considering only the naïve participants, the rate of unclear responses was similar for both the adapting (0.15) and test stimuli (0.14). The low rate at which participants responded that the stimulus was unclear suggests that forced-choice tasks are not required in order to produce a reliable negative aftereffect. However, it is possible that the naïve participants, who were all experienced psychophysical observers accustomed to forced-choice tasks, used a conservative criterion for responding that the stimulus was unclear (or a liberal criterion for choosing a direction).

4 .4 Experiment 7

While no evidence for speed tuning was found in Experiment 6, it is possible that speed tuning might have been detected under different experimental conditions. It is possible that the ceiling effects observed with some participants may have led to an underestimation of the differences in the strength of the tMAE for different adapting speeds. Because of this, Experiment 7 involved several modifications to the design used in Experiment 6 in order to reduce the strength of the tMAE, and reveal any effects of different adapting speeds more clearly.

First, adaptation effects have been shown to increase with adapting time (Goldstein, 1957; Hollins et al., 1990; Sekuler & Pantle, 1967; Wedell & Cummings, 1938), so the stimulus presentation time was reduced to 3s (from 10s) for both the adapting and test stimuli. Second, unique adapt-test stimulus combinations were no longer blocked in separate sessions, but were mixed and presented in a random sequence. This was also designed to reduce the amount of adaptation because on any given trial, the previous trial might have involved adaptation in the same or the opposite direction.

Third, because the differences in tMAE strength in Experiment 6 were evident with the lower adapting speeds, a range including lower speeds was used. The four adapting speeds used were 19, 27, 45 and 136mms^{-1}, corresponding to ISOIs of 69.1, 43.5, 26.1 and 8.7ms, and step frequencies of 16, 23, 38 and 115Hz. In case of broad tuning channels for low and high speeds, test speeds at the extremes of our range were included to maximise the possibility of detecting any speed tuning. The two test speeds were 19 and 136mm^{-1}.

In addition, only the central four columns of the Optacon were used, instead of all six. This was done because the outer two columns had the least reliable contact with the finger, which may have contributed random noise to the data. Finally, Experiment 6 showed that a forced-choice procedure is unlikely to have artificially generated the reliable negative tMAE found in previous studies that used a dynamic stimulus as evidenced by the similarly reliable negative tMAE observed when 'unclear' responses were allowed. For this reason, a two alternative forced choice procedure was used because it improved the efficiency of data collection.

The aim of Experiment 7 was to test the effects of adapting speed on the tMAE under a different set of conditions to Experiment 6. The goal was to test whether there is any evidence for speed tuning of the tMAE under these different conditions, and also to test whether the intensive code for speed observed in Experiment 6 is robust.

Procedure

Participants did six 10-minute runs, in which the test speed (19, 136mms^{-1}), the adapting speed (19, 27, 45, 136mms^{-1}, none) and the adapting direction (proximal, distal) were randomly selected for each trial. For each participant, each combination of adapting and test speeds was repeated 48 times in total (24 times for each adapting direction). In each trial, the adapting stimulus was presented for 3s, followed by the test stimulus for 3s. The stimuli were separated by breaks of 1s in which the rods did not vibrate. In the trials without an adapting stimulus, the test stimulus was presented directly after the test stimulus of the previous trial (Figure 4.8). Participants reported the perceived direction of each 3s stimulus (both the adapting and test stimuli) as either 'distal' or 'proximal' by pressing a button.

Results

Consistent with Experiment 6 results, a clear tMAE is evident, with perceived direction of the two-component test stimulus being biased toward the direction opposite to the preceding adapting motion. Figure 4.9 shows the proportion of stimuli that each participant reported as distal motion following adaptation to either distal or proximal motion. The proportions following proximal adaptation are generally higher than those following distal adaptation indicating an aftereffect in the opposite direction to the adapting motion, as expected. While in some cases, ceiling effects were still observed (EOM, WC), they appear to be fewer than in Experiment 6.

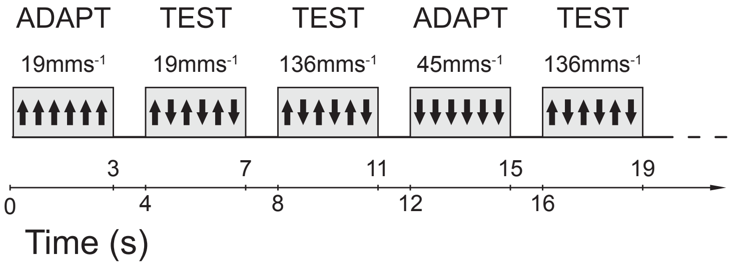

Figure 4.8. An example stimulus sequence used in Experiment 7. Each trial consisted of 3 seconds of the adapting stimulus followed by 3 seconds of the two-component test stimulus. There were additional 'catch' trials with only a test stimulus and no preceding adapting stimulus (shown here at the third stimulus presentation). Each combination of adapting speed (19, 27, 45, 136mms^{-1}, none) and test speed (19, 136mms^{-1}) was repeated 48 times in a random order. Breaks of 1.5s separated the stimulus presentations.

Unlike in Experiment 6, some participants had DIs close to 0 for test stimuli that followed adaptation in the distal direction. This may be a result of two factors: one, a bias to perceive the test stimulus as moving distally, as seen where the adapting speed equals 0 (i.e. no adaptation), an effect that was also observed in Experiment 6; and two, the deliberate efforts to reduce the strength of the tMAE to avoid the ceiling effects observed in Experiment 6. It is possible that the weaker distal adapting stimulus that produces a proximal tMAE is competing with the distal bias, resulting in a net neutral percept. It should be noted that the ceiling effects observed in both experiments predominantly occurred with distal tMAEs (Figure 4.3, Figure 4.9).

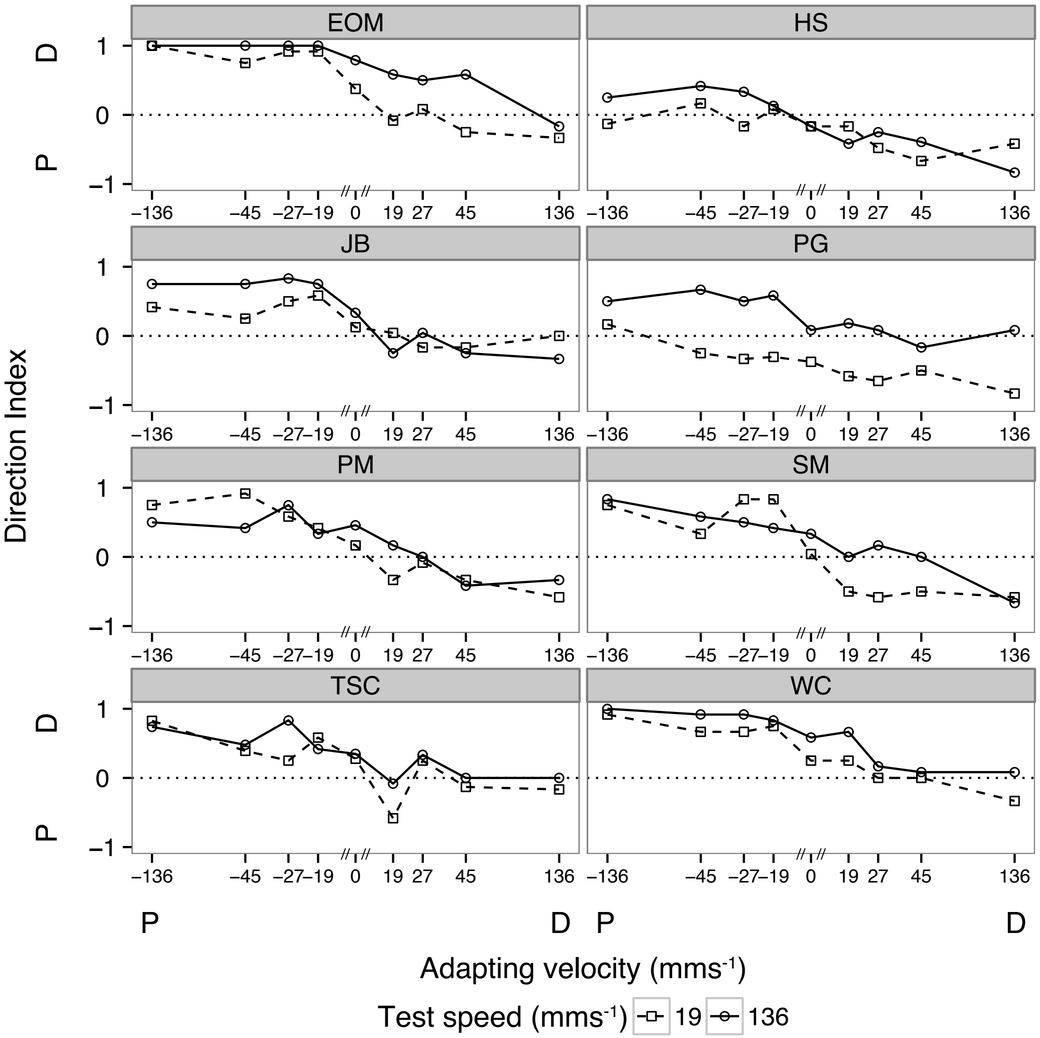

Figure 4.9. Individual data showing perceived direction of the two-component test stimulus following adaptation, Experiment 7. Same format as **Figure 4.3**.

Similar to the analysis done for Experiment 6, the DI difference score was calculated as in Equation 2, and for the repeated measures ANOVA, was rescaled and logit transformed. The median DI difference score for the test stimulus was -0.71 (95% confidence interval: -0.82, -0.62), which was significantly less than 0 (Wilcoxon signed rank test, W = 0, $p < .001$), indicating that the aftereffect was in the predicted direction, opposite to that of the adapting stimulus. Figure 4.10 shows the effect of adapting speed on the strength of the aftereffect. A repeated measures ANOVA revealed a significant effect of adapting speed ($F_{3,21} = 8.0$, $p = .001$, $\eta^2 = .52$), but test speed had no significant effect ($F_{1,7} = 0.6$, $p = .454$, $\eta^2 = .08$), nor was there a significant interaction ($F_{3,21} = 0.7$, $p = .544$, $\eta^2 = .10$).

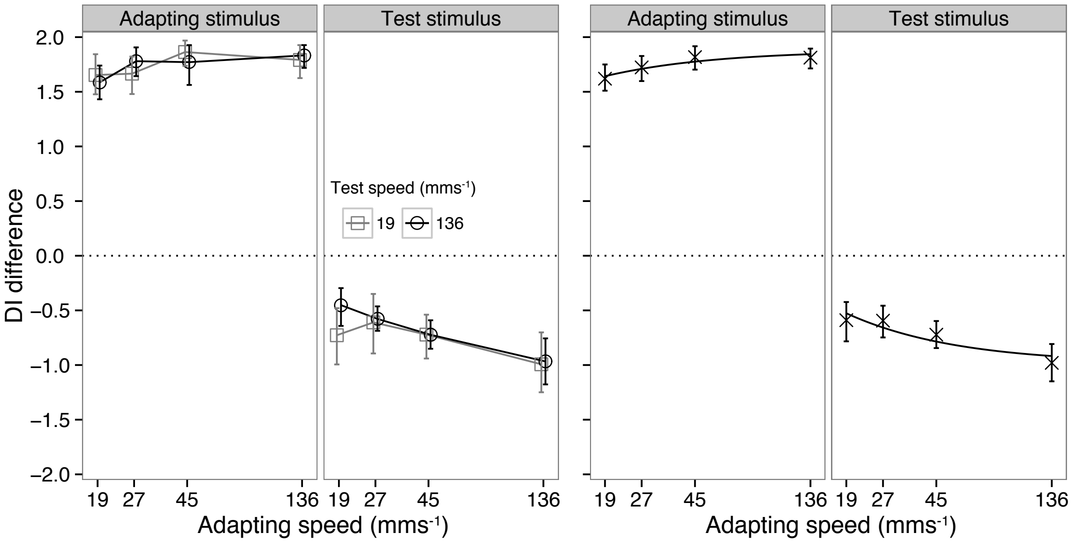

Figure 4.10. Group data showing perceived direction of both the adapting and test stimuli, Experiment 7. Same format as **Figure 4.4**.

The relationship between DI difference score and adapting speed is shown in Figure 4.10. Similar to Experiment 6, no evidence was found for speed tuning of the tMAE. That is, even under a modified experimental paradigm and testing a range including slower speeds, the strength of the aftereffect does not appear to depend on any correspondence with the test speed. Also similar to Experiment 6, the strength of the tMAE increased with adapting speed. A linear contrast was conducted on the transformed DI difference, with contrast weights reflecting the spacing of the log of the adapting speeds used in the experiment. The contrast was significant ($F_{1,7} = 24.5$, p =

.002, $\eta^2 = .78$), indicating a positive relationship between adapting speed and the strength of the aftereffect. This effect did not significantly interact with test speed ($F_{1,7}$ = 0.6, p = .464, $\eta^2 = .08$).

Perceived direction of adapting stimuli

The median DI difference for the adapting stimuli was 1.75 (95% confidence interval: 1.70, 1.83), which was significantly greater than 0 (Wilcoxon signed rank test, W = 2080, p < .001). The magnitude of the DI difference score for the test stimulus (-0.71) was significantly less than that of the adapting stimulus (paired Wilcoxon signed rank test, W = 2080, p < .001). A repeated measures ANOVA found that there was no significant effect of speed ($F_{1,7}$ = 3.6, p = .099).

First trials

In the experimental paradigm described here, using an apparent motion stimulus, adapting to unambiguous motion and testing perceived direction with the two-component test stimulus with motion in both directions, the tMAE was remarkably robust. Taking only the first trial of each of the six sessions for each participant, the test stimulus was perceived as moving in the direction opposite to the adapting stimulus 74% of the time.

4 .5 Discussion

The results reported here provide evidence that a reliable tMAE can be obtained on the finger with a variety of combinations of adapting and test speeds over the range 19 – 136mms^{-1}. The tMAE is sensitive to the speed of the adapting stimulus, with greater speeds causing a stronger bias to perceive motion in the direction opposite to the adapting motion. To our knowledge, this was the first study to look for speed tuning of the tMAE. No evidence for it was found; the strength of the tMAE did not appear to be affected by the extent to which the speeds of the adapting and test stimuli were similar.

The novel test stimulus used was effective in eliciting a tMAE, with a reliable aftereffect observable with only three seconds of adaptation. The test stimulus used is dynamic, a feature shared with test stimuli used by other researchers to reliably elicit a negative tMAE. The novel feature of the test stimulus used here is that it is composed of motion in two directions –the same as, and the opposite to the adapting stimulus. There were individual differences in perception of these combined opposing motion signals when not preceded by adaptation, with a tendency to more readily perceive one or the other direction of motion. Even so, a consistent bias was observed in all participants to perceive the test stimulus as motion in the opposite direction to the preceding adapting motion. Furthermore, in contrast to historical difficulties in eliciting a static tMAE, ceiling effects were reported here under some conditions, indicating that the dynamic tMAE is strong.

The reliable negative tMAE observed here is consistent with previous studies using a dynamic test stimulus (Watanabe et al., 2007; Konkle et al., 2009), and with a distribution shift explanation. The adapting motion caused a gain reduction of motion signals in its direction, resulting in more weight for the other direction signal present in the test stimulus – the opposite direction, which dominated perceptual judgments. The dynamic test stimulus activated relevant motion pathways to reveal the effects of adaptation.

The tMAE grew stronger with increases in adapting speed, but no differences were observed in the strength of the tMAE for test stimuli of different speeds, and there was no evidence that the tMAE was tuned for a match between the speed of the adapting and test stimuli. In addition, the variations in the strength of the tMAE were not simply a result of the clarity, or strength of the direction signal, of the adapting motion. The different adapting stimuli that varied in speed were similarly discriminable, with no significant differences in the DI difference scores.

It is possible that no effect of test speed was observed because the interleaved columns of the test stimuli that moved in different directions could not be separately resolved. This may have resulted in perceived speed being either different to the nominal speed, unclear or inconsistent, and tactile motion processes may be insensitive to the different speeds of the test stimuli. Conscious discrimination of the two test stimuli, while not necessary for the test speed to have influenced the tMAE, would be a sufficient indicator that test speed can influence perceptual processes. Informal observation indicates that the fast and slow test stimuli used in Experiment 7 were distinguishable, but discrimination was not formally tested. It is possible that with different stimuli, evidence for speed tuning might have been found in addition to the observed monotonic increase in tMAE strength with increasing adapting speeds.

The apparent motion stimuli used in this study always had the same step distance (1.18mm), which means that faster speeds had a higher step frequency, or temporal frequency (TF). The observed differences in tMAE strength with different adapting stimuli could therefore have been due to their differences in TF, rather than speed. However, the similarity between the results here and those observed for the tSAE in Experiment 5 (Chapter 3), which were shown to depend on speed rather than TF, suggests that the speed of the adapting stimulus is more likely to be responsible for the effect. Regardless of whether adapting speed or adapting TF is responsible for the differences in tMAE strength, the effect must be central. This is because the vibration frequency of individual rods was always the same, 230Hz, which means that information about either speed or TF is available only by comparing activity across primary afferents.

The similarity of the dynamic tMAE to its visual counterpart is limited. The strength of the dynamic vMAE also depends on the speed of the adapting stimulus, but the relationship is different. The vMAE shows an inverted U shaped function with regard to adapting speed, peaking at around 5-8degs^{-1} (Ashida & Osaka, 1995), and the relationship is different for different test stimuli (Alais et al., 2005). This contrasts with the results reported here, which showed a monotonic increase in the strength of the tMAE with adapting speed, and did not vary with test speed. While it is possible that a different pattern might be revealed with a wider range of adapting speeds, the range of speeds used in the experiments reported here (19-136mms^{-1}) covers the speeds typically used in humans' spontaneous movements during surface exploration (20-86mms^{-1}; Connor et al., 1990; Smith et al., 2002; Yoshioka et al., 2011), and therefore accounts for the speeds most relevant to tactile sensory function.

The observed relationship between adapting speed and tMAE strength is similar to what was observed between adapting speed and the tSAE reported in Experiments 4 and 5 (Chapter 3). For both aftereffects, speed appears to be an intensive property of the adapting motion, with the degree of adaptation increasing with speed. This may serve the function of maintaining appropriate calibration of neural and perceptual signals to the environment in which the most commonly experienced velocity across the skin is zero. A persistent motion signal of non-zero velocity would then indicate a miscalibration with an imbalance between opposing directions. Adaptation to this persistent signal may trigger a recalibration to bring the signalled velocity closer to zero; the faster the speed of the adapting motion, the greater the recalibration required.

A plausible site for the neural population underlying the tMAE is in the primary somatosensory cortex (SI), where direction-sensitive neurons have been observed that increased activity to their preferred direction of motion when speed was increased (Ruiz et al., 1995; Whitsel et al., 1978, 1972). On the other hand, Pei, Hsiao, Craig and Bensmaïa (2010) reported that the variations in direction selectivity due to speed were not always because of increased firing in the preferred direction, but could alternately be caused by decreased firing in the anti-preferred direction, or both. Furthermore, while across the population, greater speeds were associated with greater direction selectivity (they tested speeds 10 - 80mms^{-1}), individual neurons varied in their response to speed, with some increasing in direction selectivity with speed, some decreasing, and others peaking in direction selectivity at particular speeds. Because of this variation in individual neurons, perceived direction is most likely based on the population response of SI neurons. This is also suggested by the fact that most individual direction selective neurons in SI are broadly tuned (Costanzo & Gardner, 1980), but direction can be predicted by a speed-weighted population code (Ruiz et al., 1995) with a precision (16 - 46°) similar to human perceptual judgments (23-35°) made under similar conditions (Drewing et al., 2005).

The results presented here show that a tMAE can be elicited reliably and consistently in the negative direction when using a dynamic test stimulus designed to activate adapted neural populations. This dynamic tMAE is sensitive to adapting speed, increasing monotonically with increases in adapting speed. A likely neural basis of the tMAE is direction sensitive neurons in S1 that encode speed intensively.

Chapter 5: General Discussion

5 .1 Summary of results

The experiments described here used aftereffects of adaptation to tactile motion in order to uncover the processes involved in perception of the speed and direction of movement across the skin. A robust tactile speed aftereffect (tSAE) was reported, with adaptation causing a moving ridged rubber surface to consistently appear slower by about 30% of its perceived speed when unadapted (Experiments 1, 4 and 5). In Experiments 1 and 2 (Chapter 2), it was found that the tSAE was not direction sensitive, i.e. the strength of the tSAE (the amount of illusory slowing relative to baseline) was about the same whether the adapting stimulus moved in the same or the opposite direction to the test stimulus, and this despite the stimulus successfully engaging directional mechanisms, as evidenced by the ability of participants to accurately judge the direction of the stimulus, even after sustained exposure (Experiment 3, Chapter 2).

The strength of the tSAE was found to be sensitive to the speed of the adapting stimulus, with faster speeds producing a stronger tSAE (Experiments 4 and 5, Chapter 3). This is consistent with an intensive speed code, in which increasing firing rates in the neurons that encode speed is associated with increasing perceived speed. It was also found that the proportional reduction in perceived speed of the test stimulus induced by a given adapting stimulus was not a constant proportion of the baseline perceived speed, but was greater for slower test stimuli, and decreased as the test stimulus increased up to the speed of the adapting stimulus (Experiment 4).

It was shown in Experiment 5 (Chapter 3), that these variations in the strength of the tSAE were due to the speed of the adapting stimulus, and could not be attributed to the spatial period of the ridged surface or the temporal frequency with which the ridges crossed the skin. Together, these results suggest that perceived speed is based on a central neural population with an intensive code for speed, in which increasing speed is associated with increasing firing rates. The strength of the tSAE under different adapting conditions is summarised in Table 5.1.

Table 5.1. The strength of the tSAE observed in Experiments 1, 4 and 5. The strength of the tSAE is given both as the absolute change in PSE, and as the percentage change in PSE, from the baseline condition in which the same test stimulus was judged without any preceding adaptation. For a given test speed, the strength of the tSAE shows a similar pattern (dependence on adapting speed) regardless of the measure used.

Experiment	**Adapting speed (mms^{-1})**	**Test speed (mms^{-1})**	**Change in PSE (mms^{-1})**	**Percentage change in PSE**
Experiment 1 (n = 9)	81	81		
	Same direction		-23 ± 8	-30 ± 10%
	Opposite direction		-26 ± 7	-34 ± 9%
Experiment 4	Slower (n = 2)			
	30	81	-10 ± 1	-12 ± 1%
	30	144	-15 ± 92	-10 ± 11%
	30	242	-32 ± 418	-10 ± 28%
	Matched (n = 6)			
	30	30	-8 ± 5	-28 ± 17%
	81	81	-23 ± 18	-27 ± 18%
	144	144	-37 ± 43	-24 ± 26%
	242	242	-77 ± 42	-31 ± 12%
	Faster (n = 6)			
	242	30	-14 ± 4	-48 ± 14%
	242	81	-39 ± 13	-46 ± 12%
	242	144	-58 ± 37	-39 ± 21%
Experiment 5 (n = 6)	tSAE. Adapting speed (test = 40mms^{-1}):			
	20	40	-6 ± 5	-14 ± 11%
	40	40	-13 ± 6	-31 ± 14%
	81	40	-20 ± 6	-48 ± 14%

In Chapter 4, a robust and reliable dynamic tactile motion aftereffect (tMAE) was reported, using a novel two-component test stimulus to produce a negative tMAE, with illusory motion perceived in the opposite direction to the adapting motion. The strength of the tMAE was measured as the extent of directional bias in responses to the test stimulus (using the relative number of responses in the same direction, and in the opposite direction, to the adaptation). Similar to the tSAE, the strength of the tMAE was found to depend on the speed of the adapting stimulus, with greater speeds producing a stronger tMAE. There was no speed tuning of the tMAE, i.e. it was not the case that the strongest aftereffect depended on a correspondence between the adapting and test speeds. Furthermore, the speed of the test stimulus was unimportant, with different test speeds producing a similar strength tMAE, which depended on the absolute speed of the adapting stimulus.

Dynamic test stimulus

A dynamic test stimulus was used in the tMAE experiments because dynamic test stimuli yield consistent and reliable negative tMAEs (Konkle et al., 2009; Kuroki et al., 2011; Watanabe et al., 2007). When a static test stimulus is used instead, illusory motion is sometimes but not always produced. When present, it varies in direction, sometimes reported in the same direction as the adapting stimulus (a positive tMAE), sometimes the opposite (a negative tMAE), while at other times orthogonal motion or other sensations are felt. While the dynamic and static tMAEs are distinct, they share common features. Planetta and Servos (2008) found that the incidence rate of the static tMAE (including both positive and negative reports) increased with the speed of the adapting stimulus (from 150 to 350mms^{-1}), as did its duration, and subjective vividness ratings. This sensitivity to speed is similar to what was reported in Experiments 6 and 7 (Chapter 4) regarding the dynamic tMAE, which increases in strength with the adapting speed. It is likely that both the static and dynamic tMAE reflect adaptation of some common perceptual processes, but the fact that the aftereffects are highly sensitive to the particular test stimulus used suggests that adaptation to tactile motion has varied effects for different perceptual contexts and tasks.

Individual differences

In circumstances in which a consistent perceptual effect was not found, individual differences were observed. First in Experiment 2, which used bilateral adaptation to test for any differences in the strength of the tSAE due to the relative direction of the adapting and test stimuli. In this experiment, no consistent group difference was found, but individuals did show differences in how fast the differently adapted stimuli felt relative to each other (Figure 2.9). The test stimuli were the same in the different conditions, so this must reflect individual differences in sensitivity to the direction of the adapting stimulus. Second, in Experiments 6 and 7, individual differences were observed in how the two-component test stimulus was felt when adapting motion did not precede it (See Figure 4.7, and Figures 4.3 and 4.9 when adapting speed = 0). Several participants had a bias to perceive the two-component stimulus to move distally, and one proximally. It is possible that these observations may be related: individual biases to perceive motion distally or proximally may translate into motion in one or the other direction producing a stronger adapting stimulus. Anisotropies in direction discrimination have been reported in previous research, with lower thresholds for motion along the proximo-distal axis (Drewing et al., 2005; Gleeson, Horschel, & Provancher, 2009; Keyson & Houtsma, 1995). It is possible that a directional bias (for either distal or proximal motion) reflects a sensitivity to the motion signals present in the two-component test stimulus, that affords greater direction discrimination when feeling real motion along the proximo-distal axis.

5 .2 Features of neural channels coding speed and direction

The observed lack of direction sensitivity of the tSAE (Experiments 1 and 2, Chapter 2) suggests that the adaptation that causes the observed reductions in perceived speed is centrally located. Primary afferents adapt to prolonged stimulation, which reduces their response rates (Bensmaïa et al., 2005; Leung et al., 2005; Lundström & Johansson, 1986; McIntyre et al., 2012; Whitsel, Kelly, Delemos, Xu, & Quibrera, 2000), but primary afferent activity is sensitive to the direction of motion (Birznieks et al., 2010, 2001; Edin et al., 1995; Goodwin & Morley, 1987a; Wheat et al., 2010). If perceived speed were based on the amount of activity in primary afferents, we would expect the sub-population of afferents preferring the adapting motion to show greater adaptation than those preferring a different direction, and this would result in a direction sensitive tSAE. The fact that perceived speed is robust to this directionally specific change in primary afferent firing rates, suggests that adaptation occurs centrally and that the observed reduction in perceived speed is not due to changes in the response rates of primary afferents.

Central adaptation is also suggested by the fact that the strength of the tSAE depends on the speed of the adapting stimulus and not its spatial period or temporal frequency (Experiment 5, Chapter 3). This implication follows because speed is not unambiguously coded in the responses of individual primary afferents, and is confounded with TF even in the mean population firing rates (Goodwin & Morley, 1987b).

Tactile speed coding is likely to be based on sequential activation of afferents with neighbouring receptive fields stimulated by the moving stimulus, with speed computed from the distance between adjacent receptive fields and the time between their activation (Darian-Smith & Oke, 1980). This computation requires information about the location of the receptive fields of stimulated afferents ('labelled line'). There is evidence that we do have access to this information: direct electrical stimulation of both cortical (Penfield & Boldrey, 1937) and peripheral (Ochoa & Torebjörk, 1983; Torebjörk, Vallbo, & Ochoa, 1987) afferents produces a sensation that can be localised on the skin, despite no mechanical stimulus being applied there. Precise timing of afferent stimulation is also required, and this is available in the response profile of the primary afferents, whose responses are precisely phase-locked to the periodicity of ridged surfaces moving across the skin (Darian-Smith & Oke, 1980; McIntyre et al., 2012; Morley & Goodwin, 1987).

This putative central computation of speed from the spatial and temporal stimulation profile of primary afferents might benefit from the redundancy associated with a periodic or repeating texture pattern scanned over the same area of skin (e.g. the finger pad); multiple stimulating ridges provide redundant cues for the same velocity. Such a process requires sufficiently densely innervated skin to resolve the ridges separately. There is evidence that spatial information about stimulation of afferents with neighbouring receptive fields is also important for judging surface roughness. When Yoshioka, Craig, Beck and Hsiao (2011) prevented use of this spatial cue by having participants feel a scanned surface indirectly via a held rigid metal probe, they found that roughness judgments varied with the scanning speed – likely because the temporal cues in the vibrations produced in the probe were the only available input (proprioceptive cues to motion were also eliminated by keeping the arm and hand stationary while the surface moved). If speed computation similarly relies on spatial information from stimulated afferents (as proposed above), then it is likely to be affected in the same way as roughness judgments when this cue is removed: speed judgments would be expected to depend entirely on vibration frequency.

The underlying neural channels for perceived speed of tactile motion seem to code speed intensively. That is, this population of neurons responds to tactile motion and shows greater activity when the speed of that motion is increased. Evidence for this was found in Chapter 3, in which the tSAE was found to be sensitive to the speed of the adapting stimulus, with greater adapting speeds producing a stronger tSAE. When adapting speed, temporal frequency and spatial period were disambiguated in Chapter 3, it was shown that speed influenced the tSAE while TF and SP did not. This also suggests a central adaptation site. While primary afferent populations do show higher firing rates for faster speeds, speed is confounded in primary afferent responses with other stimulation features such as temporal frequency and spatial period (Goodwin & Morley, 1987b), and only as a result of central processing could speed be disambiguated from these other features.

Similar to the neural population that encodes perceived speed, the neurons that are relevant to perception of motion *direction* code speed intensively. Evidence for this was found in Experiments 6 and 7 (Chapter 4), in which the strength of the tMAE increased monotonically with the speed of the adapting stimulus. An intensive code for speed can explain this result: direction sensitive neurons respond more vigorously to fast speeds, and sustained exposure to faster speeds causes greater adaptation than to slower speeds. Although in these experiments the adapting speed was not disambiguated from the adapting TF, and either parameter could be responsible for the strength of the aftereffect, the adaptation is likely to have a central basis either way. Computation of either parameter requires comparison of the responses of different primary afferents across space and time, a necessarily central process.

Furthermore, firing rates of individual primary afferents do not contain sufficient directional information for all stimuli that traverse the skin. While primary afferents are sensitive to the direction of many natural stimuli, especially those that cause lateral skin stretch (Goodwin & Morley, 1987a; Johansson, 1978; Knibestöl & Vallbo, 1970;

Knibestöl, 1975; Olausson et al., 2000; Srinivasan et al., 1990; Westling & Johansson, 1987), some apparent motion stimuli that evoke negligible direction sensitive responses from primary afferents nevertheless provide sufficient directional cues for perception of motion (Pei et al., 2010). This same apparent motion stimulus has been shown to produce a direction-selective response in some SI neurons, which show an increased firing rate for motion in their preferred direction (ibid).

In summary, the results of the experiments reported here indicate the following identifying features of the neural processing underlying perceived speed that adapts to cause the tSAE: 1) it is centrally located, 2) it codes speed intensively, and 3) its adaptation is insensitive to direction of motion. Evidence was reported for the following properties for the processing underlying perceived direction that adapts to cause the dynamic tMAE: 1) it is centrally located, 2) it codes speed (or TF) intensively, 3) its adaptation is specific to the direction of the adapting stimulus.

5 .3 The consequences of primary afferent adaptation

It was argued in the previous section that the reduction in firing rate of primary afferents following motion adaptation is unlikely to have caused either of the aftereffects (tSAE, tMAE) reported here. Instead, both speed and direction coding in the context of these aftereffects rely on central mechanisms that compare the timing and receptive field location of activity in different primary afferents. However, primary afferent adaptation is still likely to have had perceptual consequences. In Chapter 2, we reported that primary afferents showed a reduction in firing rate when exposed to prolonged motion, consistent with previous reports of adaptation to vibration (Bensmaïa et al., 2005; Leung et al., 2005; Lundström & Johansson, 1986; Whitsel et al., 2000). Furthermore, it was illustrated in a single FA1 unit that while its firing rate was reduced, the precise phase-locked response to the ridges of the surface was preserved (the preservation of this temporal code is important for the central processes for coding motion, proposed above). Before adaptation, the unit had responded with bursts of multiple spikes to each ridge (a high burst rate), but the number of spikes per ridge reduced following adaptation, so that usually only one spike was evoked. Individual units typically show higher burst rates to vibration of greater indentation amplitude, while a one-to-one entrainment pattern (1 spike per cycle) is observed with more moderate amplitudes (Johnson, 1974).

The coding of amplitude in the burst rate of primary afferents, along with the observation that adaptation reduces perceived intensity of vibrotactile stimuli (Békésy, 1959; Berglund & Berglund, 1970; Gescheider & Wright, 1968), suggests that one consequence of primary afferent adaptation is a reduction in perceived intensity of the stimulus. This is consistent with the subjective “numbness” that participants experienced when adapting to the drum (Chapter 2), which occurred despite consistent pressure applied to the surface throughout the experiment. Although no participants spontaneously reported such a sensation with the Optacon, similar adaptation is likely to have occurred because all stimuli were composed of high frequency vibration that was repeatedly applied. It is not clear whether an adaptation-induced reduction in perceived stimulus intensity has any impact on motion processing. In vision, the luminance contrast (an analogue of indentation amplitude) of a moving stimulus can influence its perceived speed (Thompson, Brooks, & Hammett, 2006; Thompson, 1982). However, in touch, the relationship between amplitude and speed has not been investigated.

5 .4 The role of lateral skin stretch and successive positions cues

Surface texture is important for speed perception, with evidence that the speed of coarser textures is easier to discriminate than for fine textures or smooth surfaces (Bensmaïa et al., 2006; Dépeault et al., 2008; Salada et al., 2004; R. J. Webster et al., 2005). However, it is not clear whether this is due to improvements in the successive positions cue or the lateral skin stretch cue, or both.

The properties of the tSAE reported in this thesis suggest that changes in speed coding derived from the successive positions cue have a substantial impact on perceived speed. The adaptation that results in the tSAE is likely to have its basis in central processes that rely on the successive positions cue (see previous section). That the tSAE is such a large effect, with reductions in perceived speed between 11 and 48%, suggests that the successive positions cue is a major contributor to perceived speed.

The adaptation that produced the tMAE reported in this thesis also has its basis in central coding of direction derived from the successive positions cue. This is due simply to the fact that the apparent motion stimulus that was used to produce the tMAE did not stretch the skin, and provided only the successive positions cue. Previous studies using apparent motion stimuli also found a negative tMAE (Konkle et al., 2009; Kuroki et al., 2011; Watanabe et al., 2007).

It remains unclear what role lateral skin stretch plays in aftereffects of adaptation to tactile motion, a question that lies beyond the scope of this thesis. Both lateral stretch and successive positions cues to motion across the skin are likely to contribute to both perceived speed and perceived direction. However, neither the extent to which these cues remain separately represented in somatosensory pathways, nor at what stage they might be combined, is known for either speed or direction coding.

5 .5 Joint or separate coding for speed and direction?

Adaptation to tactile motion affects both perceived speed and perceived direction in a similar way; the adapting speed has the same relationship to both aftereffects (the tSAE and the tMAE), with the degree of adaptation increasing with speed. In both cases, speed appears to be an intensive property of the adapting motion. A parsimonious explanation is that both aftereffects result from adaptation in the same neural population. Indeed, the adapting stimuli are similar in that they are both motion stimuli of a repeating pattern applied to a fixed region of skin (although they are not identical: when testing the tSAE a textured surface was used, while when testing the tMAE, an apparent motion stimulus was used), and are likely to stimulate, and thus adapt, common neural populations.

The possibility that the tSAE and the tMAE result from adaptation in the same neural population raises the question of whether one of these aftereffects is simply a secondary effect of the other. For example, if perceived speed were influenced by the strength of the direction signal, then a change in the strength of the direction signal caused by adaptation might induce changes in perceived speed, which need not be explained in terms of speed-specific adaptation. However, this is unlikely to be the case. If it were, the tSAE would be expected to show reductions in perceived speed that are direction specific. Yet Experiments 1 and 2 (Chapter 2) showed that this was not the case – the reduction in perceived speed following adaptation was similar whether the test stimulus moved in the same or the opposite direction to the adapting stimulus. Conversely, the tMAE cannot be attributed to secondary perceptual effects that result from the tSAE for the same reason – the tSAE shows perceived speed reduced by a similar amount for different directions, while the tMAE requires a directional bias in the level of adaptation.

The tSAE and the tMAE are likely to be separate aftereffects, both directly resulting from adaptation to motion, but the extent to which these two aftereffects reflect adaptation of common neural channels is less clear. While the adapting stimuli are similar, and no doubt cause adaptation in common neurons, the different perceptual tasks performed by the participants may rely on the activity of different subsets of the adapted neural population. When investigating the tSAE, participants are asked to judge the speed of motion, and for the tMAE, they are asked to judge its direction. For a common adaptation process to be responsible for both aftereffects requires perceived speed and perceived direction to be jointly coded, rather than being coded in different neural populations that are both adapted by sustained exposure to motion.

While it was found that both speed and directional channels have a common feature of intensive speed coding, consistent with joint coding of speed and direction, two findings reported in this thesis contrast with this, and suggest that perceived speed and direction might not be jointly coded, although neither can be considered conclusive. Firstly, the relationship between the adapting and test speeds was found to be important for the strength of the tSAE, but not for the tMAE. The strength of the tMAE depended only on the adapting speed, and not the test speed (Experiments 6 and 7). This could reflect distinct adaptation processes affecting perceived speed and direction.

On the other hand, this may simply reflect differences in the stimuli used in the two experiments, and direct comparison may not be appropriate. Both experiments involved a high adapting speed with test speeds slower than, and equal to, the adapting speed. However, the high adapting speed in the tSAE experiment was much higher (242mms^{-1}) than that in the tMAE experiment (136mms^{-1}), because of limitations of the tactile array used in the latter experiment. In the former experiment, a lower adapting speed was not sufficiently tested (n=2) to verify whether the effect of test speed in the tSAE is significant with lower adapting speeds. Alternatively, it may be that no effect of test speed was observed in the tMAE experiment because the test stimulus, which involved motion in both directions simultaneously, may have fallen below the spatial resolution threshold for motion. That is, the tactile system may not have separately resolved the interleaved columns that moved in different directions. The columns may have instead been integrated in such a way that the perceived speed was not necessarily equal to the nominal speed, and was possibly unclear or inconsistent from trial to trial. If this were the case, then the tactile motion system may have been insensitive to the differences in the speed of different test stimuli.

The second result that suggests separate coding of speed and direction is the lack of direction sensitivity of the tSAE (Experiments 1 and 2, Chapter 2). If perceived speed and perceived direction were jointly coded, one would expect that the tSAE would be sensitive to the direction of the adapting stimulus, but it was not. However, joint coding may still occur if a mechanism generalises the effects of adaptation from neurons preferring the adapted direction to neurons preferring all directions. This would result in the neurons in the population being subject to two simultaneous adaptation effects – one that disproportionately affects neurons that prefer motion in the adapting direction, and another that applies to all neurons. Something similar, described as gain control, has been observed in direction selective neurons sensitive to visual motion in flies (Harris et al., 2000).

If there are two adaptation processes, one directional and one not, acting on a single neural population, the net outcome should still result in direction sensitive aftereffects. This scenario might nevertheless produce both the directional negative tMAE and the direction-insensitive tSAE in two ways. Firstly, it is possible that perceived speed is less sensitive to small changes in firing rate in this neural population, and so a relatively small direction-specific difference in response will not be used when participants are required to judge speed. Secondly, it is possible that joint coding occurs at an intermediate stage that is subject to direction-specific adaptation effects, and that this intermediate stage projects to a later stage of motion processing that codes for speed, but not direction, in which neurons inherit adaptation in a non-directional fashion. This might be achieved if the later stage neurons receive converging inputs from neurons in the intermediate stage that prefer different directions of motion.

Previous studies provide mixed evidence regarding joint coding of speed and direction. Evidence in favour of joint coding is provided by a subset of direction selective neurons in SI that show a stronger direction preference (a greater firing rate for the preferred direction relative to other directions) when the speed of motion across their receptive fields is increased (Pei et al., 2010; Ruiz et al., 1995; Whitsel et al., 1978, 1979, 1972). Evidence suggesting separate coding of speed and direction comes from studies that have found dissociation in the preservation of the ability to make direction and speed judgments following damage to the dorsal column nuclei or the cortex. Essick, Franzén, et al. (1996) described three patients with lesions of the parietal cortex whose capacity to discriminate the direction of a brush stroked across the skin was either eliminated or severely impaired on the hand contralateral to the lesion, while capacity to scale speed (5 – 640mms^{-1}) was preserved. Wall and Noordenbos (1977) reported one case in which a patient's dorsal columns were completely severed and could not judge direction at all, but performance on a task requiring discrimination between a slow (25mms^{-1}) and a fast (100mms^{-1}) brush stroke was only slightly impaired. However, these patients may have been able to use the duration of motion stimulation as a substitute for discriminating speed, so it is not clear whether they truly constitute dissociations between direction and speed perception.

Neither previous research nor the new evidence provided in this thesis is sufficient to resolve the question of whether speed and direction are jointly coded in a common neural population. While both the existence of SI neurons sensitive to direction and speed (Pei et al., 2010; Ruiz et al., 1995; Whitsel et al., 1978, 1972), and the result that the strength of both the tSAE and the tMAE scale with adapting speed are suggestive, neither can rule out the possibility of separate coding. The evidence for separate coding in at least some stage of tactile motion processing is more compelling. The possible dissociation between the ability to judge speed and direction observed in clinical patients with both dorsal column (Wall & Noordenbos, 1977) and cortical (Essick, Franzén, et al., 1996) lesions, if genuine, suggests separate pathways, and a degree of independence for these perceptual capacities. The lack of direction sensitivity of the tSAE, if not explained by separate coding of speed and direction, requires a particular neural adaptation process to occur – neural gain control causing adaptation to generalise across neurons preferring different directions – which, while plausible, does not have any supporting evidence.

5 .6 The neural site of tactile motion processing

The primary somatosensory cortex (SI) is the current best candidate site for processing direction of tactile motion. In a human fMRI study, Planetta and Servos (2011) measured brain activity while inducing the static tMAE. They found that while the contralateral thalamus, postcentral gyrus and parietal operculum all responded to actual tactile motion compared to the stationary surface, only the postcentral gyrus (SI) showed activity during the tMAE.

Several studies of single cell responses in monkeys have reported a substantial number of direction selective, motion sensitive neurons in SI of (Essick & Whitsel, 1985a, 1985b; Gardner & Costanzo, 1980b; Hyvärinen & Poranen, 1978; Warren et al., 1986; Whitsel et al., 1972). Although neurons sensitive to motion or direction typically make up a minority of SI neurons sampled (e.g. one study found that 38% of SI neurons respond better to motion than to simple punctate stimulation, and approx. 60% of these were direction selective, Warren et al., 1986), their response properties strongly suggest a role for signalling direction of motion. Pei et al. (2010) found neurons in monkey SI that signalled the direction of motion regardless of whether the stimulus was a bar, a dot pattern or a random dot display (with varying motion coherence), and the preferred direction of these neurons remained constant over a variety of speeds and indentation amplitudes. These pattern-independent neurons were mostly found in area 1, with a small number in area 2.

Further support for SI as a neural basis of motion direction processing is provided by Experiments 6 and 7 (Chapter 4), which showed that the strength of the tMAE increases monotonically with adapting speed. This result is consistent with speed being coded as an intensive property of neurons that signal motion direction. Individual SI direction selective neurons in monkeys have been commonly observed to show a stronger direction preference (usually due to increased firing rate in the preferred direction) when the speed of motion across their receptive fields is increased (Pei et al., 2010; Ruiz et al., 1995; Whitsel et al., 1978, 1979, 1972). While some individual direction selective neurons have a different relationship to speed (Pei et al., 2010; Whitsel et al., 1979), the population response increases monotonically with speed (Pei et al., 2010).

The direction selective neurons reported by Pei et al. (2010) were investigated with an apparent motion display, which is similar to the Optacon display used in Experiments 6 and 7 (Chapter 4) to investigate the tMAE in that neither display causes any lateral skin stretch (the individual pins move vertically) , but relied on the successive positions cue to signal motion across the skin (Gardner & Palmer, 1989; Pei et al., 2010). While these neurons may also respond to lateral skin stretch, it is clear from Pei et al.'s results that the successive positions cue is sufficient to stimulate direction selective neurons in SI. It is very likely that the apparent motion stimulus used in the tMAE studies reported here also stimulated these neurons.

SI is also a candidate site for processing speed of tactile motion, although it is not clear whether the same SI neurons are used to code speed and direction (see previous section). The lack of direction sensitivity of the tSAE observed in Experiments 1 and 2 suggests that the changes in perceived speed due to adaptation must be robust to changes in firing rate of the direction sensitive primary afferents. A process in which speed is computed centrally from the distance and time between successively stimulated regions of skin, signalled by primary afferents, was proposed to account for this result. There is evidence that neurons in area 3b of SI in monkeys engage in spatio-temporal integration, evident when a region of skin outside the receptive field of an individual neuron was stimulated, and this changed the response of the neuron to stimuli within its receptive field (Reed et al., 2010). Inhibition of the response was most common, and the magnitude of the effect was also highly dependent on the relative timing of the stimulation, with the greatest inhibition observed when the stimulation outside the RF preceded stimulation inside by about 30ms (Reed et al., 2010). This could form the basis of a motion processing system in which distance and temporal offset between stimulation of input afferents are compared and used to compute speed.

The finding that the strength of the tSAE increases monotonically with adapting speed (Experiments 4 and 5, Chapter 3) also suggests that perceived speed has its basis in neurons that code speed intensively with firing rate increasing with speed. Collins and Roppolo (1980) reported SI neurons whose firing rate increased monotonically with the speed of a moving brush (although 3 of the 37 recorded neurons showed the opposite effect), and Tremblay, Ageranioti-Bélanger and Chapman (1996) also found SI neurons that increased their firing rate with increases in the speed of a surface scanned across the skin. Furthermore, some of these speed-sensitive neurons' responses were independent of surface roughness and pressure. Neither of these studies tested for direction sensitivity, so it is not known whether these neurons are the same as those described above that are sensitive to both direction and speed (Pei et al., 2010; Ruiz et al., 1995; Whitsel et al., 1978, 1979, 1972).

The responses of individual neurons in S1 may not sufficiently account for human perceptual performance, and population responses may require a later stage of processing in a different cortical region. For example, Collins and Roppolo (1980) found that the capacity of S1 neurons to discriminate between two speeds was poorer than human psychophysical results. One possible site is the secondary somatosensory cortex (S2), in which a few neurons have been found whose responses are affected by the speed with which a surface is actively scanned (Sinclair & Burton, 1993). Although the experiments reported here used passive motion, the S2 neurons' responses had a positive relationship with speed, and responses were largely independent of SP and TF, which is consistent with the relationship between adapting speed and the strength of aftereffects reported here.

A possible alternate neural site for coding of tactile motion is in the human motion complex, hMT+/V5, an area that until recently has been considered a purely visual area. For example, Zihl, von Cramon and Mai (1983) reported a patient with selective brain damage to the region whose visual motion perception was impaired while auditory and tactile motion perception remained intact. The primary function of hMT+/V5 is processing visual motion stimuli and it is also thought to play an important role in the vMAE (Kohn & Movshon, 2003).

However, recent neuroimaging studies have suggested that hMT+/V5 may be involved in multisensory processing of motion, including processing of tactile motion stimuli. Several recent fMRI studies have found that tactile motion activates hMT+/V5 (Blake, Sobel, & James, 2004; Matteau, Kupers, Ricciardi, Pietrini, & Ptito, 2010; Ricciardi et al., 2007; Summers, Francis, Bowtell, McGlone, & Clemence, 2009; Wacker, Spitzer, Lützkendorf, Bernarding, & Blankenburg, 2011), while having participants simply imagine the moving stimulus does not (Blake et al., 2004), suggesting that the involvement of hMT+/V5 in tactile perception is not due to mental imagery alone. Tactile motion may also be privileged in hMT+/V5 over other forms of tactile stimulation, as apparent motion has been found to activate hMT+/V5 more than stationary vibration does (Summers et al., 2009; Wacker et al., 2011).

There is also evidence for a specific role for hMT+/V5 in processing both speed and direction of motion. Application of TMS to anterior hMT+ interfered with participants' ability to detect changes in speed of a felt moving surface, reducing accuracy and increasing reaction times compared to when no TMS was applied or when it was applied to a control site (Basso et al., 2012; Ricciardi et al., 2011). van Kemenade et al. (2013) also found that motion direction information was present in the fMRI BOLD signal resulting from a leftward or rightward apparent motion stimulus.

While hMT+/V5 does not receive direct projections from somatosensory cortical areas, it may receive indirect input via the ventral intraparietal area (VIP), a multisensory area that responds to both visual and somatosensory stimulation, particularly motion (Duhamel, Colby, & Goldberg, 1998). The VIP receives projections from somastosensory areas (Seltzer & Pandya, 1980)and also has some fibre projections to MT and MST (Blatt, Andersen, & Stoner, 1990; Rosa, Soares, Fiorani, & Gattass, 1993).

5 .7 Functional account of tactile aftereffects

Adaptation is commonly described as a net benefit for perception by proposing that absolute accuracy is compromised for the sake of greater discrimination sensitivity (Brenner et al., 2000; Clifford & Wenderoth, 1999; Goble & Hollins, 1993, 1994; Krekelberg et al., 2006; Wainwright, 1999). This is thought to be achieved via neural gain control in which the response range of neurons is recalibrated to better inform on *changes* in stimulus intensity that are likely to arise in the environment (Maravall et al., 2007; Ohzawa et al., 1982, 1985). In the experiments on the tSAE reported here (Experiments 1, 2, 4 and 5), judgments of the speed were compromised after adaptation (motion was perceived slower than it actually was), but there was no evidence of any improvement in speed discrimination sensitivity.

Previous studies that also failed to find a discrimination advantage following adaptation (Barlow et al., 1976; De Valois, 1977; Krekelberg et al., 2006), prompted Gepshtein, Lesmes and Albright (2013) to argue for a 'system account' of sensory adaptation, contrasted with a 'stimulus account'. The system account says that rather than interpreting adaptation effects narrowly in terms of the task presented in the experiment, they should be interpreted in the broader context of any task that the adapted system might have to perform. It is certainly possible that a system optimisation account might be appropriate for the tSAE, but it is not obvious for which tasks the system is being optimised. One possibility is that functions relating to surface exploration and identification are served by the adaptation that causes the tSAE. However, when spatial cues are available perceived roughness of a surface is robust to adaptation to both surface scanning motion and vibration, and aftereffects involving a change in roughness perception are observed only when vibration frequency is the sole cue available (Hollins, Lorenz, & Harper, 2006; Washburn, Hollins, & Bensmaïa, 2001).

Another ability that is possibly optimized by adaptation is vibration frequency discrimination. However, if this were the case, one would expect to see an improvement in discrimination performance in the tSAE experiments that used adapting and test stimuli with matched speeds and surfaces (because under these conditions TF was also matched), but this was not observed. A third possibility is that the adaptation may play a role in feedback about the speed of exploratory movements across a surface, and influence the movement in a beneficial way. Although it's not clear what advantage perceiving the speed as slower would confer, the lack of direction sensitivity of the tSAE is appropriate. When free to explore a surface, observers tend to move their fingers in multiple directions, usually back and forth (Morley et al., 1983; Smith et al., 2002; Yoshioka et al., 2007), so any changes in exploration speed should occur across all directions.

A plausible functional account of the tMAE is that it plays a role in recalibrating the tactile motion system's neural signal corresponding to no motion across the skin. Most of the time, a given area of skin is not subject to lateral motion, so no motion is the overwhelming persistent state. An artificially induced persistent state of motion in the lab may trigger a recalibration process to bring the new persistent motion velocity (direction and speed) closer to the perceptual zero point. The result that the strength of the tMAE increases with adapting speed is consistent with this explanation. The greater the speed, the greater the apparent miscalibration, and the stronger a correction needs to be made.

5 .8 Conclusion

Two aftereffects of adaptation to tactile motion, the tactile speed aftereffect (tSAE) and the tactile motion aftereffect (tMAE) were revealed to have properties indicating a central site as the neural basis of adaptation. The lack of direction sensitivity of the tSAE suggests a central adaptation site because the effect is robust to changes in the firing rate of direction selective primary afferents. Both aftereffects increased in strength with increasing speed of the adapting motion, indicating an intensive code for speed in the adapted neural population underlying both perceived speed and perceived direction. This is consistent with response properties of motion sensitive neurons in the primary somatosensory cortex, which increase their firing rates with increasing speed of motion.

Separate coding of speed and direction in different neural populations is suggested by the need for both a non-directional adaptation mechanism to explain the lack of direction sensitivity of the tSAE, and for a direction-specific adaptation mechanism to explain the negative tMAE.

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Appendix A: DI scores for adapting stimuli in Experiments 6 and 7

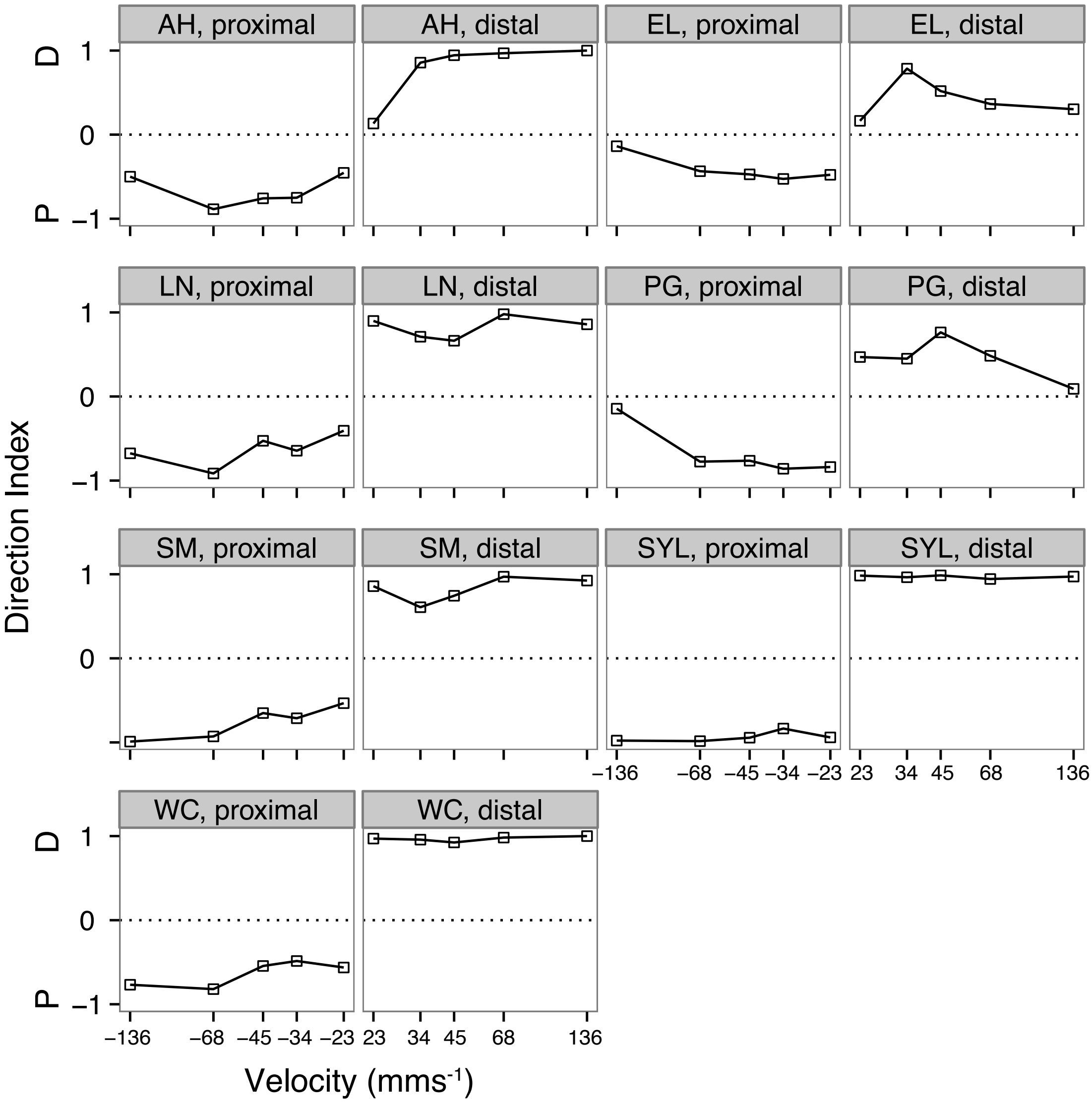

Figure A.1. Individual data showing perceived direction of the adapting motion, Experiment 6. The Direction Index (DI, see text for its calculation) is shown on the ordinate, with positive values indicating perceived direction was distal, negative values indicating perceived direction was proximal, and a value of 0 indicating a neutral percept. The speed of the adapting motion is shown on the abscissa on a log scale, with negative values indicating motion in the proximal direction and positive values indicating motion in the distal direction.

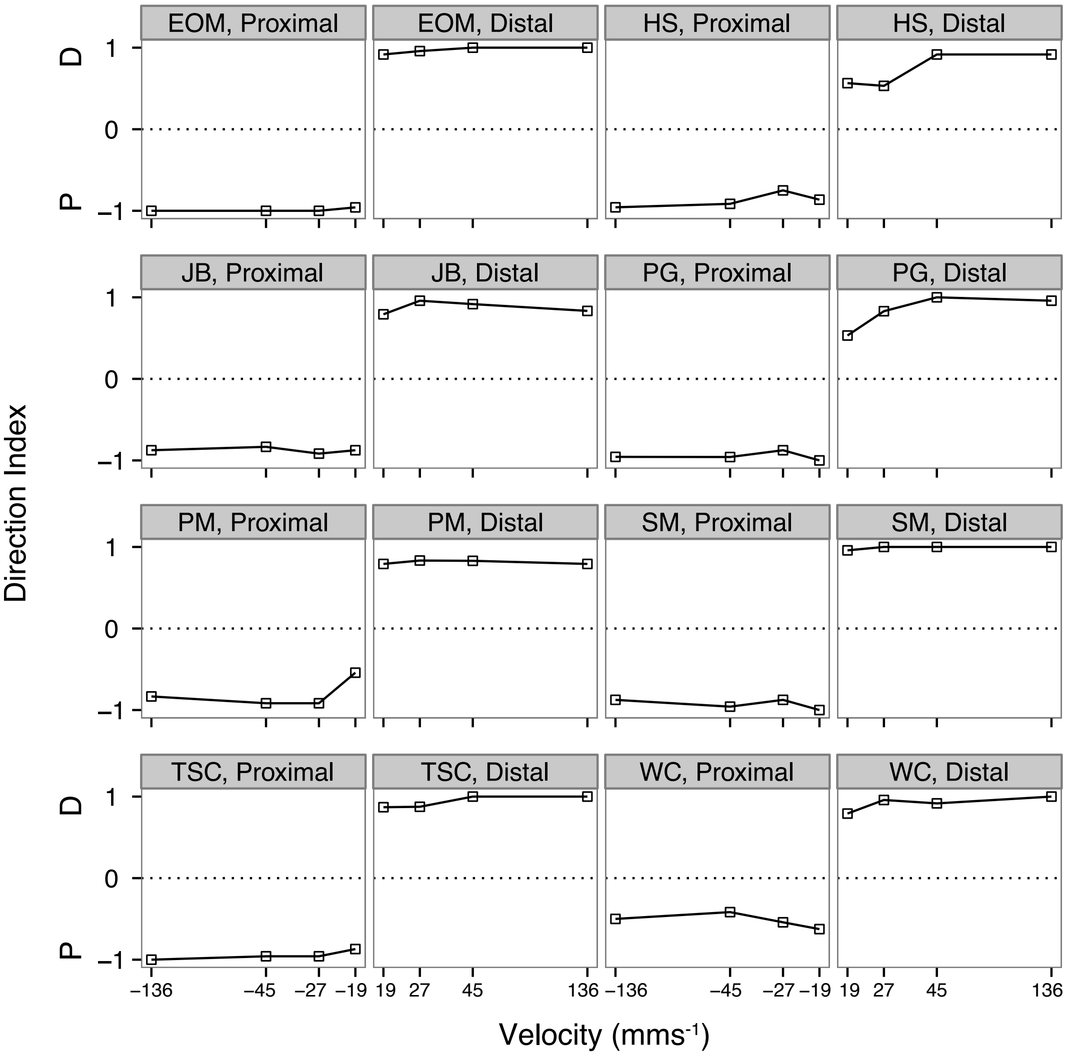

Figure A.2. Individual data showing perceived direction of the adapting motion, Experiment 7. Same format as Figure A.1.

Appendix B: Published Work