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**MODULATIONS OF VISUAL AND SOMATOSENSORY
PERCEPTION BY ACTION**

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**Thesis submitted to the University of Nottingham
for the degree of Doctor of Philosophy**

JULY 2011

Abstract

This thesis aimed to further investigate the effects of movements on modulations of visual and somatosensory perception. The first experiment (Chapter 2) investigated spatial mislocalisation of visual stimuli presented before saccade using a pointing paradigm and found that a predictive remapping of visual space occurred before saccade and the post-saccadic remapping employed spatially as well as temporally accurate memory of pre-saccadic visual stimuli. The second experiment (Chapter 3) examined relevance of saccadic chronostasis to remapping of visual space using a target displacement paradigm and found that it did not serve as a mechanism that fills in a perceptual gap during saccadic suppression. The third (Chapter 4) and fourth (Chapter 5) experiments adopted a target blanking paradigm and found that the pre-saccadic stimuli predictively remapped before saccade were anchored to the location of the pre-saccadic target remapped using a precise efference copy and neither saccade landing sites nor remembered locations of pre-saccadic targets were used in this process. Behavioural (Chapter 6) and fMRI (Chapter 7) studies were conducted to investigate modulations of tactile perception by manual movements and found that the tactile attention induced by the cued index finger facilitated processing of tactile stimuli presented to the responded hand. The somatosensory ROIs mainly showed a bias towards contralateral tactile stimulation in comparison with ipsilateral tactile stimulation. The right primary motor cortex (right M1), the left precuneus (left PreC) and the left middle frontal gyrus (left MFG) showed significant modulations of somatosensory processing by the Moving condition compared to the Non Moving condition. The final chapter included summaries and conclusions of each chapter and proposals for future investigations.

Acknowledgements

I am grateful to a number of people who made this thesis possible and I would like to take this opportunity to thank them.

I would first like to thank my supervisor, Stephen Jackson, for giving me a chance to do a PhD in the first place and for his supervision, teaching and guidance over the last few years. I would also like to thank Denis Schluppeck for his valuable suggestions and his attention to my PhD life. I wish to thank Jane Fowlie for her kindness to me.

I would like to thank the past and present members of the lab for their sincere help and honest advice and for their friendships: Åsa Pellijeff, Suzanne Ryan, Sally Pears, Catherine Preston, Rebecca Fisher, Kirsten McKenzie, Duncan Astle, Violet Yang, Amy Parkinson, Elena Georgiadi, Turki Abualait, Laura Condon, Lisa Everton, Chris Mason, Martin Schürmann and Roger Newport. I would also like to show my gratitude to all those, who participated in my experiments, for their time and effort.

Thanks to Hideo Kato for encouraging me and comforting me with tasty Japanese food. I owe my deepest gratitude to Selwyn and Judy Norton who looked after me while I was learning English in Bournemouth.

Thanks in particular to Park Han-Na for her patience and prayer for me. And last, but by no means least, at home thanks to my father (Nam Ki-Chon), my mother (Choi Gab-Soon) and my sister (Nam Eun-Jin) for their support and love.

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Chapter 1: Literature Review

1.1. Introduction

Stable perception of visual space is a natural phenomenon. However, questions can be raised about this phenomenon termed as space constancy or spatial stability given that eye movements occur two to three times per second and the peak velocity of eye movements is often more than 500 degrees per second.

Similar answers to the question about the stable perception of the surroundings during saccades were given by two researchers (Sperry, 1950; von Holst, 1954). von Holst (1954) used a few terminologies to explain space constancy. A signal produced by a stimulus was termed as afference and a general term for a motor signal was efference. The same sensory-receptors process stimuli produced both by animals' own movements and by movements of the environment. The former was termed as re-afference and the latter as ex-afference. According to the theory, when a movement is intended, a motor signal, efference, is sent to an effector from motor areas and a copy of the efference is also sent to visual or somatosensory areas or somewhere in the CNS where sensory consequences of the movement might be found. A re-afference is produced by the effector and the re-afference is compared to the efference copy. If there is no difference between them, the efference copy compensates for the re-afference and nothing takes place. However, if there is a difference, according to the theory, the difference can affect the movement or produce a perception. For example, when an eye was fixed and muscle receptors were anaesthetised, intention to turn the eye to the right produced a perception of surroundings jumping to the right since the efference copy was not cancelled by re-

afference which could not be produced as a result of anaesthesia. When the paralysed eye was passively moved to the right, another false perception of the surroundings jumping to the left was experienced as the surroundings moved on the retina and an afference was produced. However, when the intention to move the eye and the passive movement of the eye were combined, no movement of the surroundings was perceived as the efference copy and the re-afference nullified each other.

Sperry (1950) observed a forced circling of fish after he surgically rotated the left eyeball 180 degrees. The origin of the circling was thought to be central as part of the motor signal for the eye movement. It was suggested that the motor signal have a corollary discharge into visual areas to compensate for the retinal displacement induced by the eye movement. The direction and velocity of the eye movement are used to compensate for each change in advance to the onset of the eye movement. This anticipatory compensation was considered to be operating to maintain spatial stability during the onset of abrupt eye, head and body movement. When retinal field of fish was surgically rotated 180 degrees, the anticipatory control did not cancel out the retinal displacement, but amplified the movement of the surroundings.

Earlier studies provided evidence contrary to efference copy or corollary discharge hypotheses of space constancy. Retinal displacements of the stimuli were not compensated by efference copy of a motor command as participants reported perceived locations of the visual stimuli according to their relative retinal locations (Matin & Pearce, 1965). Visual stimuli flashed prior to eye movements were mislocalised in the direction of the eye movements in the dark (Dassonville et al., 1992; Schlag & Schlag-Rey, 1995) and visual space was compressed towards a

saccadic goal before, after and during eye movements (Burr et al., 2001; Ross et al., 1997). Misperceptions of temporal order or duration of stimuli were also observed around saccades (Morrone, Ross et al., 2005). These studies will be described in the subsequent sections. It appears that visual stability is maintained in the unstable and rapidly changing environment. Maybe there is no contradiction between stable perception of the world and spatial mislocalisation and temporal misjudgement observed around saccadic eye movements. It is possible that spatial mislocalisation and temporal misjudgement can be by-products of a mechanism that induces stable perception of the world. Further investigation into spatial mislocalisation of visual stimuli presented around eye movements could reveal possible parts played by efference copy or corollary discharge in space constancy in advance of eye movements.

An internal forward model was proposed for a system to predict the consequences of a motor command (Wolpert & Flanagan, 2001). It simulates a forward or causal relationship between actions and their outcomes. Forward models can be updated by computing prediction errors between the predicted and actual consequences of a motor command. Sensory prediction might then be utilised to cancel the sensory consequences of movements. As a result, effects of significant sensory information can be enhanced by suppressing sensory consequences of self-generated movements. For instance, identical tactile stimuli are perceived to be less ticklish when they are self-generated.

Sensory consequences of self-generated movements can be attenuated by efference copy of a motor command according to forward models (Blakemore et al., 1999;

Shergill et al., 2003), but it was also shown that externally-generated tactile stimuli are also attenuated prior to, during and after movements (Collins et al., 1998; Shimazu et al., 1999; Starr & Cohen, 1985; Voss et al., 2006). The pre-motor theory of attention claimed that when a goal-directed movement is prepared, the shared cortical circuits are activated for spatial attention (Rizzolatti et al., 1994). Different motor tasks can activate different cortical circuit for spatial attention. The theory also suggested that the preparation to reach a target should improve capacity to process sensory information presented the location of the target in the same way as the preparation to make an eye movement does. Accordingly, studies shows enhanced tactile processing during action preparation (Deubel & Schneider, 1998; Eimer et al., 2005; Juravle & Deubel, 2009). Further investigation is needed as only a few studies were conducted to investigate modulations of tactile perception around manual movements.

The rest of this chapter contains descriptions and relevance of studies to modulations of visual and tactile perceptions around eye movements and manual movements. The last section includes the aim of the thesis and plans for each study. Introductions of each study specify a detailed motive for the study based on the literature review in this chapter.

1.2. Spatial mislocalisation

1.2.1. With eye movements

Perception of visual space is rather volatile around a saccade. It was reported that there can be either a match or a mismatch between retinal locations of visual stimuli

and their perceived relative locations, depending on the locations of visual stimuli in the visual field when they were flashed prior to and during saccadic eye movements (Matin & Pearce, 1965). In the first experiment, the participants made eye movements from an initial fixation (IF) to the saccadic target (ST) located to the right of IF and a visual stimulus was flashed to the right of ST. The participants reported the direction of the visual stimuli relative to ST. The retinal locations of visual stimuli were varied as the eyes moved from IF to ST. Participants reported 'left' when the retinal location of the flashed visual stimuli was to the left of the retinal location of ST and 'right' when the retinal location of the flashed visual stimuli was to the right of the retinal location of ST although the visual stimuli were presented to the right of ST. Thus, the participants reported the perceived locations of the visual stimuli according to their relative retinal locations and the retinal displacements of the stimuli were not compensated by efference copy of a motor command. In the subsequent experiment, the participants reported the direction of the visual stimuli relative to IF and the visual stimuli were flashed either to the left or to the right of IF. Interestingly, participants reported 'right' in response to the flash presented to the right of IF when the retinal location of visual stimuli was to the left of the retinal location of IF. In other words, the visual stimuli flashed between IF and ST during saccades were perceived as shifted in the direction of saccades even though their retinal location was in the opposite direction. The result also implied that retinal displacements of the visual stimuli were compensated by efference copy of a motor command. Thus, the retinal location of visual stimuli presented during saccades does not impinge on their perceived location.

Studies showed that visual stimuli presented before or during saccadic eye movements were mislocalised in the direction of the eye movements while those presented immediately after the saccadic eye movements were mislocalised in the opposite direction of the eye movements. This phenomenon has been attributed to the inaccurate hypothetical eye position signal (EPS) and the mislocalisation is thought to reflect a gap between EPS and the actual eye position. EPS might be estimated by subtracting the retinal error of a visual target from the perceived location of the target and was shown to begin to develop before the onset of saccades and slowly reach the actual eye position slightly after the end of saccades. Thus, the time course of EPS is different from that of the actual eye movement (Dassonville et al., 1992, 1993; Honda, 1997; Schlag & Schlag-Rey, 1995; Schlag & Schlag-Rey, 2002). In a study of oculomotor localisation, five human and one non-human participants made an eye movement from a fixation point (F) to a first saccadic target (S1). A second saccadic target (S2) was presented before, during or after the first saccade and participants made a targeting saccade from S1 to S2. The targeting saccades were accurate for stimuli presented well before and well after the first saccade, but S2 was mislocalised in the direction of the first saccade when it was presented near the onset of saccades (Dassonville et al., 1992). In the dark two stimuli flashed at the same position near the onset of saccades were perceived separated from each other and the distance was reached maximum at the onset of saccades (Schlag & Schlag-Rey, 1995).

A study using a double-step task with a 100 ms target duration showed mislocalisation errors in the opposite direction of the saccade when stimuli were presented before the eye movements in a dark room (Jeffries et al., 2007). Trials that started with a rightward first saccade elicited leftward mislocalisation, while those

that started with a leftward first saccade elicited rightward mislocalisation, that is, a perisaccadic mislocalisation in the opposite direction of saccades. As this mislocalisation pattern could not be explained by the damped eye position theory, the results were attributed to an ambiguous remapping, in which a single stimulus is represented by multiple location signals from cortical areas such as LIP and its connected areas that have an anticipatory attribute before the onset of eye movements. However, the ambiguous remapping can also be used to explain perisaccadic mislocalisation errors in the direction of saccades (Kusunoki & Goldberg, 2003).

Mislocalisation of visual stimuli flashed in the dimly illuminated background showed a different pattern from that of visual stimuli flashed in the dark (Honda, 1993). In the dark, stimuli presented before and during saccades showed mislocalisation in the direction of saccades while stimuli presented after saccades showed mislocalisation in the opposite direction of saccades. However, in the dimly lit structured background the mislocalisation pattern was different depending on the locations at which the stimuli were presented. Stimuli flashed at the location on the left of the fixation point were mislocalised in a similar pattern to those presented in the dark. Stimuli flashed at the location between the fixation point and the saccadic target showed decreased mislocalisation in the direction of the saccade and increased mislocalisation in the opposite direction of saccades. Stimuli flashed at the location on the right of the saccadic target did not show mislocalisation in the direction of the saccade, but only showed huge mislocalisation errors in the opposite direction of the saccade. Another difference between the two conditions was the timing of mislocalisation. In the dark the mislocalisation began about 100 ms before the onset

of the saccade, whereas in the illuminated background it started about 50 ms before the onset of the saccade.

When observers made eye movements and a probing bar was presented at one of three locations (e.g. a location on the left of the initial fixation, a location between the initial fixation and the saccadic target or a location beyond the saccadic target), perceived locations of the bar before the onset of the saccade were not mislocalised in the same direction. The bars presented at the location on the left of the fixation and the location between the fixation and the target showed a strong mislocalisation in the direction of the saccade before the onset of the saccade, whereas the bars presented beyond the saccadic target showed mislocalisation errors in the opposite direction of saccades. Consequently, it appears that space is compressed towards the saccadic target before the onset of the saccade (Kaiser & Lappe, 2004; Morrone et al., 1997; Ross et al., 1997). Spatial compression of visual space towards the saccadic goal might be related to transition of the coordinate system from one fixation to another (Morrone et al., 1997).

It has been argued that in complete darkness, the extraretinal eye position signal is the only informative source for saccadic eye movements to a target and using this signal leads to uniform perisaccadic mislocalisation in direction and magnitude. However, when post-saccadic visual references are available, the target is localised not egocentrically, but relative to other visual information. Consequently, stimuli in the pre-saccadic visual coordinate are remapped in the post-saccadic visual coordinate formed by visual information, resulting in a compression of visual space (Lappe et al., 2000). However, it was shown that post-saccadic visual references are

not essential to induce compression of visual space (Morrone, Ma-Wyatt et al., 2005). When the perceived location of a saccadic target, which was drawn towards a flashed target, was taken into account, mislocalisation errors of the flashed target showed a typical pattern of spatial compression in the dark (Awater & Lappe, 2006).

When all visual references were removed by a shutter 75 ms after bar presentation, participant's verbal report of locations of the probing bars presented within 50 ms prior to saccadic eye movements verified a typical compression of space towards the saccadic target just as all the visual information was available (Burr et al., 2001). Instead of verbal reporting, observers responded using their index finger in a different condition. The blind pointing condition, in which they responded with their eyes closed, did not induce either perisaccadic mislocalisation of probing bars in the direction of the saccade or compression towards the saccade target. That is, their pointing responses were accurate. When visual references were available, the pointing condition induced a typical pattern of compression of visual space. It was suggested that visual space is represented by separate systems for conscious perception and action. While the system for conscious perception is susceptible to distortion, the system for action represents space accurately. The susceptible system tends to override the veridical one when visual information is available (Burr et al., 2001). As the veridical representation of space in the blind pointing condition illustrated, accurate information about visual stimuli presented before, during and after saccades has been shown to be available although perceptual representation of space is distorted.

It seems that the visual system maintains visual information obtained during saccades. Immediately after the initiation of saccades towards a saccadic target, the saccadic target stepped forwards, backwards or remained constant for less than the duration of the primary saccade and then blanked for 250 to 300 ms. It was shown that an accurate secondary saccade was made towards the invisible jumped target during the blanking period (Hallett & Lightstone, 1976). Accurate localisation of targets flashed prior to, during and after saccades were also illustrated when the localisation was carried out by striking the perceived location of the target with a hammer. It was suggested that there was accurate temporal concurrence between eye positions and eye position signals during saccades (Hansen & Skavenski, 1985). It seems that information about visual stimuli flashed during saccades is not completely lost and the information held in the visual system is veridical.

1.2.2. With head movements

The mechanism that is involved in localising visual objects presented prior to saccadic eye movements seems to be different from that used for localisation while making a slower form of movements. A participant, AI who had a congenital ophthalmoplegia, carried out localisation tasks while making saccadic head movements with a velocity of around 50°/sec. The localisation of probing bars presented prior to saccades was accurate and did not differ from that carried out while the eyes were fixated. It was suggested that visuospatial mislocalisation accompanied by saccadic eye movements was closely related to the fast movements made by the ocular system and the anticipatory remapping of visual space prior to eye movements. A link between motor prediction systems and rapid forms of movements was tentatively proposed (Jackson et al., 2005).

When rapid head movements with a mean velocity of more than 256°/sec and a maximum velocity of 552°/sec are made, auditory spatial compression is observed. The auditory stimuli were presented prior to the head movements and the bidirectional pattern of mislocalisation towards the head-turn target was analogous to that found in the visual system. It was hypothesised that auditory receptive fields of bimodal superior colliculus neurons would be shifted in advance of the saccade-like head movements characterised by high velocity and rapid reaction times (Leung et al., 2008). It seems that mislocalisation errors towards a target location observed prior to rapid movements might indicate anticipatory activity of the brain to facilitate information processing which can be delayed by rapid movements.

1.3. Saccadic suppression

1.3.1. Visual sensitivity

It has been known that a suppression of visual sensitivity occurs just before saccades (Ross et al., 2001). It was shown that saccadic suppression began around 50 ms before the onset of saccades and lasted until around 50 ms after the offset of saccades (Diamond et al., 2000). The time course of saccadic suppression is similar to that of spatial compression (Ross et al., 2001). As visual stimuli presented during saccades were accurately localised (Hallett & Lightstone, 1976; Hansen & Skavenski, 1985), there is no complete loss of information about the visual objects.

When an image is stationary, high spatial frequency contents are more visible, whereas at saccadic velocity, low spatial frequency contents of an image are more

visible and detectable (Burr & Ross, 1982). Contrast sensitivity curves for sinusoidal gratings moving at five different velocities were obtained. Participants were asked to detect the direction of motion while fixating a large fixation point. The curves showed almost identical peak sensitivity and general width. However, for gratings of higher velocity the peak sensitivity was reached at low spatial frequencies and for stationary gratings or gratings of lower velocity the peak sensitivity was reached at high spatial frequencies. On the contrary, while contrast sensitivity of horizontal gratings presented for 20 ms in normal viewing showed little loss of sensitivity from the peak sensitivity as spatial frequencies decreased, during saccades contrast sensitivity was dramatically impaired at low spatial frequencies compared to the loss of sensitivity in normal viewing (Burr et al., 1982). Thus, low spatial frequency components of an object which are otherwise conspicuous in normal viewing are blurred during saccades.

It was claimed that the suppression is closely related to motion signals (Burr et al., 1994). Contrast sensitivities for luminance-modulated gratings (yellow – black) and colour-modulated gratings (red – green) were measured during saccades and in normal viewing. There was no difference in contrast sensitivity for colour-modulated gratings in both saccade and normal viewing conditions. For one participant, sensitivity was even higher during saccades than in normal viewing. However, for luminance-modulated gratings, there was a great loss of sensitivity at low spatial frequencies during saccades compared to the normal viewing condition. There was no difference in contrast sensitivity at high spatial frequencies in both conditions. As it is accepted that while parvocellular stream provides colour information, the magnocellular stream is sensitive to brief and fast objects of low spatial frequency,

the results implied an impairment of the magnocellular pathway. Thus, it was suggested that motion sensitivity was impaired during saccades since the magnocellular pathway sends signals to motion areas (Burr et al., 1994; Ross et al., 2001).

Although there is a loss of motion sensitivity during saccades and observers can detect a change or displacement, they do not experience a sense of disruption (Burr et al., 1982). Thresholds for a backward displacement of moving gratings were measured during saccades and in normal viewing. Thresholds for both conditions rose as a function of velocity. The threshold during saccades was about three times larger than that in normal viewing. While participants perceived disruption in normal viewing when a threshold was reached, during saccades they had no sense of disruption even though they detected the displacement. When a line of random dot triplets was rotated 90 degrees, participants perceived an obvious change when it was triggered by hand. However, when it was triggered during a saccade they did not feel disruption even though they noticed a change of orientation.

With each eye movement, a centre of the coordinate system is changed from the initial fixation point to the saccadic goal. During this transition it may be possible that certain stimuli presented during saccadic suppression are visible or even salient and the surrounding visual scene is blurred, but not disturbing, that is, the visual stimuli can be detected without any sense of disruption. The impairment of motion sensitivity by saccadic suppression (Burr et al., 1994; Ross et al., 2001) and elimination of the blur by visual masking (Wurtz, 2008) during saccades may play a

significant role in a smooth transition of coordinate system from one fixation to another.

1.3.2. Target displacement

Target displacement is not detected just before the onset of saccades and the suppression of target displacement is maximal during saccades (Bridgeman et al., 1975). The target displacement went undetected when the magnitude was less than one third of a saccade. It was proposed that degradation of visual information played a key role in suppressing target displacement since the target displacement was not detected although the retinal displacement of the target after the target displacement was larger than the magnitude of corollary discharge, which was supposed to cancel out the initial retinal displacement of the target before the target displacement. Failure to detect target displacement during saccades can also be related to the loss of motion sensitivity during saccadic suppression (Burr et al., 1994).

According to the reference object theory, detection of target displacement across saccades can be obtained by comparing pre-saccadic and post-saccadic locations of the target. The high threshold for detecting a target displacement might indicate either that spatial information about pre-saccadic and post-saccadic locations of objects is not available or that a comparison between the pre-saccadic and post-saccadic locations is not performed if it is not necessary. Continuous presence of visual objects immediately after saccades is a significant factor to maintain perceived stability of the objects. A saccadic target and a distractor were closely placed and either of them were displaced right or left. Participants' task was to report which one was displaced. The results showed that continuously present objects were perceived

as stable since blanked one was frequently perceived as displaced as long as displaced one was present after saccades. It was also shown that when both the target and the distractor were present after saccades without blanking, the detection of the saccadic target displacement was not better than that of the distractor displacement. In other words, non-target object can act as a stable reference (Deubel et al., 1998).

The blanking paradigm revealed information which improved detection of target displacement, That is, enhanced capability to assess the target's post-saccadic position relative to its pre-saccadic position (Deubel et al., 1996). Perceived direction of a saccadic target, which was displaced forward or backward during saccades, was measured. When the saccadic target was displaced during saccades and present after the saccades, the judgment on displacement direction showed a high inter-subject variability. The participants showed a strong tendency of reporting forward target displacements. This phenomenon was noticeable especially when there was no target displacement. When the saccadic target was blanked for 250ms after the onset of saccades, participants accurately reported the direction of target displacements and inter-subject variability was removed. It was put forward that the absence of a visual stimulus immediately after saccades destabilises the visual system and the system has to employ other available information such as efference copy or remembered target location. It was claimed that a precise extraretinal signal about the location of a saccadic target and its displacement is available and utilised especially when visual information is not available after saccades. Thus, the accurate evaluation of inter-saccadic target displacement implies presence of accurate information about pre-saccadic target position, magnitude and direction of saccades and target's retinal error after saccades.

1.4. Temporal misjudgements

1.4.1. With eye movements

Visual objects presented before saccadic eye movements are not only mislocalised, but temporal perception of them was also distorted. It was reported that perceived time of visual stimuli presented before saccades is compressed and temporal order of visual stimuli flashed just before saccades is reversed (Morrone, Ross et al., 2005). Perceived intervals between two pairs of horizontal bars were compared after larger horizontal saccades. For the test pairs, the interval was fixed at 100 ms and they were presented well before or just before the onset of saccades. The intervals of the test pairs were compared the variable intervals of the control pairs presented 2 seconds after the test pairs. The perceived interval of the test pairs presented between -400 and -200 ms before the onset of saccades was a mean of 100 ms whereas that of the test pairs presented between -100 and -50 ms before the onset of saccades was a mean of 50 ms. That is, the perceived interval of visual stimuli presented just before saccades was compressed. When participants made temporal order judgements of a pair of horizontal bars presented just before saccades, the temporal order was reversed for pairs of bars whose separation was small (20 – 44 ms and 44 – 75 ms bins). When the bar separation was large (75 – 200 ms bin), the temporal order judgement was accurate.

Lengthening of perceived duration of saccadic targets after saccades, which was termed as saccadic chronostasis, was observed (Yarrow et al., 2001). Participants made either 22° or 55° saccades to a numerical counter. A voluntary eye movement changed the digit from 0 to 1. The duration of the number 1 was varied and the subsequent numbers (2, 3, and 4) were presented for 1 s. Participants were required

to indicate whether the duration of the number 1 was longer or shorter than the duration of the subsequent numbers. The results showed that the subjective duration of the number 1 was 1 s while the actual duration was shorter than 1 s. It was claimed that the lengthening of the percept of the saccadic target illustrates backdating of the percept of the saccadic target to a moment before the onset of saccades. Therefore, the backward extension of perception of a saccadic target may be related to bridging the perceptual gap during the saccadic suppression to maintain perceptual continuity.

Contrary to this post-saccadic phenomenon, observers experience fixating a saccadic target before their eyes have actually landed on it (Hunt & Cavanagh, 2009). When observers moved their gaze to a clock with a hand moving at a rate of 1 rps and judged the time their eyes landed the clock, the perceived time was 39 ms earlier than the actual arrival time on the clock. In the control condition, the eyes were fixed and the clock moved to the location of the fixation. The perceived time was 27 ms later than the actual arrival time. Thus, this result implies a predictive remapping of the saccadic target just before the eye movement. However, the saccadic chronostasis implies a mechanism of a post-saccadic remapping of pre-saccadic visual space (Yarrow et al., 2001).

1.4.2. With manual movements

Anticipatory awareness of voluntary movements was observed. It was shown that the perceived time of the first keypress precedes the actual keypress by 96 ms (Haggard et al., 1999). Participants were requested either to prepare to type a string of one, three or five letters presented at the beginning of each trial during warning signals and type the letter string after a go signal in the Sternberg condition or to watch a

rotating clock and spontaneously type the presented string and give a verbal indication of the position of the clock hand at the time of the first keypress in the Libet condition. In the Stenberg condition, latency between the go signal and the first keypress was measured, while in the Libet condition, a time difference between real and indicated clock hand positions at the time of the first keypress was measured to see whether awareness of the first keypress was anticipatory or delayed. As it was suggested that motor programmes for each keypress were stored in a motor output buffer in a random order, the reaction time for the first keypress was expected to increase in proportion to the buffer size or the length of the string. If awareness of movement preceded the buffer search, a negative correlation between the time awareness for the first keypress and the reaction time for the first keypress would be expected. The results illustrated that in the Stenberg condition, the increase in the latency between the go signal and the first keypress was proportional to the length of the letter string, whereas in the Libet condition, the time of the first keypress was perceived earlier as the length of the letter string increased. Thus, it was suggested that an anticipatory awareness of intentional actions originated from cortical process of the action rather than sensory feedback.

The duration of tactile stimulation immediately after an arm movement is overestimated (Yarrow & Rothwell, 2003). Participants were instructed to make long (50 cm), short (15 cm) or double reaching movements to a strain gauge mounted on a vibrator. When participants first reached to the strain gauge, it was vibrating at 120 Hz. After variable time, it vibrated at 60 Hz, 120 Hz and then 60 Hz for 1000 ms respectively. The participants reported whether the duration of the first vibration (120 Hz) was longer or shorter than the subsequent three vibrations. The results

showed that participants overestimated the duration of the first vibration felt immediately after touching the vibrator by 90 – 120 ms compared to the static arm control condition. The backward extension of tactile perception to a moment during the arm movement is similar to saccadic chronostasis, which shows a backward extension of percept of a saccadic target to a moment around 50 ms before the onset of saccades. The difference is the manual chronostasis is not affected by the magnitude of movements.

Lengthening of percept of a visual object is not only restricted to saccades. Voluntary movements influence perceived time of visual stimuli (Park et al., 2003). The method was adopted from the saccadic chronostasis study (Yarrow et al., 2001). A change in the numerical counter was triggered by a key press or a voice command by observers. The results illustrated that the duration of visual stimulus was overestimated when the change of the counter was triggered by the key press or the voice command without delay. When a delay was inserted between a key press and a change of the numerical counter and the delay was estimated, the delay was overestimated. Thus, it was proposed that illusory extension of time would be experienced when voluntary actions trigger the onset of an event.

1.5. Facilitation of visual, auditory and tactile processing prior to saccadic eye movements

Processing of visual, auditory and tactile targets can be facilitated by linking different modalities. The links can be made either by covert shift of attention or by overt shift of attention.

Cross-modal links between vision, audition and touch were shown in covert spatial attention (Spence et al., 1998). Attention shifts by visual and auditory cues induced fast and accurate tactile discriminations when the cues and tactile targets were on the same side. Tactile cues presented prior to visual and auditory targets also induced faster and more accurate elevation judgements when the cues and visual and auditory targets were on the same side.

The pre-motor theory of attention claimed that when a goal-directed movement is prepared, the shared cortical circuits are activated for spatial attention. The theory put forward that the preparation to make an eye movement should improve capacity to process sensory information presented the location of the target (Rizzolatti et al., 1994).

Studies showed a close link between saccadic eye movements and shift of spatial attention (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). A shift of visual attention precedes saccadic eye movements (Hoffman & Subramaniam, 1995). This was shown by enhanced detectability of visual information presented at the location of intended saccades. This improvement took place before participants foveated on the stimulus array as the stimulus array was disappeared well before the onset of saccades. A second experiment was carried out to see if attentional allocation can be separated from saccadic eye movements. Better target detection was found at the location of saccadic goals regardless of where the participants were instructed to attend. Thus, the allocation of attention was determined by the direction of eye movements. In addition, it was shown that attention cues were not ignored since the saccades were faster when the attention cue

and the direction of saccades were congruent compared to when they were incongruent.

Auditory attention is shifted in the direction of intended saccades just as visual attention shifts to the location of intended saccades (Rorden & Driver, 1999). Participants fixated on the central fixation LED. They made a 15° eye movement either to the left or to the right saccade markers when the LED turned from yellow to either red or green. An auditory target was presented from one of four loudspeakers located above and below the saccade markers. The participants judged whether the sound came from the upper or lower loudspeaker regardless of its laterality. It was found that auditory elevation discriminations were faster for auditory targets presented on the same side as the direction of saccades. The improved discriminations were also observed in the trials in which auditory targets were terminated before the onset of saccades. Thus, auditory attention shifted towards saccade destination prior to saccadic eye movements.

A link between tactile attention and saccadic eye movements was demonstrated using a target detection paradigm (Juravle & Deubel, 2009; Rorden et al., 2002). It was shown that tactile attention shifted by saccadic eye movements can facilitate the processing of tactile stimuli (Juravle & Deubel, 2009). In Experiment 1, an auditory cue, either low or high, prepared participants to make an eye movement from a fixation cross either to the right or to the left index finger respectively. The offset of the auditory cue prompted the participant to execute the eye movement and a tactile stimulus was presented to one of the fingers for 100 ms. The tactile stimulus was an increase in the vibration intensity (2.9 V, 140 Hz) from the base vibration intensity

(0.63 V, 60 Hz) which was presented with the auditory cue from the beginning of each trial. Participants were requested to respond to the tactile stimulus by pressing the foot pedal. The results showed that tactile stimuli presented at the finger of the planned saccade were detected faster than those presented at the opposite finger of the planned saccade. Thus, tactile attention shifts to the location of saccades and facilitates the processing of tactile stimuli.

1.6. Modulations of tactile and visual perception around manual movements

Sensory consequences of self-generated movements were shown to be attenuated by efference copy of a motor command according to forward models (Blakemore et al., 1999; Shergill et al., 2003). It was also illustrated that externally-generated tactile stimuli were also attenuated prior to, during and after movements (Shimazu et al., 1999; Starr & Cohen, 1985; Voss et al., 2006). However, the pre-motor theory of attention supports enhanced tactile processing during action preparation (Rizzolatti et al., 1994).

When a force was self-generated, the perception of the force was attenuated by about a half. Consequently, self-generated forces could not match externally-generated forces of the same magnitude (Shergill et al., 2003). When participants were requested to match perceived forces, which were delivered to the left index finger by a torque motor, by pressing on the left index finger through a force transducer using the right index finger, the forces generated by the right index finger were significantly higher than the forces applied by the torque motor.

Perception of self-administered tactile stimulation was attenuated compared to that of tactile stimulation delivered externally and the attenuation was affected by temporal and spatial relationships between sensory predictions of tactile stimuli and actual sensory feedbacks (Blakemore et al., 1999). For self-administered stimulation, participants moved a robot arm with their left hand to deliver a tactile stimulus on their right palm via a second robot. They reliably rated self-administered stimuli as being less ticklish, intense and pleasant than when they were externally delivered by a robot. In the subsequent experiments, time and direction of tactile stimuli were manipulated. There was a delay between the movement of the left hand and delivery of tactile stimuli on the right hand. The direction of the tactile stimuli was modulated as a function of the direction of the left hand movement. The rating of ticklishness increased as the delay and the perturbation increased. It was suggested that the efference copy of the motor command could not cancel the sensory consequence of the left hand movement because there was an unpredicted discrepancy between the sensory prediction of the movement and the actual sensory feedback as a result of the delay and the perturbation.

According to pre-motor theory, different motor tasks can activate different cortical circuit for spatial attention. The theory proposed that the preparation to reach a target is expected to enhance capacity to process sensory information presented the location of the target in the same way as the preparation to make an eye movement does (Rizzolatti et al., 1994).

A link between visual attention and reaching movements, similar to the link between visual attention and saccadic eye movements, was found (Deubel & Schneider, 1998).

In a dual-task paradigm, participants made a reaching movement and indicated the identity of the discrimination symbols ('E' or '3') centred between distractors. The discrimination targets and the distractors were disappeared before the onset of the reaching movements. The results showed that discrimination of mirror image symbols was better when the symbol was the target for the reaching movements than when they were different. Thus, it was argued that it is not possible to maintain perceptual processing capacity for discriminating targets while directing a movement to a spatially irrelevant location. It was also suggested that preparation of a goal-directed action implied in the dorsal stream combines perceptual capacity of the ventral stream with the target object.

Action preparation can improve the processing of tactile stimuli (Juravle & Deubel, 2009). In Experiment 2, an auditory cue, either low or high, prepared participants to lift the right or left index finger respectively while fixating on a central fixation cross. The offset of the auditory cue prompted the participant to execute finger-lifting movement and a tactile stimulus was presented to one of the fingers for 100 ms. The tactile stimulus was an increase in the vibration intensity from the base vibration intensity which was presented with the auditory cue from the beginning of each trial. Participants were requested to respond to the tactile stimulus by pressing the foot pedal. The results showed that tactile stimuli presented at the finger of the planned movement were detected faster than those presented at the opposite finger of the planned movement. Thus, the shift of covert tactile attention to the location of the planned movement improved the processing of tactile stimuli. It was argued that the timing of the tactile target delivery is a crucial factor and that the processing of

tactile stimuli was facilitated when the tactile target was delivered during the response-preparation period rather than the response-execution period

An event-related potential (ERP) study illustrated that shifts of tactile attention can be induced by the covert preparation of unimanual responses (Eimer et al., 2005). ERPs were recorded during the interval between a response-hand selection cue and a subsequent action cue (Go/Nogo signal) while participants were preparing to lift their left or right index finger. During the response preparation period before the action cue (Go/Nogo signal), three attentional ERP components were observed. At anterior recording sites, there was an initial negativity (starting 350 ms after the hand-selection cue) over the hemisphere contralateral to the cued attentional shift compared to the hemisphere ipsilateral to the cued attentional shift ('anterior directing attention negativity, ADAN). This frontal negativity was followed by parietal positivity (starting 600 ms after the cue) over the contralateral hemisphere ('late directing attention positivity', LDAP) at posterior recording sites. Another subsequent contralateral negativity (starting 900 ms after the cue) was recorded over the primary motor cortex ('lateralised readiness potential', LRP). It was suggested that the ADAN and LDAP components are related to attentional orientating processes and the LRP is related to motor preparation. Somatosensory ERP components were boosted when task-irrelevant tactile stimuli were delivered to the prepared finger early (520 ms after the hand-selection cue) or late (920 ms after the hand-selection cue) during the response preparation period. When the tactile stimuli were delivered early, the N140 component was increased for tactile stimuli delivered to the cued index finger compared to those delivered to the uncued index finger in both contralateral and ipsilateral hemispheres (F3/4 and C3/4) to the stimulated hand.

When the tactile stimuli were delivered late, the N140 component was also increased for the tactile stimuli delivered to the cued finger in the contralateral hemisphere (F3/4 and C3/4) to the stimulated finger. During this late period, the P90 component was boosted for the stimuli delivered to the cued finger in the ipsilateral hemisphere (F3/4 and C3/4) to the stimulated finger.

However, studies reported attenuation of somatosensory evoked potentials (SEPs) before the onset of movements (Shimazu et al., 1999; Starr & Cohen, 1985). An electric stimulus was delivered to the right median nerve at the wrist after an auditory warning signal. Participants were instructed to extend the right fingers on receiving the stimulation. The SEP was not confounded by afferent input induced by the movement as the mean of EMG activities was around 75 ms. The frontal N30, parietal P30 and central N60 components of the SEP were shown to be gated compared to the SEP components at rest. It was proposed that the attenuation of the SEP components must have originated from the central area of motor preparation as the tactile stimulation preceded the finger movements (Shimazu et al., 1999).

It was also demonstrated that cutaneous sensory thresholds were elevated during movement (Angel & Malenka, 1982). Electric shocks were delivered to the right index finger while it remained stationary or was moving at one of three velocities. The results showed that the detectability of the electric shocks was negatively correlated with the speed of finger movement. As the speed of finger movement increased, there was also an increase in sensory suppression.

A relationship between human muscular sense and movements was investigated (Collins et al., 1998). Participants were instructed to report muscle twitches while making fast (3 Hz) or slow (1 or 0.5 Hz) flexion-extension wrist movements. Muscular sense was also tested while participants remained at rest or the movements were passively made. It was shown that muscular sense was significantly attenuated by the fast movement condition compared to the slow, passive or static conditions. The attenuation during slow and passive movements was not different from the static condition. When the participants were requested to make reaching movements to touch or grasp a target, muscular sense was significantly attenuated when reaching movements were made with the stimulated arm compared to when the arm remained static or reaching movements were made with the unstimulated arm. The time course of the attenuation was also investigated. A response cue to initiate the wrist movement was preceded 1s by a warning signal. 120-160 twitches were applied during the interval between the warning signal and just after the end of the movement. Attenuation of twitch perception was observed before, during and after the movement compared to the static condition. It was suggested that the origin of the attenuation was central as the attenuation was found during the active movement, but not passive movement and was observed prior to the onset of the movements.

Dependency of sensory attenuation on central signals generated during motor preparation was demonstrated (Voss et al., 2006). Electrical cutaneous stimuli were delivered to the left and right index finger and point of subjective equality (PSE) was measured. The left finger acted as a reference and received electrical stimuli of a fixed intensity. Participants were requested to lift the right index finger with the last of three auditory signals and the right finger received stimuli of a varied intensity.

The movement of the right index finger triggered the onset of cutaneous stimulation. The PSE value was increased by 169 % in the movement condition compared to that in the control condition in which the left finger remained relaxed. In other words, the cutaneous stimulation to the moving finger had to be 2.69 times stronger to be perceived as equal in intensity as the stimulation to the finger at rest. When the movement was delayed by transcranial magnetic stimulation (TMS) applied to the left primary motor cortex and cutaneous stimuli were delivered during the delayed period, the PSE value was increased by 147 % compared to that of the control condition. Thus, it was put forward that an efferent signal prior to the movement is the main factor for sensory suppression and the actual movement is not essential. However, when cutaneous stimuli were delivered 50 – 120 ms prior to the onset of the movement, nonsignificant attenuation was observed (25 % increase in the PSE value). As the cutaneous stimuli were applied at the onset of the movement in the movement condition and during the delayed period in the TMS-delayed movement condition, it can be postulated that sensory suppression originated from an efferent signal during motor preparation mainly functions during the movement rather than prior to the movement onset.

1.7. Overview of empirical studies

The aim of this thesis is to further investigate the effects of movements on modulations of visual and tactile perception and elucidate theoretical relevance of the modulations to hypotheses or theories suggested by previous studies.

It appears that visual stability is maintained in the unstable and rapidly changing environment. Regardless of perceived stability of the world, retinal displacements of

visual stimuli are not compensated by efference copy of a motor command and visual stimuli presented around eye movements are mislocalised in the direction of saccades or towards a saccadic goal. Thus, the first experiment (Chapter 2) was designed to further investigate spatial mislocalisation of visual stimuli presented prior to the onset of saccades. The second experiment (Chapter 3) was designed to examine the relevance of saccadic chronostasis to remapping of visual space since it was suggested that a mechanism of saccadic chronostasis might fill in a perceptual gap during saccadic suppression. The third (Chapter 4) and fourth (Chapter 5) experiments were designed to investigate how visual stimuli in the pre-saccadic coordinate were updated in the post-saccadic coordinate, for example, relative to saccade landing sites, the location of post-saccadic target or the location obtained using efference copy.

Studies contradict each other on changes in tactile perception around manual movements. Perception of externally-generated tactile stimuli applied around manual movements was either attenuated or enhanced. Further investigation into modulations of tactile perception is needed as very few studies were carried out for clarification. Thus, behavioural (Chapter 6) and fMRI (Chapter 7) studies were conducted using the same experimental paradigm.

The final chapter includes summaries and conclusions of each chapter and suggestions for future studies.

Chapter 2: An investigation into spatial mislocalisation prior to the onset of saccade

2.1. Introduction

Retinal images are displaced whenever eyes move. It was believed that these retinal displacements were adjusted by efference copy of a motor command (von Holst, 1954) or a corollary discharge (Sperry, 1950) and the stable perception of the surroundings is maintained. However, it was found that retinal displacements of visual stimuli were not compensated (Matin & Pearce, 1965) and visual stimuli were mislocalised in the direction (Dassonville et al., 1992; Honda, 1997; Schlag & Schlag-Rey, 1995) or in the opposite direction (Jeffries et al., 2007) of saccades or towards a saccadic goal (Burr et al., 2001; Jackson et al., 2005; Kaiser & Lappe, 2004; Morrone et al., 1997; Ross et al., 1997). Visual information after saccades was found to be a significant factor for the perception of spatial compression towards a saccadic goal (Lappe et al., 2000), but the compression of visual space was shown without post-saccadic visual references (Awater & Lappe, 2006; Morrone et al., 2005). It was suggested that spatial compression of visual space towards a saccadic goal might indicate a transition of the coordinate system from a centre of the pre-saccadic coordinate system to a centre of the post-saccadic coordinate system (Burr et al., 2001; Morrone et al., 1997). However, there is no empirical evidence to support the hypothesis.

The present study was designed to further investigate spatial mislocalisation of visual objects presented prior to the onset of saccades. The present study adopted a pointing

paradigm (Burr et al., 2001). A similar method using a hammer showed accurate localisation of visual objects flashed prior to, during and after saccades (Hansen & Skavenski, 1985). In the study, participants were requested to point to the perceived location of visual objects while they were fixating the saccadic goal. Previous studies did not control participants' eye movements immediately after saccades before they responded although the visual space is remapped with each eye movement and this remapping could have an effect on the results.

Visual objects presented in the previous studies of spatial localisation appeared to be highly predictable as few stimuli were presented. In the present study, nine vertical bars were presented in the whole visual field including the initial fixation point and the saccadic target and participants made eye movements in two directions (left-to-right trials or right-to-left trials).

Previous studies showed that mislocalisation started from 50 ms before the onset of saccades (Burr et al., 2001; Honda, 1993; Jackson et al., 2005; Ross et al., 1997). Saccadic suppression of visual sensitivity was shown to begin around 50 ms before the onset of saccades and last until around 50 ms after the offset of saccades (Diamond et al., 2000) and the time course of saccadic suppression and that of spatial compression are similar (Ross et al., 2001). A phenomenon termed as saccadic chronostasis proposed that backward extension of perception of a saccadic target to a moment around 50 ms before the onset of saccades may be linked to bridging a perceptual gap during the saccadic suppression to maintain perceptual continuity (Thilo & Walsh, 2002; Yarrow et al., 2001). Thus, the range of data collected in the

study was within 100 ms before the onset of saccades and the behavioural difference was observed between two intervals (-100 to -50 ms and -50 to 0 ms).

If the visual system held accurate information about visual objects presented before the onset of saccades, the localisation of visual objects would be accurate. Otherwise, a pattern of mislocalisation errors would be expected either in the direction of saccades or in the opposite direction of saccades or both.

2.2. Methods

2.2.1. Participants

Six right-handed observers, three males and three females, with normal or corrected vision participated in the study. Their mean age was 26.7 (range: 24 ~ 32).

2.2.2. Apparatus/Materials

A pupil and dual first Purkinje image Video Eyetracker with an EyeLock headrest was fixed on a Vision Science height-adjustable workbench (Cambridge Research System). The sampling frequency of the video eye-tracker was 250 Hz and the accuracy was 0.25 - 0.125° of visual angle. The headrest was used to maintain the participant's head position and the viewing distance (400 mm). During the experiment, the stimuli were perceived binocularly, but only the movement of the right eye was recorded. The investigator could see a video image of the participant's eye displayed on a separate screen, which made it possible to monitor the eye position in the eye tracker throughout the experiment. In a built-in calibration procedure, twenty white circular dots (subtending 0.25°) presented on a grey

background. They were randomly presented one by one for 500 ms in a 5 x 4 grid calibration area set to 70% of the total screen area. The calibration procedure was repeated until all the dots were accurately foveated.

The experiment was written in Matlab and the stimuli were generated utilising Cogent Graphics (developed by John Romaya at the Laboratory of Neurobiology, Wellcome Department of Imaging Neuroscience, UCL, UK), MATLAB CRS (Cambridge Research System) Toolbox and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a 17-inch ELO Touchscreen ($46^\circ \times 37^\circ$) with a resolution of 1024 x 768 pixels at a frame rate of 60 Hz.

The stimuli were composed of a black fixation cross (subtending 0.86°) and a vertical green bar ($1.5^\circ \times 37^\circ$) presented for one screen refresh rate (16.7 ms) on a red background. The fixation cross was presented 7° to the left the midline of the screen and jumped to 7° to the right of the midline of the screen for the left-to-right trials or vice versa for the right-to-left trials. The probing bar was presented at one of nine positions. The positions of the probing bar presented to the left of the midline of the screen were denoted by negative numbers (-14° , -10.5° , -7° , -3.5°) and the positions of the probing bar presented to the right of the midline of the screen were denoted by positive numbers (14° , 10.5° , 7° , 3.5°). The position of the probing bar presented at the midline was denoted as 0° (see Figure 2.1). A speaker was used to play an auditory tone (1000 Hz) and the study was carried out in a dimly lit laboratory.

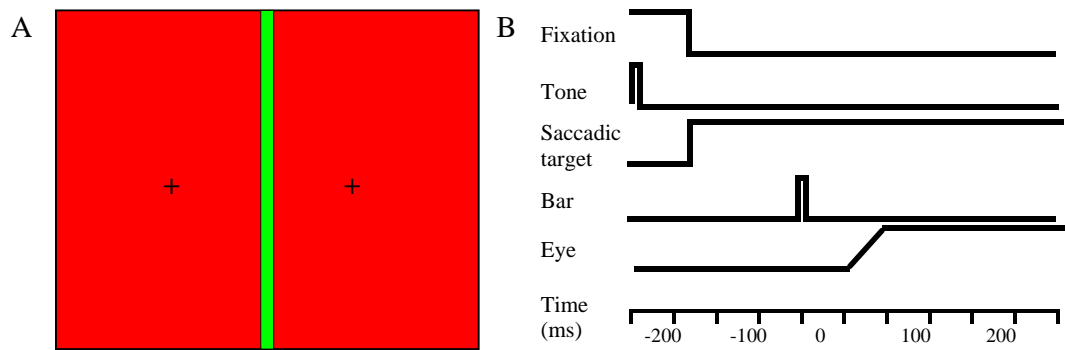


Figure 2.1: Stimuli (A) and time course (B) for the spatial localisation task.

2.2.3. Design

A two-way (3 x 2) repeated measures design was utilised. There were two independent variables, Location and Time. The Location variable represented the positions of the probing bar and consisted of three levels: Before, Middle, After. The positions of the probing bar were collapsed to simplify the analysis and the collapsed location could represent the whole spatial area. Before referred to two positions (-10.5° and -14° for the left-to-right trials and 10.5° and 14° for the right-to-left trials) before the fixation cross. Middle referred to three positions (-3.5° , 0° and 3.5° for both the left-to-right trials and the right-to-left trials) between the fixation cross and the saccadic target. After referred to two positions (10.5° and 14° for the left-to-right trials and -10.5° and -14° for the right-to-left trials) beyond the saccadic target. The Time variable represented presented time of the probing bar and consisted of two levels: -100 to -50 ms and -50 to 0 ms. -100 to -50 ms represented an interval between -100 and -51 ms before saccadic onset and -50 to 0 ms represented an interval between -50 and 0 ms before saccadic onset. The dependent variable was a

mislocalisation error (Deg) between the veridical bar position and the apparent bar position.

2.2.4. Procedure

Observers were required to make a saccade from a fixation cross presented 7° to the left of the midline of the screen to an identical saccadic target presented 7° to the right of the midline for the left-to-right trials or vice versa for the right-to-left trials. They were instructed to respond using their index finger by pointing to the position of a vertical probing bar presented briefly just before the saccade while fixating the saccadic target. The stimuli were presented on a uniform red background.

Calibration was carried out before each block began. Observers viewed a 17-inch ELO Touchscreen ($46^\circ \times 37^\circ$) from a distance of 40 cm through a liquid crystal lenses. Once the eye-tracker had determined that the observer was correctly fixating within 2.86° (20 mm) around a fixation cross for 500ms, a tone was presented for 150 ms, indicating the start of each trial. After a various duration ($M = 1000$ ms, $SD = 125$ ms), a saccadic target was presented to the other side of the screen. The observers made a 14° saccade to the saccadic target and pointed to the position of a probing bar ($1.5^\circ \times 37^\circ$). The screen then went blank (red background). The observers were asked not to blink after the tone until they had responded (see Figure 2.2).

The order of the bar positions was pseudo-randomly determined in each block by the computer. The saccadic latency of each trial was measured and a median latency was determined from every nine trials. The median latency was used to predict a saccadic

onset of a subsequent trial. The probing bar was presented 35 ms (for one half of each trial type) or 75 ms (for the other half of each trial type) before saccadic onset.

Each block consisted of 36 trials (half left-to-right trials and half right-to-left trials). Observers performed two sessions on a different day. Each session was composed of two practice blocks and ten experimental blocks.

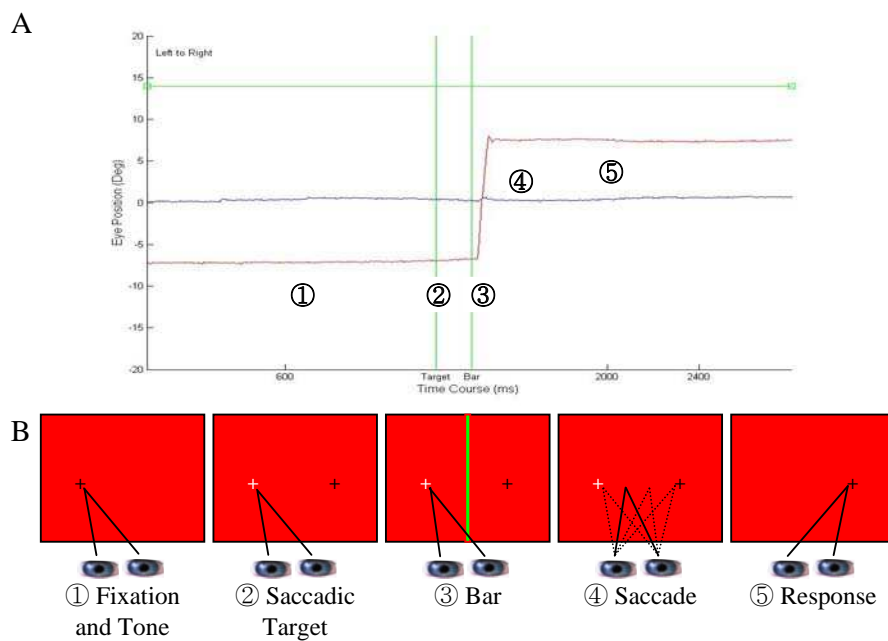


Figure 2.2: Plot of eye movement trace (A) and Schematic illustration of experimental procedure (B). The plot was used to analyse each trial. The red trace represents horizontal eye movements (x coordinate) and the blue trace represents vertical eye movements (y coordinate). The two solid vertical green lines represent a saccadic target time (Target) and a probing bar time (Bar) and the horizontal solid green line represents the position of the probing bar presented on the screen. The numbers on the plot correspond to the time course of the experimental procedure. In each trial, a tone went off when participants fixated a black cross (①). After an interval, a saccadic target was presented on the other side of the screen (②). A vertical green bar was presented (③) before they made an eye movement to

the saccadic target (④). They indicated a perceived position of the bar using their index finger while fixating the saccadic target (⑤). The white cross represents a trace of the fixation cross.

2.3. Results

Data analysis:

Eye movement trace for each trial was plotted using x and y coordinates from eye-position data recorded every 4 ms. Noisy trials showing excessive blinks, head movements or an early eye movement to the saccadic target were discarded. The latency was defined as a time difference between the onset of a saccadic target and the initiation of the saccade, which was determined when a difference between two data points exceeded more than 0.5° in the x coordinate (see Figure 2.2). Mislocalisation errors between the veridical bar position and the apparent bar position were obtained. For the left-to-right trials it was calculated by subtracting the veridical bar position from the apparent bar position and for the right-to-left trials it was calculated by subtracting the apparent bar position from the veridical bar position. Thus, a positive value indicated a mislocalisation error in the direction of the saccade and a negative value indicated a mislocalisation error in the opposite direction of the saccade.

Scatter graphs were used to plot mislocalisation errors of a probing bar presented at nine positions. Mislocalisation errors for the left-to-right trials and those for the right-to-left trials were separately plotted. As the patterns of mislocalisation errors for both trial types were near-identical, data from both trial types were collapsed. For example, mislocalisation errors of a probing bar at -14° (-10.5° , -7° , -3.5° , 0° , 3.5° ,

7°, 10.5°) for the left-to-right trials and 14° (10.5°, 7°, 3.5°, 0°, -3.5°, -7°, -10.5°) for the right-to-left trials were pooled. The collapsed data were presented as a left-to-right trial type. Two positions (-10.5° and -14°) of the collapsed data were pooled and referred to as a Before location. Three positions (-3.5°, 0° and 3.5°) were pooled and referred to as a Middle location. Two positions (10.5° and 14°) were pooled and referred to as an After location. Data of probing bars presented at the fixation cross and the saccadic target were excluded for the analysis. The collapsed data in each location were divided with regard to intervals between the onset of a probing bar and the initiation of saccades: -100 to -50 ms and -50 to 0 ms before saccadic onset. For statistical analysis, mean mislocalisation errors for two intervals (-100 to -50 ms and -50 to 0 ms) of three locations (Before, Middle and After) were calculated for each individual (see Figure 2.3).

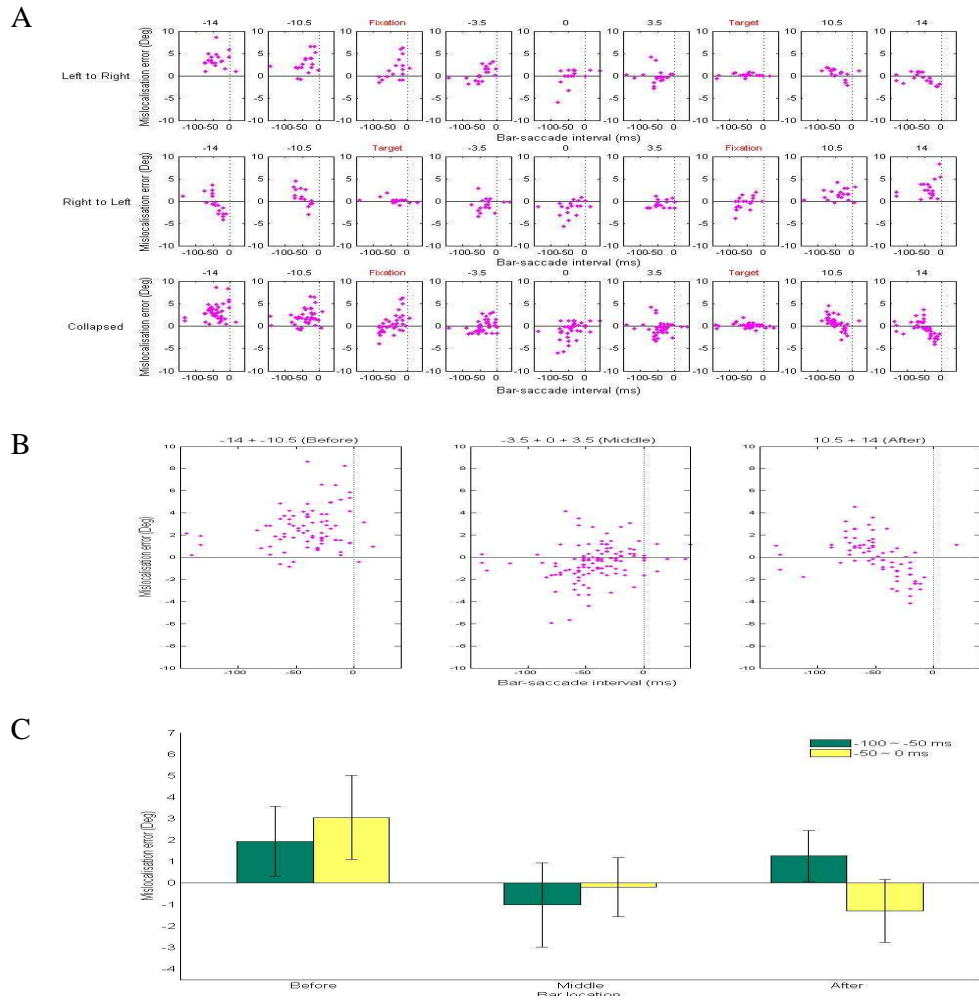


Figure 2.3: Procedure of data analysis for each participant.

Mislocalisation errors for the left-to-right trials and those for the right-to-left trials were separately plotted using scatter graphs. As the patterns of mislocalisation errors for both trial types were near-identical, data from both trial types were collapsed and presented as a left-to-right trial type (A). Two positions (-10.5° and -14°) before the fixation cross, three positions (-3.5° , 0° and 3.5°) in the middle and two positions (10.5° and 14°) after the saccadic target of the collapsed data were pooled and referred to as Before, Middle and After locations respectively (B). The collapsed data in each location were divided in terms of two bar-saccade intervals: -100 to -50 ms and -50 to 0 ms before saccadic onset. Mean mislocalisation errors for two intervals of three locations were calculated for each individual. Error bars represent standard deviations (C).

A two-way 3 (Location: Before, Middle, After) x 2 (Time: -100 to -50 ms, -50 to 0 ms) repeated measures ANOVA was carried out on mean mislocalisation errors of 6 observers (see Figure 2.4). There was a significant main effect of Location, $F(2, 10) = 17.02$, $p = .001$, $\eta_p^2 = 0.77$. Post-hoc tests using a Bonferroni adjustment showed that there was a significant difference in mean mislocalisation errors between Before ($M = 2.63$, $SEM = 0.64$) and Middle ($M = -0.42$, $SEM = 0.26$) locations; $F(1, 5) = 28.50$, $p = .009$, $\eta_p^2 = 0.85$ and between Before ($M = 2.63$, $SEM = 0.64$) and After ($M = -0.11$, $SEM = 0.22$) locations; $F(1, 5) = 14.06$, $p = .040$, $\eta_p^2 = 0.74$. However, there was no significant difference in mean mislocalisation errors between Middle ($M = -0.42$, $SEM = 0.26$) and After ($M = -0.11$, $SEM = 0.22$) locations; $F(1, 5) = 0.70$, $p = 1.000$, $\eta_p^2 = 0.12$. The results showed that there was no significant main effect of Time, $F(1, 5) = 0.17$, $p = .697$, $\eta_p^2 = 0.03$. However, there was a significant interaction between Location and Time, $F(2, 10) = 68.11$, $p < .001$, $\eta_p^2 = 0.93$. A simple main effects analysis illustrated that there was a significant effect of Time in Before ($F(1, 5) = 94.86$, $p < .001$, $\eta_p^2 = 0.95$), Middle ($F(1, 5) = 28.76$, $p = .003$, $\eta_p^2 = 0.85$) and After ($F(1, 5) = 41.37$, $p = .001$, $\eta_p^2 = 0.89$) locations.

One-sample t-tests were carried out on mean mislocalisation errors for two intervals of three locations. In the Before location, mean mislocalisation errors were positive and significant for both -100 to -50 ms ($M = 2.11$, $SD = 1.58$, $t(5) = 3.27$, $p = .022$) and -50 to 0 ms ($M = 3.16$, $SD = 1.57$, $t(5) = 4.93$, $p = .004$) intervals. In the Middle location, the mean mislocalisation error for the -100 to -50 ms interval was negative and significant ($M = -1.14$, $SD = 0.51$, $t(5) = -5.48$, $p = .003$), but that for the -50 to 0 ms interval was not significant ($M = 0.31$, $SD = 0.88$, $t(5) = .86$, $p = .427$). In the

After location, the mean mislocalisation error for the -100 to -50 ms interval was positive and significant ($M = 1.03$, $SD = 0.97$, $t(5) = 2.61$, $p = .048$), but that for the -50 to 0 ms interval was negative and significant ($M = -1.26$, $SD = 0.19$, $t(5) = -15.87$, $p < .001$).

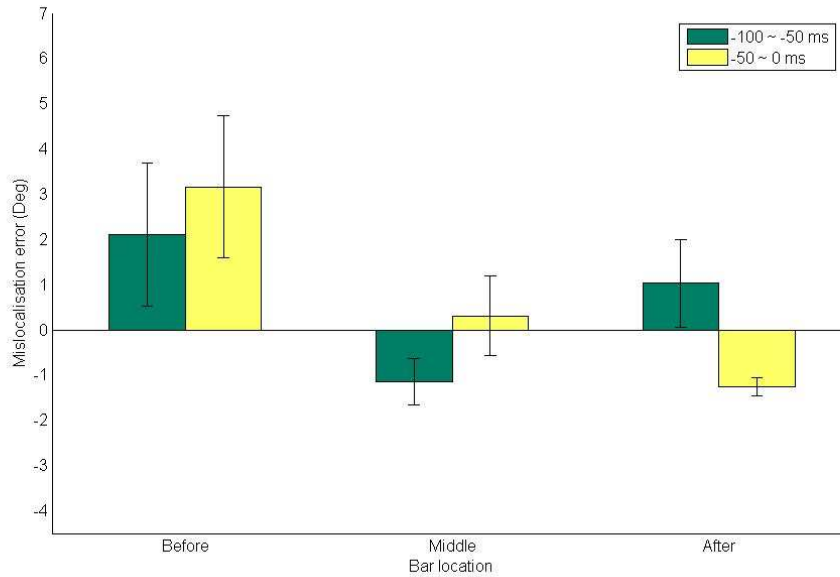


Figure 2.4: Mean mislocalisation errors of 6 observers.

Mean mislocalisation errors are presented with regard to two separate intervals (-100 to -50 ms and -50 to 0 ms) of three different locations (Before, Middle, After). Error bars represent standard deviations.

2.4. Discussion

The significant interaction between Location and Time and the significant effects of Time in three locations indicate that two different remapping mechanisms are involved in two separate intervals. At the interval of -50 to 0 ms, the mean mislocalisation error in the Before location was in the direction of saccades, but that

in the After location was in the opposite direction of saccades. They together show a pattern of spatial compression towards the saccadic target. At the interval of -100 to -50 ms, the mean mislocalisation errors in the Before and After locations were in the direction of saccades, but that in the Middle location was in the opposite direction of saccades. The mean mislocalisation errors in the Before and Middle locations show a pattern of spatial compression towards the initial fixation cross.

The double compressions within 100 ms before the onset of saccades can be indicative of an effortless transition of a coordinate system from one fixation to another (Burr et al., 2001; Ross et al., 2001). In a visual memory study, observers showed a tendency to mislocalise a briefly presented visual stimulus closer towards the centre of gaze, regardless of presence of the fixation point (Sheth & Shimojo, 2001). The stimuli presented both left and right visual fields were perceived as compressed towards the centre of gaze. When observers made an eye movement to another fixation point and remained fixated while responding, the pre-saccadic visual stimulus presented at least 500 ms before the onset of saccades was still mislocalised towards the initial fixation point. In other words, the visual stimulus presented well before the onset of saccades was remapped in exocentric coordinates rather than egocentric coordinates. However, visual stimuli presented within 50 ms before saccades were perceived as compressed towards a saccadic goal and thus remapped in egocentric coordinates rather than exocentric coordinates (Burr et al., 2001; Jackson et al., 2005; Lappe et al., 2000; Ross et al., 1997). Thus, the post-saccadic remapping of pre-saccadic visual space in the present study demonstrates that stimuli presented at the interval of -100 to -50 ms are represented in the coordinate system

with the initial fixation point as a centre and the stimuli presented at the interval of -50 to 0 ms are represented in the coordinate system with the saccadic goal as a centre.

The separate representation of pre-saccadic visual space at two intervals in the present study illustrates that the post-saccadic remapping employs spatially as well as temporally accurate memory of pre-saccadic visual stimuli. It seems that stimuli presented at the interval of -100 to -50 ms were remapped in the coordinate system before transition occurred and stimuli presented at the interval of -50 to 0 ms were remapped in the coordinate system after transition occurred. That is, a visual input coded in the pre-saccadic coordinate was updated in the post-saccadic coordinate (Duhamel et al., 1992). 58 % of the visuomovement cells in the frontal eye field also discharged for a vanished stimulus after saccades (Umeno & Goldberg, 2001). It was suggested that the remapping of pre-saccadic visual space after saccades plays a role in linking information about a stable object from one fixation to another (Gottlieb, 2007).

Some information about the pre-saccadic stimulus was kept and used after saccades (Khayat et al., 2004a, 2004b). Monkeys were trained to make a sequence of two saccades along a target curve and to ignore the other distracting curve. Each trial started when the monkey fixated on the initial fixation (FP1). The next fixation (FP2) and the final fixation were connected on the target curve, but they were disconnected on the distracting curve. In normal trials, the monkeys made a saccade to FP2 and then to the final fixation at the end of the target curve. Saccadic reaction time between the offset of FP2 and the onset of the saccade to the final fixation was measured. In catch trials, during the first saccade from FP1 to FP2 the previously

disconnected segment was connected and vice versa. The catch trials tested effects of incongruence between pre-saccadic and post-saccadic visual information. If the monkeys had no information about the pre-saccadic stimulus, there would be no difference in saccadic reaction time between normal trials and catch trials. Saccadic reaction time for the normal trials was significantly shorter than that for the catch trials. The early neural activity relies on the pre-saccadic visual information rather than the post-saccadic one (Khayat et al., 2004a). Receptive fields of area V1 neurons were located on a segment between FP2 and the final fixation of the target or distracting curve while the monkeys were fixating on FP1 before making a saccade to FP2. The neural activity to the target segment was greater than that to the distracting segment. This pre-saccadic attentional modulation appeared to be restored after saccades. In normal trials, a saccade to FP2 brought a receptive field to the target or distracting segment. In catch trials, a saccade to FP2 triggered a change in the stimulus configuration. A target segment became a distracting segment and vice versa. It took significantly longer time for the catch trials to show attentional modulation with the neural activity to the target segment greater than that to the distracting segment. This was because the early attentional modulation in the catch trials showed a greater neural activity to the distracting segment than to the target segment since there was incongruence between the pre-saccadic and post-saccadic stimulus configuration. Thus, the early neural activity relies on the pre-saccadic visual information rather than the post-saccadic one (Khayat et al., 2004a). It was suggested that predictive and useful pre-saccadic information is incorporated into a new coordinate system with a new fixation as a centre (Melcher, 2005). Visual information such as tilt, basic shape and face can be maintained across saccades and impinge on subsequent perception of a stimulus in the same location. When an

adaptor and a test stimulus were presented in the same location, visual-form aftereffects were transferred across saccades.

The compression of pre-saccadic stimuli closer towards a saccadic goal illustrates that visual stimuli presented within 50 ms before saccades are remapped in a coordinate system with the saccadic goal as a centre, that is, a predictive remapping. 44% of the parietal neurons showed characteristics of predictive remapping (Duhamel et al., 1992). The receptive field of the neurons shifted about 80 ms before the onset of saccades to remap a stimulus in the post-saccadic location of the receptive field. This type of remapping seems to rely on the existence of visual stimuli and the implementation of saccades. Mere shifting of attention to a saccadic target did not induced discharge of the neurons. 66 % of visual cells in the frontal eye field discharged for a flashed stimulus before saccades (Umeno & Goldberg, 2001). They also showed a predictive response to a continuously present stimulus. Tilt adaptation was transferred from the initial fixation position to the future fixation position before saccades (Melcher, 2007). The adapting stimulus was shown at the initial fixation position. A test stimulus was presented at either the initial fixation position or the future fixation position before or after saccades. Before onset of saccades there was a remarkable drop in the tilt adaptation aftereffect (TAE) at the initial fixation position, but there was a large increase in the TAE at the future fixation position before saccades. There was no transfer of TAE to a future fixation position by a mere shift of spatial attention. A part of the full TAE at the initial fixation position after saccades also showed an integration of pre and post-saccadic information. The continuous increase of the TAE at the future fixation position after saccades illustrates that predictively remapped tilt adaptation was updated after

saccades in a new coordinate system just as the probing bar remapped predictively into the coordinate system with the saccadic goal as a centre was represented in the post-saccadic coordinate system after saccades. A predictive interhemispheric remapping before saccades was demonstrated using event-related potentials (Parks & Corballis, 2008). Horizontal saccades caused a visual stimulus to shift either within the same visual field (within condition) or between two visual fields (cross condition). The within condition required remapping within the same hemisphere whereas the cross condition required remapping between two hemispheres. The results illustrated that in the hemisphere ipsilateral to the visual stimulus, two pre-saccadic potentials such as antecedent potential (AP) and spike potential (SP) showed greater amplitudes for the cross condition compared to the within condition.

There is growing evidence that visual memory is closely related to compression of visual space towards a saccadic goal. The present study showed that at the interval of -50 to 0 ms, the mean mislocalisation errors were increased as the visual stimuli were presented farther away from the saccadic goal (see Figure 2.3 and 2.4). Peripherally presented flashed stimuli were mislocalised towards a fixation cross and the magnitude of foveal mislocalisation was enlarged as a function of eccentricity of presentation (Musseler et al., 1999; Osaka, 1977; Sheth & Shimojo, 2001; van der Heijden et al., 1999). Stimulus contrasts affect perception and visual memory. Low-contrast random visual stimuli were more difficult to process than high contrast stimuli (Harley et al., 2004). Less obvious stimuli can cause larger mislocalisation errors. Thus, stimulus contrast can have a strong effect on compression of visual space. Low contrast probes induced greater compression than high contrast probes (Michels & Lappe, 2004). In the same vein, when stimuli with near-threshold or

above-threshold luminance were presented in the dark-adapted or light-adapted conditions, near-threshold stimuli with low visibility showed larger mislocalisation errors than more conspicuous above-threshold stimuli (Georg et al., 2008). In a dark room, visual stimuli presented in the retinal periphery were mislocalised towards a fixation point (Osaka, 1977; Sheth & Shimojo, 2001). After a dark adaption, participants were instructed to point to the location of a target presented in the periphery while fixating on a fixation point. Mislocalisation errors were made towards the fixation point and increased as a function of retinal eccentricity of the target (Osaka, 1977). It was suggested that pre-saccadic spatial compression would not occur without a visual spatial reference present after saccades and post-saccadic visual references play the most significant part in transsaccadic spatial localisation (Lappe et al., 2000). However, it was demonstrated that post-saccadic visual references are not essential to induce compression of visual space (Morrone et al., 2005). A translucent shutter was used to remove visual references. In a dark room, with the closure of the shutter, the display of the monitor was changed from red to black. A saccadic target was displayed while the shutter was open and shown following saccades at the participant's request. The perceived position of a probing bar was measured together with the perceived position of the saccadic target and the distance between the saccadic target and the bar. Participants showed different results for verbal report at a shutter latency of 25 ms after the onset of saccades. When the probing bar was localised taking into account the relative distance from the position of the saccadic target, the results showed a typical pattern of spatial compression. Without taking into account the relative distance from the saccadic target, there was no sign of compression of visual space. It turned out that participants, who took into account the relative distance from the position of the

saccadic target for verbal report, made accurate judgments on the position of the saccadic target. However, the participant, who did not consider the relative distance from the position of the saccadic target, made considerable errors. The saccadic target turned out to be perceived towards the probing bar. After the errors for the location of the saccadic target were corrected, the result showed a typical pattern of spatial compression.

A mechanism of a post-saccadic remapping of pre-saccadic visual space was implied in a study of a temporal illusion termed as chronostasis (Yarrow et al., 2001). In the experiment, participants made either 22° or 55° saccades to a numerical counter. The average durations for the 22° and 55° saccades were 72 ms and 139 ms respectively. A voluntary eye movement changed the digit from 0 to 1. The duration of the number 1 was varied and the subsequent numbers (2, 3, and 4) were presented for 1 s. Participants' task was to indicate whether the duration of the number 1 was longer or shorter than the duration of the subsequent numbers. The results showed that although participants actually saw the number 1 for only 880 ms for the 22° saccade or 811 ms for the 55° saccade, their subjective duration of the number 1 was 1 s. In other words, the subjectively-defined second was shorter than 1 s by the duration of the eye movement plus 50 ms. Consequently, the saccadic chronostasis backdated the percept of the saccadic target to a moment around 50 ms before the onset of saccades. Therefore, it was suggested that the backward extension of perception of a saccadic target may be related to bridging the perceptual gap during the saccadic suppression to maintain perceptual continuity (Thilo & Walsh, 2002; Yarrow et al., 2001).

The post-saccadic localization of stimuli presented before saccades in the present study showed a spatially and temporally accurate representation of the pre-saccadic visual space. The double compression of visual space before the onset of saccades illustrated a transition of the coordinate system from one fixation to another. Especially, the pre-saccadic compression towards a saccadic goal at the interval -50 to 0 ms clearly showed a predictive remapping of visual space. The saccadic chronostasis suggested that an illusory perception of temporal continuity by backdating the perception of a saccadic target may play a role in remapping of visual space during saccadic suppression.

It was suggested that the saccadic chronostasis relies on stability of a saccadic target (Yarrow et al., 2001). When the positional stability of the saccadic target was disrupted by displacing it up to 9° during saccades, the illusion of chronostasis was not experienced whether the shift of the saccadic target was noticed or not. However, when the shift of the saccadic target was not perceived, the illusion was not completely eradicated. Thus, it would be of interest to see if a displacement of a saccadic target could influence localisation of stimuli presented during saccadic suppression. If it increased uncertainty of stimuli, larger mislocalisation errors would be expected.

Chapter 3: An investigation into the effect of saccadic chronostasis on filling in a perceptual gap during saccadic suppression

3.1. Introduction

A loss of visual sensitivity occurs just before saccades and the time course of saccadic suppression is similar to that of spatial compression (Ross et al., 2001). Saccadic suppression begins around 50 ms before saccades and lasts until around 50 ms after saccades (Diamond et al., 2000). A study of a temporal illusion termed as saccadic chronostasis suggested a mechanism of a post-saccadic remapping of pre-saccadic visual space. Yarrow et al. (2001) claimed that backward extension of perception of a saccadic goal to a moment around 50 ms before the onset of saccades may be related to filling a perceptual gap during saccadic suppression to maintain perceptual continuity. However, Georg and Lappe (2007) found that saccadic chronostasis is only relevant to a saccadic target rather than the entire visual field.

The present study was designed to investigate the relevance of saccadic chronostasis to the gap-filling of visual space during saccadic suppression. Yarrow et al. (2001) shown that when positional stability of a saccadic target was broken by a saccadic target displacement during saccades, saccadic chronostasis disappeared whether participants perceived the displacement or not. Thus, the present study adopted a target displacement paradigm, in which a saccadic target was displaced during saccades. If the target displacement paradigm disrupted bridging a perceptual gap during saccadic suppression, it would increase uncertainty of visual stimuli.

Consequently, the magnitude of mislocalisation errors for visual stimuli presented during the interval of -50 to 0 ms would rise.

3.2. Methods

3.2.1. Participants

Eight right-handed observers, two males and six females, with normal or corrected vision participated in the study. Their mean age was 27.3 (range: 23 ~ 35).

3.2.2. Apparatus/Materials

Apparatus and Materials utilised were the same as those explained in Chapter 2 except for a change in a screen refresh rate from 60 Hz (16.7 ms) to 75Hz (13.3 ms).

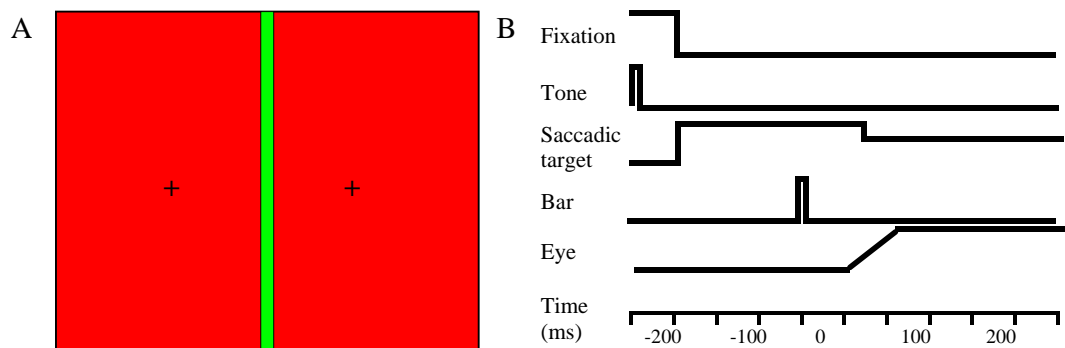


Figure 3.1: Stimuli (A) and time course for the spatial localisation task with a saccadic target displacement paradigm (B). In this paradigm, a saccadic target was displaced 1° forward or backward during saccades or remained constantly.

3.2.3. Design

A three-way (3 x 3 x 2) repeated measures design was utilised. There were three independent variables, Condition, Location and Time. The Condition variable represented three different conditions of the present experiment: Control, Forward, Backward. Control referred to a spatial localisation task with no manipulation. Forward referred to a spatial localisation task with a saccadic target displacement in the direction of saccades. Backward referred to a spatial localisation task with a saccadic target displacement in the opposite direction of saccades. The saccadic target displacement took place during saccades. The Location variable represented the positions of the probing bar and consisted of three levels: Before, Middle, After. The positions of the probing bar were collapsed to simplify the analysis and the collapsed location could represent the whole spatial area. Before referred to two positions (-10.5° and -14° for the left-to-right trials and 10.5° and 14° for the right-to-left trials) before the fixation cross. Middle referred to three positions (-3.5° , 0° and 3.5° for both the left-to-right trials and the right-to-left trials) between the fixation cross and the saccadic target. After referred to two positions (10.5° and 14° for the left-to-right trials and -10.5° and -14° for the right-to-left trials) beyond the saccadic target. The Time variable represented intervals between time of a probing bar presented and the initiation of saccades and consisted of two levels: -100 to -50 ms and -50 to 0 ms. -100 to -50 ms represented an interval between -100 and -51 ms before saccadic onset and -50 to 0 ms represented an interval between -50 and 0 ms before saccadic onset. The dependent variable was a mislocalisation error (measured in degrees) between the veridical bar position and the apparent bar position.

3.3.4. Procedure

The procedure was the same as that described in Chapter 2 except for a saccadic target displacement during saccades. The target displacement took place when a saccadic velocity exceeded $200^{\circ}/\text{sec}$ after the onset of saccades. It was emphasised that participants had to fixate the saccadic target before they responded.

The saccadic latency of each trial was measured and a median latency was determined from every five trials instead of every nine trials as in Chapter 2. The median latency was used to predict a saccadic onset of a subsequent trial. The probing bar was presented 35 ms (for one half of each trial type) or 75 ms (for the other half of each trial type) before saccadic onset.

Each block consisted of 54 trials (half left-to-right trials and half right-to-left trials). After 27 trials, participants had a break and completed each block following the same calibration procedure. Observers performed two sessions on a different day. Each session was composed of two practice blocks and ten experimental blocks.

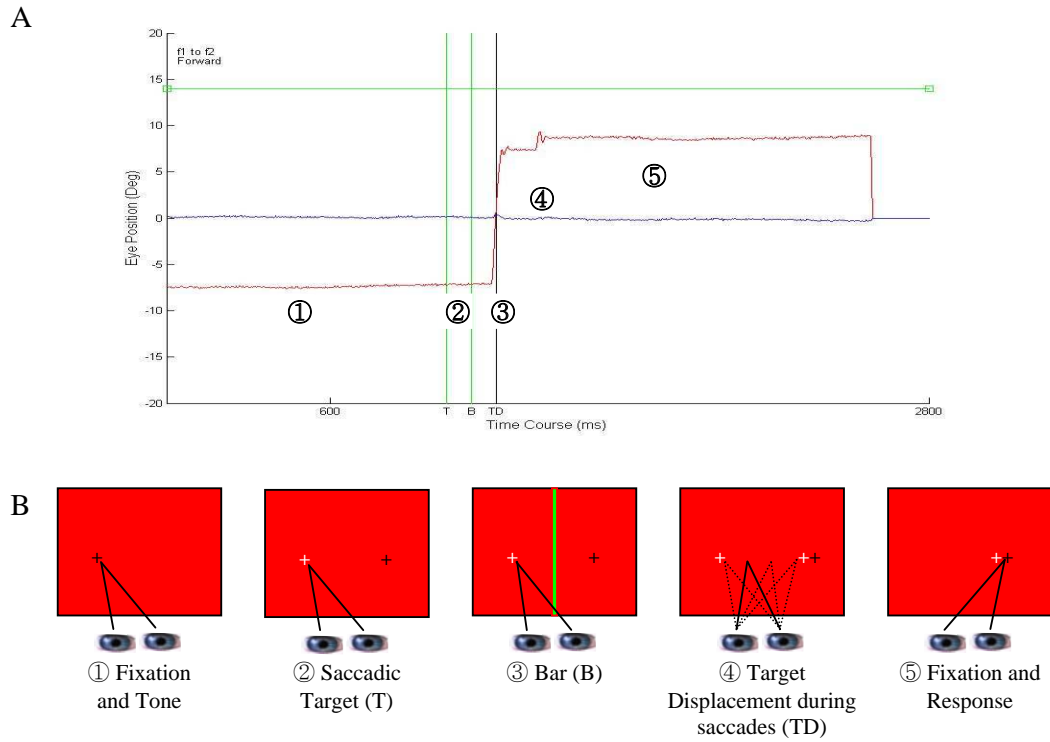


Figure 3.2: Plot of eye movement trace (A) and Schematic illustration of experimental procedure with a saccadic target displacement paradigm (B).

The plot was used to analyse each trial. The red trace represents horizontal eye movements (x coordinate) and the blue trace represents vertical eye movements (y coordinate). The two solid vertical green lines represent a saccadic target time (T) and a probing bar time (B). The solid vertical black line represents a saccadic target displacement time (TD). The horizontal solid green line represents the position of the probing bar presented on the screen. The numbers on the plot correspond to the time course of the experimental procedure. In each trial, a tone went off when participants fixated a black cross (①). After an interval, a saccadic target was presented on the other side of the screen (②). A vertical green bar was presented (③) before they made an eye movement to the saccadic target. During the saccade, the saccadic target was displaced 1° forward or backward or remained constantly (④). They indicated a perceived position of the bar using their index finger while fixating the saccadic target (⑤). The white crosses represent traces of the fixation cross and the saccadic target.

3.3. Results

Data analysis for the present study was the same as one described in Chapter 2.

Figure 3.3 shows a data analysis procedure for the Forward condition. Control and Backward conditions were analysed using the same procedure.

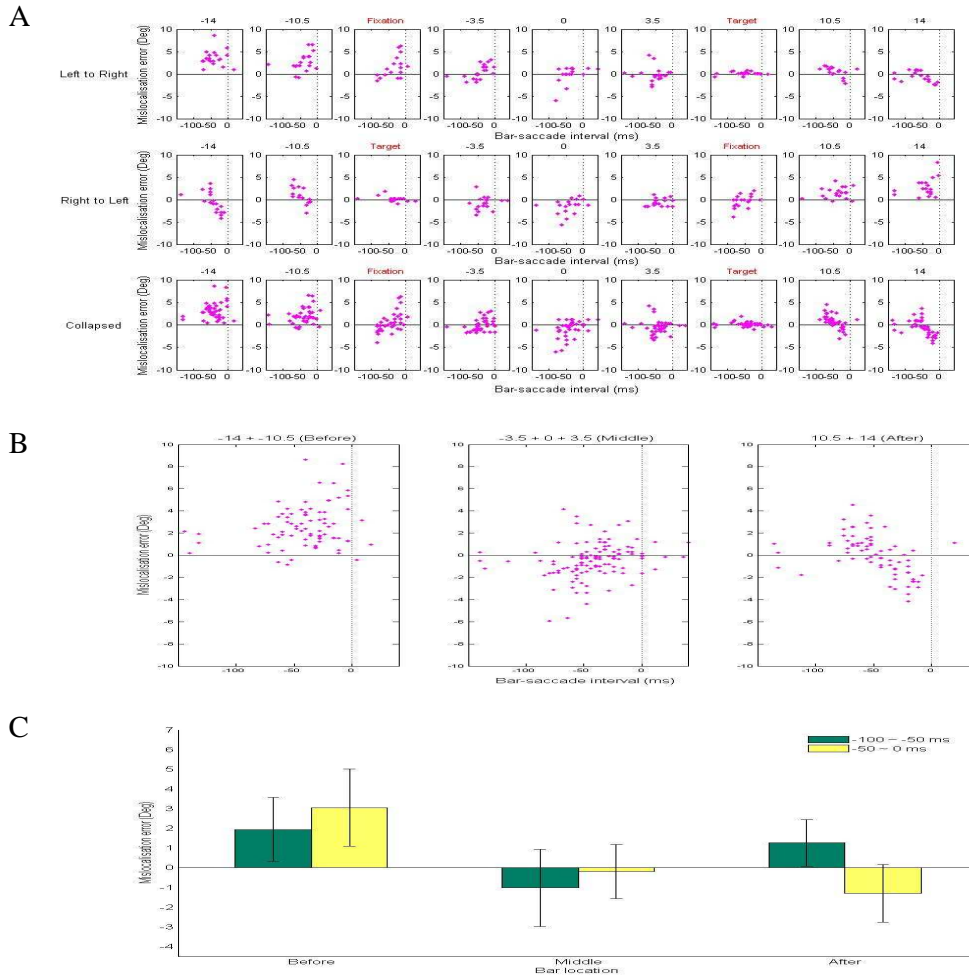


Figure 3.3: Procedure of data analysis for the Forward condition of a participant.

A three-way 3 (Condition: Control, Forward, Backward) x 3 (Location: Before, Middle, After) x 2 (Time: -100 to -50 ms, -50 to 0 ms) repeated measures ANOVA was carried out on mean mislocalisation errors of eight observers (see Figure 3.4). There was no significant main effect of Condition, $F(2, 14) = 0.49$, $p = .624$, $\eta_p^2 = 0.07$. There was a significant main effect of Location, $F(2, 14) = 19.54$, $p = .001$, $\eta_p^2 = 0.74$. Post-hoc tests using a Bonferroni adjustment showed that there was a significant difference in mean mislocalisation errors between Before ($M = 2.85$, $SEM = 0.57$) and Middle ($M = -0.49$, $SEM = 0.31$) locations; $F(1, 7) = 43.97$, $p = .001$, $\eta_p^2 = 0.86$ and between Before ($M = 2.85$, $SEM = 0.57$) and After ($M = -0.88$, $SEM = 0.38$) locations; $F(1, 7) = 21.11$, $p = .008$, $\eta_p^2 = 0.75$. However, there was no significant difference in mean mislocalisation errors between Middle ($M = -0.49$, $SEM = 0.31$) and After ($M = -0.88$, $SEM = 0.38$) locations; $F(1, 7) = 0.42$, $p = 1.000$, $\eta_p^2 = 0.06$. There was no significant main effect of Time, $F(1, 7) = 0.98$, $p = .356$, $\eta_p^2 = 0.12$.

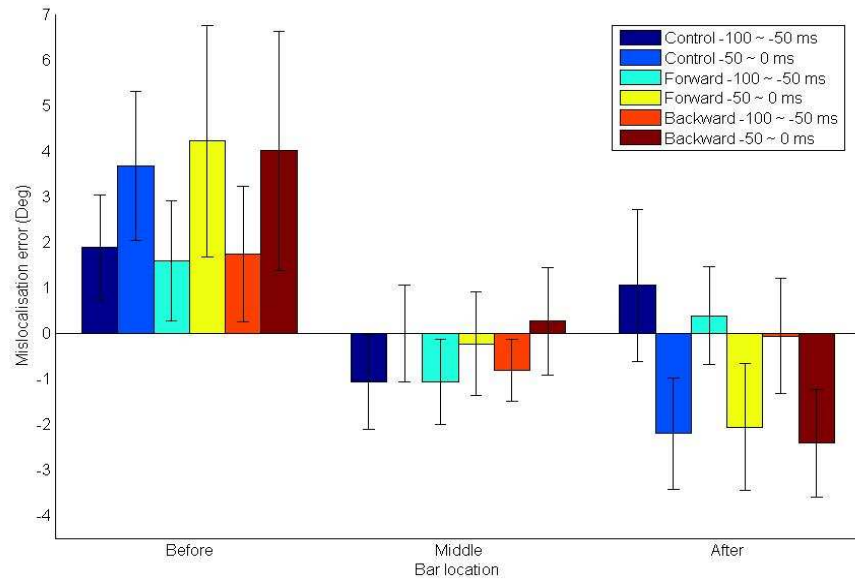


Figure 3.4: Mean mislocalisation errors of eight observers.

Mean mislocalisation errors of three conditions are presented with regard to two separate intervals (-100 to -50 ms and -50 to 0 ms) of three different locations (Before, Middle, After). Error bars represent standard deviations.

The results illustrated that there was a significant interaction between Condition and Location, $F(4, 28) = 3.17$, $p = .029$, $\eta_p^2 = 0.31$ (see Figure 3.5). A simple main effects analysis showed that there was no significant effect of Condition in Before ($F(2, 14) = 0.14$, $p = .869$, $\eta_p^2 = 0.02$) and Middle ($F(2, 14) = 2.32$, $p = .135$, $\eta_p^2 = 0.25$) locations. However, there was a significant effect of Condition in the After location, $F(2, 14) = 6.44$, $p = .010$, $\eta_p^2 = 0.45$. Post-hoc tests using a Bonferroni adjustment showed that there was no significant difference in mean mislocalisation errors between Control ($M = -0.57$, $SEM = 0.46$) and Forward ($M = -0.8$, $S4EM = 0.35$) locations; $F(1, 7) = 1.24$, $p = .908$, $\eta_p^2 = 0.15$ and between Forward ($M = 2.85$,

SEM = 0.57) and Backward (M = -0.88, SEM = .38) locations; $F(1, 7) = 5.27$, $p = .166$, $\eta_p^2 = 0.43$. However, there was a significant difference in mean mislocalisation errors between Control (M = -0.49, SEM = 0.31) and Backward (M = -0.88, SEM = 0.38) locations; $F(1, 7) = 25.45$, $p = .004$, $\eta_p^2 = 0.78$.

There was a significant interaction between Condition and Time, $F(1.12, 7.86) = 6.92$, $p = .028$, $\eta_p^2 = 0.50$ (see Figure 3.5). Since Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(2) = 9.11$, $p = .010$, corrected values of degrees of freedom were calculated using Greenhouse-Geisser estimates of sphericity ($\epsilon = 0.56$). A simple main effects analysis showed that there was no significant effect of Time for Control ($F(1, 7) = 0.53$, $p = .492$, $\eta_p^2 = 0.07$), Forward ($F(1, 7) = 2.16$, $p = .185$, $\eta_p^2 = 0.24$) or Backward conditions ($F(1, 7) = 3.47$, $p = .105$, $\eta_p^2 = 0.33$). However, the graph indicates that for the Control condition, the mean mislocalisation error for the interval of -100 to -50 ms was greater than that for the interval of -50 to 0 ms, but for Forward and Backward conditions, the mean mislocalisation error for the interval of -50 to 0 ms was greater than that for the interval of -100 to -50 ms.

There was a significant interaction between Location and Time, $F(1.15, 8.08) = 25.34$, $p = .001$, $\eta_p^2 = 0.78$ (see Figure 3.5). Since Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(2) = 7.91$, $p = .019$, corrected values of degrees of freedom were calculated using Greenhouse-Geisser estimates of sphericity ($\epsilon = 0.58$). A simple main effects analysis illustrated that there was a significant effect of Time in Before ($F(1, 7) = 14.43$, $p = .007$, $\eta_p^2 = 0.67$), Middle

($F(1, 7) = 15.61, p = .006, \eta_p^2 = 0.69$) and After ($F(1, 7) = 35.04, p = .001, \eta_p^2 = 0.83$) locations. One-sample t-tests illustrated that in the Before location, mean mislocalisation errors were positive and significant for both -100 to -50 ms ($M = 1.74, SEM = 0.45, t(7) = 3.83, p = .006$) and -50 to 0 ms ($M = 3.97, SEM = 0.79, t(7) = 5.05, p = .001$) intervals. In the Middle location, the mean mislocalisation error for the -100 to -50 ms interval was negative and significant ($M = -0.98, SEM = 0.29, t(7) = -3.53, p = .010$), but that for the -50 to 0 ms interval was not significant ($M = 0.01, SEM = 0.39, t(7) = 0.03, p = .979$). In the After location, the mean mislocalisation error for the -100 to -50 ms interval was not significant ($M = 0.46, SEM = 0.46, t(7) = 1.00, p = .352$), but that for the -50 to 0 ms interval was negative and significant ($M = -2.27, SEM = 0.43, t(7) = -5.19, p = .001$). There was no significant interaction among three factors, $F(4, 24) = 2.09, p = .109, \eta_p^2 = 0.23$.

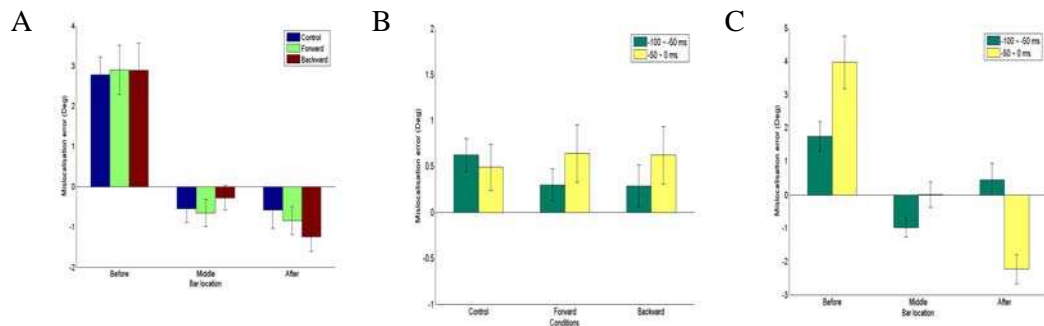


Figure 3.5: Graphs for simple effects analysis between Condition and Location (A), between Condition and Time (B) and between Location and Time (C).

3.4. Discussion

There was no significant difference among three conditions. A simple main effects analysis for the significant interaction between Condition and Location shows that in the After location, the mean mislocalisation error for the Backward condition was in the opposite direction of saccades and significantly different from that for the Control condition. The mean mislocalisation error for the Forward condition was somewhere between the other two conditions. Although a simple main effects analysis did not show any significance, a significant interaction between Condition and Time shows that for the Control condition, the mean mislocalisation error for the interval of -100 to -50 ms was greater than that for the interval of -50 to 0 ms, but for Forward and Backward conditions, the trend was reversed. The significant interaction between Location and Time and the significant effects of Time in three locations illustrate that two different remapping mechanisms are involved in the two intervals. At the interval of -50 to 0 ms, the mean mislocalisation error in the Before location was in the direction of saccades, but that in the After location was in the opposite direction of saccades. They together show a pattern of spatial compression towards the saccadic target. At the interval of -100 to -50 ms, the mean mislocalisation error in the Before was in the direction of saccades, but that in the Middle location was in the opposite direction of saccades. The mean mislocalisation errors in the Before and Middle locations show a pattern of spatial compression towards the initial fixation cross. The three conditions showed the same pattern of interactions between Location and Time.

Since a displacement of a saccadic target during saccades was suggested to reduce or remove saccadic chronostasis, it was expected that the perceptual gap during the

saccadic suppression would not be filled optimally and consequently cause an increase in uncertainty of stimuli. The main interest of the present study was whether a displacement of a saccadic target during saccades could increase the magnitude of mislocalisation errors for the stimuli presented at the interval of -50 to 0 ms by increasing uncertainty of stimuli. The results showed that a displacement of a saccadic target during saccades did not influence the magnitude of mislocalisation errors for stimuli presented during saccadic suppression. Consequently, there was no change in the interaction between Location and Time.

Saccadic chronostasis does not seem to serve as a mechanism that remaps visual stimuli presented during saccadic suppression. If saccadic chronostasis did not occur in other locations except a saccadic target, it would imply that saccadic chronostasis is not related to remapping of the entire visual field. An experiment was carried out to investigate whether saccadic chronostasis takes place in the entire visual field and consequently involves in a mechanism that remaps visual space during saccadic suppression (Georg & Lappe, 2007). In the experimental condition, the clock was presented at a location between the initial fixation point and the saccadic target. The typical chronostasis phenomenon was occurred at the location of the saccadic target, but not at the location halfway between the initial fixation point and the saccadic target. Thus, temporal illusion of chronostasis, which is suggested to bridge a perceptual gap during saccadic suppression, does not match with the phenomenon of spatial compression towards the saccadic target during saccadic suppression as spatial compression is illustrated in the entire visual field. Another difference is that saccadic chronostasis is a post-saccadic gap-filling mechanism while spatial compression towards the saccadic target is a phenomenon of a predictive remapping

of visual space. A predictive shift of gaze direction could match with a predictive transition of a coordinate system from one fixation to another shown in the spatial compression phenomenon (Hunt & Cavanagh, 2009). When observers moved their gaze to a clock with a hand moving at a rate of 1 rps and judged the time their eyes landed the clock, the perceived time was 39 ms earlier than the actual arrival time on the clock. In the control condition, the eyes were fixed and the clock moved to the eyes. The perceived time was 27 ms later than the actual arrival time. The observers experienced fixating a saccadic target before their eyes actually landed on it. It was proposed that this predictive remapping of the saccadic target just before the eye movement plays an important role in moving visual activity from the current foveal location to the next foveal location to maintain a representation of visual space across eye movements.

Concerning the concept of a perceptual gap during saccades, it may be worth mentioning that there is no complete loss of visual sensitivity for stimuli presented during saccadic suppression. While contrast sensitivity of horizontal gratings presented for 20 ms in normal viewing showed little loss of sensitivity from the peak sensitivity as spatial frequencies decreased, contrast sensitivity during saccades was dramatically impaired at low spatial frequencies compared to the loss of sensitivity in normal viewing (Burr et al., 1982). Thus, low spatial frequency components of an object are greatly suppressed during saccades. Contrast sensitivities for luminance-modulated gratings (yellow – black) and colour-modulated gratings (red – green) were measured during saccades and in normal viewing (Burr et al., 1994). There was no difference in contrast sensitivity for colour-modulated gratings in both saccade and normal viewing conditions. For one participant, sensitivity was even higher

during saccades than in normal viewing. For luminance-modulated gratings, although there was no difference in contrast sensitivity at high spatial frequencies in both saccade and normal viewing conditions, there was a great loss of sensitivity at low spatial frequencies during saccades compared to the normal viewing condition. In the present study, at the interval of -50 to 0 ms, the mean mislocalisation errors showed a pattern of spatial compression towards the saccadic target whereas at the interval of -100 to -50 ms, the mean mislocalisation errors showed a pattern of spatial compression towards the initial fixation cross. Saccadic suppression began around 50 ms before the onset of saccades and lasted until around 50 ms after the offset of saccades (Diamond et al., 2000). Thus, it can be speculated that the results might have been caused by a difference in visual sensitivity at the difference intervals. However, it is believed that the two separate patterns of spatial compression were not induced by visual sensitivity for stimuli presented within 100 ms before saccades as equiluminant stimuli were used.

Although modulations in stimulus contrast and luminance can change magnitude of spatial compression (Georg et al., 2008; Michels & Lappe, 2004), spatial compression is not due to lack of information about stimuli presented during saccadic suppression (Hamker et al., 2008). A letter 'E' was used as a probe and the horizontal line '-' of the letter was used as a location marker. The location marker was shown from the beginning of the trial and indicated the location of the probe. The probe was presented around the onset of saccades and perceived location of the probe was reported after saccades. The location marker and the saccade target were remained until the end of the trial. The results illustrated the compression of the flashed probe towards the saccadic target even though the precise location of the

probe was shown throughout the trial. Even when the participants had to make a memory guided saccade to location of the saccadic target and consequently, the location marker was only visible reference, perceived location of the probe still showed a pattern of compression towards the saccadic target. Thus, it is not vague perception of stimuli caused by loss of visual sensitivity or short duration of presentation that induced compression of visual space.

The present study showed that saccadic chronostasis is not involved in a mechanism that fills the perceptual gap during saccadic suppression since the displacement of the saccadic target does not affect perception of stimuli presented during saccadic suppression and consequently does not change magnitude of mislocalisation errors towards the saccadic target. It was also suggested that there is no complete loss of visual sensitivity during saccadic suppression and compression of visual space is not due to uncertainty of stimuli during saccades.

There is a mismatch between a saccadic target and a saccade landing site when a saccadic eye movement is made. This mismatch is regular and if it is large enough, it results in a corrective saccade. However, it does not cause conscious disturbance. This seems to be a way that the visual system maintains trans-saccadic visual stability (Findlay & Gilchrist, 2003). This mechanism may play a role in smooth transition of a coordinate system from one fixation to another. Thus, a stable localisation of a saccadic target would be an important factor for a stable integration of pre-saccadic visual space with the initial fixation as a centre into the post-saccadic visual space with the saccadic target as a centre. Deubel et al. (1996) suggested that a saccadic target found after the end of saccades is relocalised. If the saccadic target is

not found, for example, as a result of post-saccadic target blanking, the visual system uses other information to localise the saccadic target such as efference copy and remembered target location since temporal contiguity of visual space is disturbed. Adopting a target blanking paradigm might help to investigate how predictively remapped pre-saccadic visual space is updated in the post-saccadic visual space. It can be updated in the post-saccadic visual space relative to saccadic landing sites, a location remapped using efference copy, a remembered target location or a location of the post-saccadic target if the saccadic target is not available immediately after the end of saccades.

Chapter 4: An investigation into effects of a saccadic target blanking on post-saccadic remapping of pre-saccadic visual space

4.1. Introduction

Visual information coded before the onset of saccades was updated after the end of saccades. The memory trace of stimuli flashed long or immediately before saccades was remapped after saccades (Duhamel et al., 1992). Gottlieb (2007) suggested that post-saccadic remapping of pre-saccadic visual space plays a part in linking information about a stable object across saccades. However, target displacements occurred just before the onset of saccades were not detected and the suppression of target displacement was maximal during saccades (Bridgeman et al., 1975). According to the reference object theory, the high threshold for detecting a target displacement might indicate either that spatial information about pre-saccadic and post-saccadic locations of objects is not available or that a comparison between the pre-saccadic and post-saccadic locations is not performed if it is not necessary (Deubel et al., 1998). It was demonstrated that continuous presence of visual objects immediately after saccades is a significant factor to maintain perceived stability of the objects. A saccadic target and a distractor were closely placed and either of them were displaced right or left. Participants' task was to report which one was displaced. The results showed that continuously present objects were perceived as stable since blanked one was frequently perceived as displaced as long as displaced one was present after saccades. A blanking paradigm was shown to reveal information which improved detection of a target displacement (Deubel et al., 1996). When the saccadic target was blanked for 250 ms after the onset of saccades, participants accurately reported the direction of target displacements. It was proposed that the absence of a

visual stimulus immediately after saccades destabilises the visual system and the system has to employ other available information such as efference copy or remembered target location. Deubel et al. (1996) also claimed that a precise extraretinal signal about the location of a saccadic target and its displacement is available and utilised especially when visual information is not available after saccades.

In the previous study, there was no difference in magnitudes of mislocalisation errors between the Control condition and the target displacement conditions (Forward and Backward) where the saccadic target was displaced during saccades. It seems that when a saccadic target is available after saccades, pre-saccadic visual space is integrated into post-saccadic visual space without any disturbance. However, according to the reference object theory, it is not clear what would be used as a reference point when pre-saccadic visual space was remapped in the post-saccadic visual space since the theory predicts that spatial information about pre- and post-saccadic locations of a saccadic target is neither available nor compared if the saccadic target is available after saccades. The results of the previous study showed that the displaced target was not used as a reference point for post-saccadic remapping of pre-saccadic visual space. Thus, it is necessary to carry out further studies to find out a potential mechanism for post-saccadic remapping of pre-saccadic visual space.

The present study was designed to investigate effects of the saccadic target blanking on the post-saccadic remapping of pre-saccadic visual space. It is known that there are regular mismatches between a saccadic target and a saccade landing site when an

eye movement was made and corrective saccades are made to adjust these differences (Findlay & Gilchrist, 2003). Findlay and Gilchrist (2003) suggested that the visual system seems to maintain trans-saccadic visual stability by removing perceptual disturbance caused by these adjustments. Deubel et al. (1982) demonstrated that if a saccadic target is blanked, a corrective saccade is not made until it appears again. Thus, the target blanking paradigm can be used to examine if saccadic landing sites were used as a reference point for updating pre-saccadic visual space. As mentioned earlier, the absence of the saccadic target causes the visual system to utilise other information such as the location of the saccadic target remapped by efference copy or remembered location of the saccade target. The blanked target location may also be used as a reference point and the blanking duration could affect the post-saccadic remapping.

4.2. Methods

4.2.1. Participants

Eight right-handed observers, four males and four females, with normal or corrected vision participated in the study. Their mean age was 28 (range: 22 ~ 35).

4.2.2. Apparatus/Materials

Apparatus and Materials utilised were the same as those explained in Chapter 2 except for a change in a screen refresh rate from 60 Hz (16.7 ms) to 75Hz (13.3 ms).

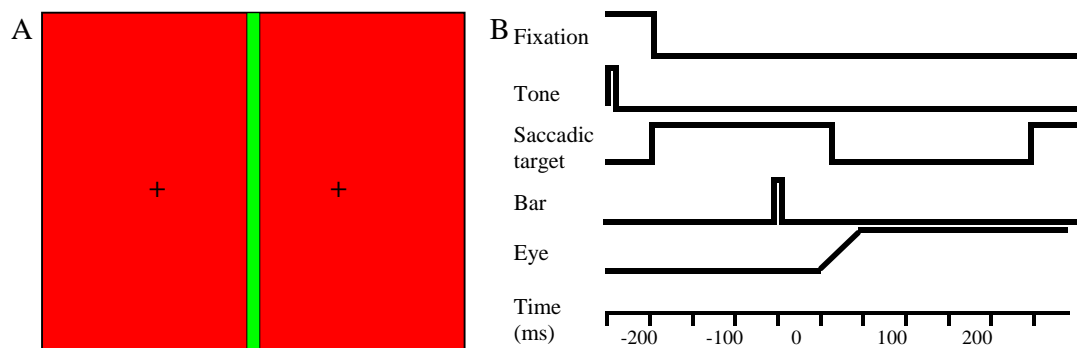


Figure 4.1: Stimuli (A) and time course for the spatial localisation task with a saccadic target blanking paradigm (B). In this paradigm, the saccadic target disappeared during saccades and appeared again 200 ms after the offset of saccades.

4.2.2. Design

A three-way (2 x 3 x 2) repeated measures design was utilised. There were three independent variables, Condition, Location and Time. The Condition variable represented two different conditions of the present experiment: Control and Blanking. Control referred to a spatial localisation task with no manipulation. Blanking referred to a spatial localisation task with a saccadic target blanking for 200 ms after the offset of saccades. The saccadic target blanking began during saccades. The Location variable represented the positions of the probing bar and consisted of three levels: Before, Middle, After. The positions of the probing bar were collapsed to simplify the analysis and the collapsed location could represent the whole spatial area. Before referred to two positions (-10.5° and -14° for the left-to-right trials and 10.5° and 14° for the right-to-left trials) before the fixation cross. Middle referred to three positions (-3.5° , 0° and 3.5° for both the left-to-right trials and the right-to-left trials) between

the fixation cross and the saccadic target. After referred to two positions (10.5° and 14° for the left-to-right trials and -10.5° and -14° for the right-to-left trials) beyond the saccadic target. The Time variable represented intervals between time of a probing bar presented and the initiation of saccades and consisted of two levels: -100 to -50 ms and -50 to 0 ms. -100 to -50 ms represented an interval between -100 and -51 ms before saccadic onset and -50 to 0 ms represented an interval between -50 and 0 ms before saccadic onset. The dependent variable was a mislocalisation error (measured in degrees) between the veridical bar position and the apparent bar position.

4.2.4. Procedure

The procedure was the same as that described in Chapter 2 except for a saccadic target blanking for 200 ms after the offset of saccades. The saccadic target disappeared when a saccadic velocity exceeded $200^\circ/\text{sec}$ after the onset of saccades. It appeared again 200 ms after the offset of saccades, which was detected when the saccadic velocity decreased to less than $100^\circ/\text{sec}$. It was emphasised that participants had to fixate the saccadic target before they responded.

The saccadic latency of each trial was measured and a median latency was determined from every five trials instead of every nine trials as in Chapter 2. The median latency was used to predict a saccadic onset of a subsequent trial. The probing bar was presented 35 ms (for one half of each trial type) or 75 ms (for the other half of each trial type) before saccadic onset.

Each block consisted of 36 trials (half left-to-right trials and half right-to-left trials). Observers performed two sessions on a different day. Each session was composed of two practice blocks and 15 experimental blocks.

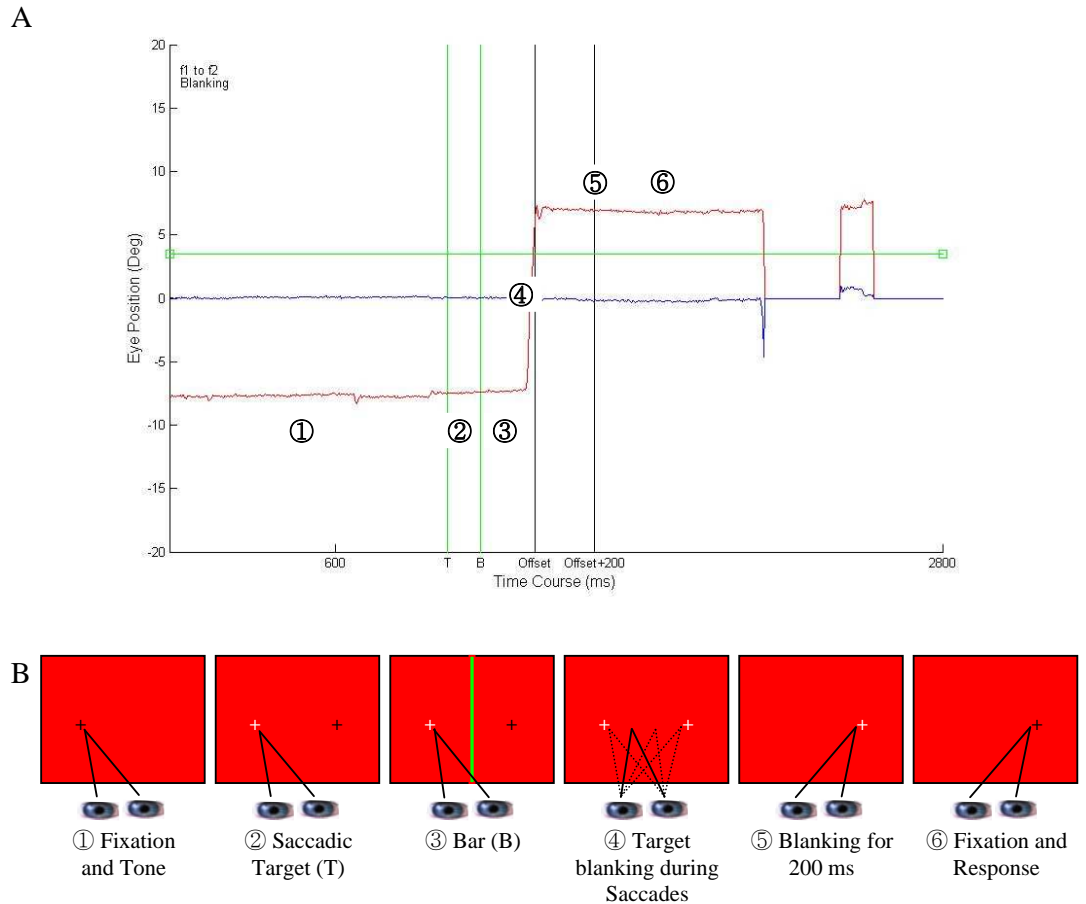


Figure 4.2: Plot of eye movement trace (A) and Schematic illustration of experimental procedure with a saccadic target blanking paradigm (B).

The plot was used to analyse each trial. The red trace represents horizontal eye movements (x coordinate) and the blue trace represents vertical eye movements (y coordinate). The two solid vertical green lines represent a saccadic target time (T) and a probing bar time (B). The two solid vertical black lines represent the offset of saccades (Offset) and 200 ms after the offset of saccades (Offset+200). The horizontal solid green line represents the position of the probing bar presented on the screen. The numbers on the plot correspond to the time course of the experimental procedure. In

each trial, a tone went off when participants fixated a black cross (①). After an interval, a saccadic target was presented on the other side of the screen (②). A vertical green bar was presented (③) before they made an eye movement to the saccadic target. During the saccade, the saccadic target disappeared (④). The saccadic target was blanked for 200 ms after the offset of saccades (⑤). They indicated a perceived position of the bar using their index finger while fixating the saccadic target (⑥). The white crosses represent traces of the fixation cross and the saccadic target.

4.3. Results

Data analysis for the present study was the same as one described in Chapter 2. Figure 4.3 shows a data analysis procedure for the Blanking condition. The Control condition was analysed using the same procedure.

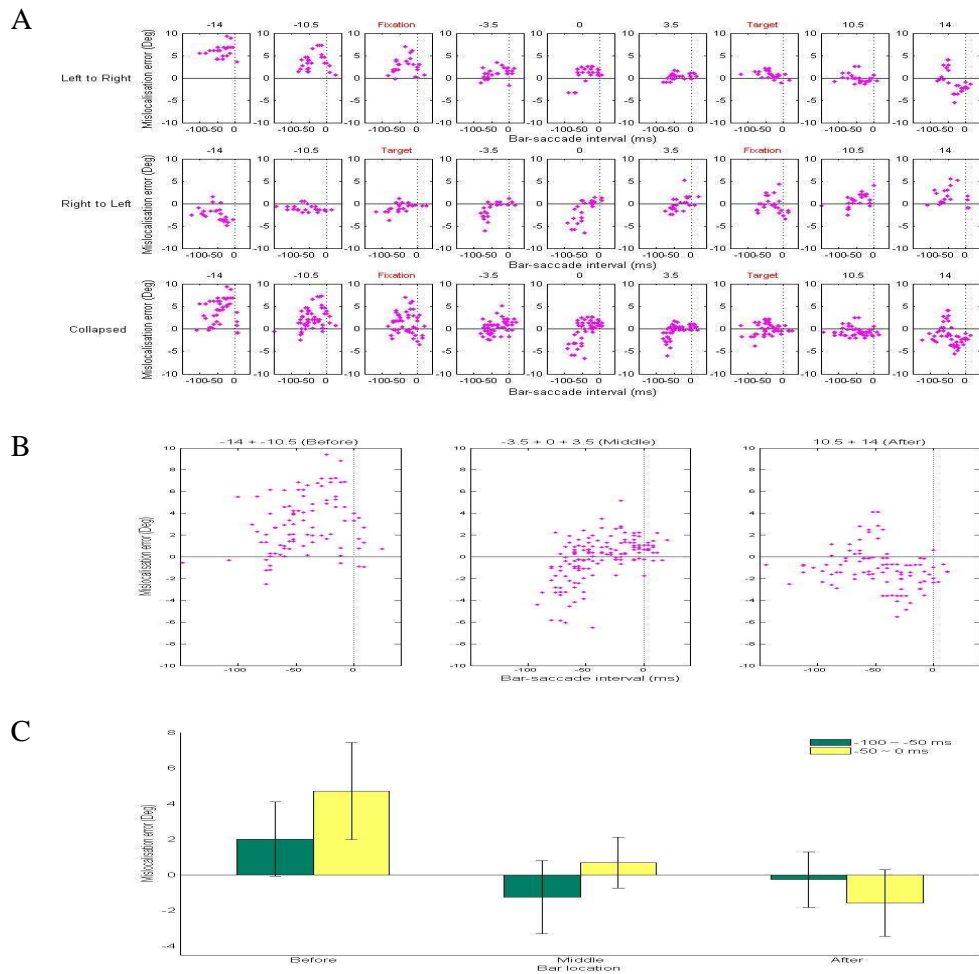


Figure 4.3: Procedure of data analysis for the Blanking condition of a participant.

A three-way 2 (Condition: Control, Blanking) x 3 (Location: Before, Middle, After) x 2 (Time: -100 to -50 ms, -50 to 0 ms) repeated measures ANOVA was carried out on mean mislocalisation errors of eight observers (see Figure 4.4). There was no significant main effect of Condition, $F(1, 7) = 0.26$, $p = .629$, $\eta_p^2 = 0.04$. There was a significant main effect of Location, $F(2, 14) = 43.73$, $p < .001$, $\eta_p^2 = 0.86$. Post-hoc tests using a Bonferroni adjustment showed that there was a significant difference in mean mislocalisation errors between Before ($M = 3.81$, $SEM = 0.34$)

and Middle ($M = 0.50$, $SEM = 0.39$) locations; $F(1, 7) = 103.45$, $p < .001$, $\eta_p^2 = 0.94$ and between Before ($M = 3.81$, $SEM = 0.34$) and After ($M = -0.72$, $SEM = 0.37$) locations; $F(1, 7) = 81.24$, $p < .001$, $\eta_p^2 = 0.92$. However, there was no significant difference in mean mislocalisation errors between Middle ($M = 0.50$, $SEM = 0.39$) and After ($M = -0.72$, $SEM = 0.37$) locations; $F(1, 7) = 3.70$, $p = .287$, $\eta_p^2 = 0.35$. There was no significant main effect of Time, $F(1, 7) = 0.90$, $p = .375$, $\eta_p^2 = 0.11$.

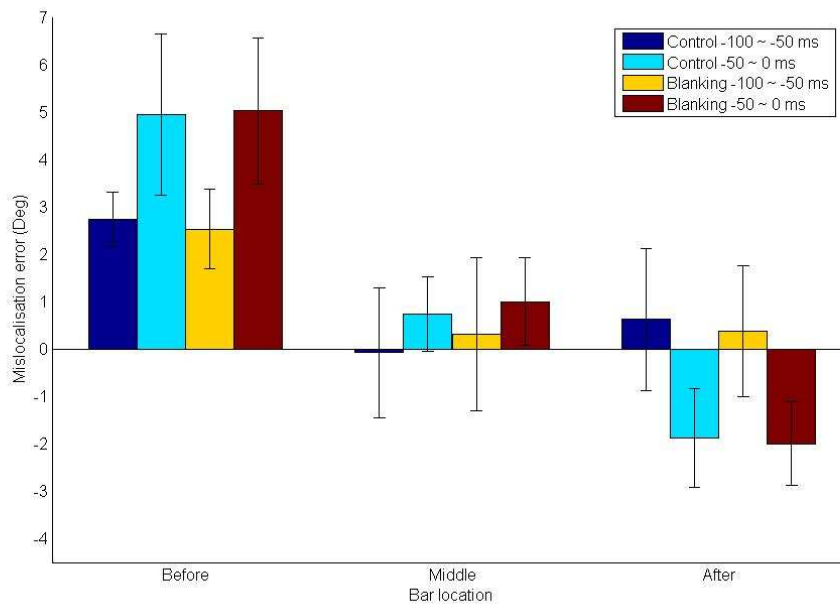


Figure 4.4: Mean mislocalisation errors of eight observers.

Mean mislocalisation errors of two conditions are presented with regard to two separate intervals (-100 to -50 ms and -50 to 0 ms) of three different locations (Before, Middle, After). Error bars represent standard deviations.

The results illustrated that there was no significant interaction between Condition and Location, $F(2, 14) = 2.53$, $p = .115$, $\eta_p^2 = 0.27$. There was no significant interaction between Condition and Time, $F(1, 7) = 0.20$, $p = .665$, $\eta_p^2 = 0.03$. However, there

was a significant interaction between Location and Time, $F(2, 14) = 36.24, p < .001, \eta_p^2 = .84$ (see Figure 4.5). A simple main effects analysis illustrated that there was a significant effect of Time in Before ($F(1, 7) = 27.10, p = .001, \eta_p^2 = 0.80$) and After ($F(1, 7) = 32.91, p = .001, \eta_p^2 = 0.83$) locations, but not in the Middle ($F(1, 7) = 5.04, p = .060, \eta_p^2 = 0.42$) location. One-sample t-tests illustrated that in the Before location, mean mislocalisation errors were positive and significant for both -100 to -50 ms ($M = 2.64, SEM = 0.21, t(7) = 12.80, p < .001$) and -50 to 0 ms ($M = 4.99, SEM = 0.54, t(7) = 9.30, p < .001$) intervals. In the Middle location, the mean mislocalisation error for the -100 to -50 ms interval was not significant ($M = 0.12, SEM = 0.52, t(7) = 0.23, p = .828$), but that for the -50 to 0 ms interval was positive and significant ($M = 0.87, SEM = 0.30, t(7) = 2.92, p = .022$). In the After location, the mean mislocalisation error for the -100 to -50 ms interval was not significant ($M = 0.50, SEM = 0.51, t(7) = 0.98, p = .358$), but that for the -50 to 0 ms interval was negative and significant ($M = -1.93, SEM = 0.32, t(7) = -6.02, p = .001$). There was no significant interaction among three factors, $F(2, 14) = 0.28, p = .759, \eta_p^2 = 0.04$.

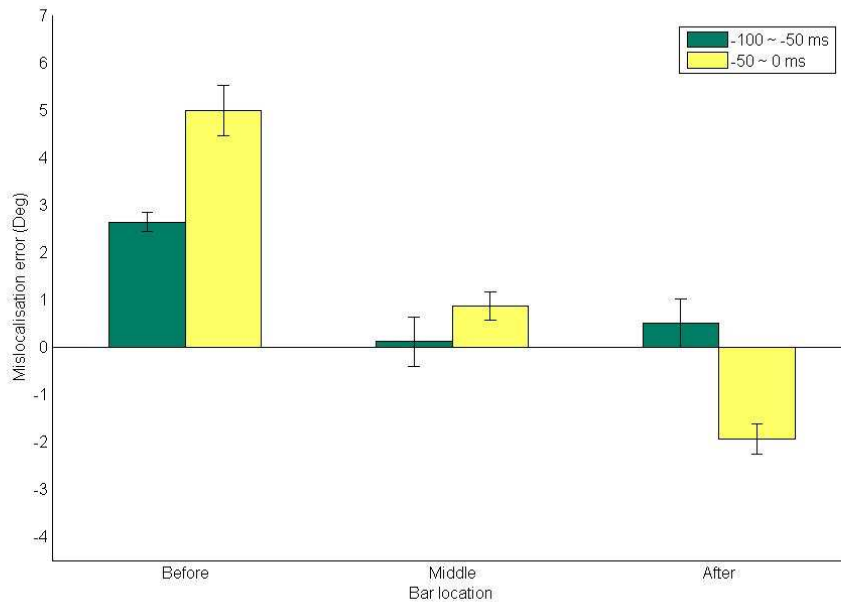


Figure 4.5: Graph for simple effects analysis between Location and Time.

4.4. Discussion

There was no significant difference between two conditions. The significant interaction between Location and Time and the significant effects of Time in Before and After locations indicate that two different remapping mechanisms are involved in the two intervals. At the interval of -50 to 0 ms, the mean mislocalisation error in the Before location and the Middle locations was in the direction of saccades, but that in the After location was in the opposite direction of saccades. They together show a pattern of spatial compression towards the saccadic target. At the interval of -100 to -50 ms, the mean mislocalisation errors in the Before was in the direction of saccades. The two conditions showed the same pattern of interactions between Location and Time.

The present study adopted a target blanking paradigm to study how predictively remapped pre-saccadic visual space is updated in the post-saccadic visual space. Deubel et al. (1996) suggested that the visual system employs other information to localise the saccadic target such as efference copy and remembered target location when temporal continuity of the saccadic target is disturbed and It was demonstrated that if a saccadic target is blanked, a corrective saccade is not made until it appears again (Deubel et al., 1982). Thus, it was expected that the target blanking paradigm could induce disruption of remapping of pre-saccadic visual space as the predictively remapped visual stimulus could be anchored relative to a saccadic landing site, a remembered location of the pre-saccadic target or a location of the post-saccadic target found after the end of saccades. However, the results showed that the absence of the saccadic target after the end of saccades did not disrupt remapping of predictively remapped pre-saccadic visual space as there was no significant change in the magnitude of mislocalisation errors for stimuli presented at the interval of -50 to 0 ms and consequently, there was no significant difference between two conditions in the interaction between Location and Time.

As Deubel et al. (1982) illustrated that primary saccades tend to undershoot about 1 deg for 10–15 deg saccades and if a saccadic target is not present, a corrective saccade is not carried out until reappearance of the saccadic target, it was hypothesised that the saccadic landing site could be used to remap the predictively remapped pre-saccadic visual stimulus into the post-saccadic visual space. However, the results indicated that it was not used to anchor pre-saccadic visual stimuli to the post-saccadic coordinate system.

When the saccadic target was displaced during saccades and present after the saccades, the judgment on displacement direction showed a high inter-subject variability (Deubel et al., 1996). The participants showed a strong tendency of reporting forward target displacements. This phenomenon was noticeable especially when there was no target displacement. If the visual system used an inaccurate memory of the location of the pre-saccadic target to remap pre-saccadic stimuli, there would be a change in the magnitudes of mislocalisation errors for stimuli presented at the interval of -50 to 0 ms. However, the results also showed that a remembered location of the pre-saccadic target was not utilised to remap pre-saccadic visual stimuli to the post-saccadic visual space.

When the saccadic target was blanked for 250ms after the onset of saccades, participants accurately reported the direction of target displacements and inter-subject variability was removed (Deubel et al., 1996). The improved judgment of target displacements in the blanking condition was not predicted by the post-saccadic refixation error, but by the actual target displacement. This result implies that the judgment on target displacements was not made relative to the saccadic landing site, but to the location of the saccadic target remapped using a precise extraretinal signal. Thus, although the saccadic target was not visible immediately after saccades, the location of the saccadic target was available and could be used to integrate pre-saccadic visual stimuli into the post-saccadic coordinate system.

Availability of post-saccadic visual references immediately after saccades is the defining factor for pre-saccadic compression of visual space (Lappe et al., 2000). The ruler used as a visual reference also provided marks that could indicate positions for

the initial fixation point and the saccadic target. It seems that one of the marks that was in the position of the saccadic target played a main role in inducing compression of stimuli towards the saccadic target. The gap condition in which the ruler was blanked for 250 ms with the presentation of the bar caused confusion since the magnitude of compression found in the gap condition was not different from those found in the conditions in which the ruler was either present or absent throughout the trials and it fell somewhere between two conditions. Thus, in the present study it was also possible that the blanked target was used as a reference point for remapping of pre-saccadic stimuli.

The present study showed that a saccadic landing site and a remembered location of the pre-saccadic target was not utilised to remap pre-saccadic stimuli. However, in the present study it is not clear whether a saccadic target remapped using efference copy or a location of the blanked post-saccadic target found after saccades is used to remap pre-saccadic stimuli. As the blanking paradigm elicits information about a location of the pre-saccadic target using efference copy and a location of the post-saccadic target relative to the pre-saccadic target (Deubel et al., 1996), if the post-saccadic target reappeared after blanking in a location other than the location of the pre-saccadic target, it would be possible that the location of the blanked post-saccadic target could be used for remapping of the pre-saccadic stimuli.

Chapter 5: An investigation into effects of a displaced target after blanking on post-saccadic remapping of pre-saccadic visual space

5.1. Introduction

The previous study with a saccadic target blanking paradigm illustrated that saccade landing sites and remembered locations of the pre-saccadic target were not used as a reference point for post-saccadic remapping of pre-saccadic visual space. However, it was difficult to conclude whether the location of a pre-saccadic target remapped using efference copy or the post-saccadic target reappeared after blanking was used as a reference point. First, as the blanking of a saccadic target makes both the location of a pre-saccadic target and its displacement relative to the pre-saccadic target available to the visual system, it is possible that the location of a pre-saccadic target and the displaced location of a pre-saccadic target are used a reference point (Deubel et al., 1996). Second, the presence of a visual reference immediately after saccades induces spatial compression towards a saccadic target (Lappe et al., 2000). In the study, the visual reference provided marks for the initial fixation and the saccadic target. In a gap condition, the visual reference was blanked for 250 ms with the presentation of a probing bar. The results showed that the magnitude of compression of the gap condition fell between conditions in which the visual reference was either present or absent throughout the trials. The compression index of the present condition was significantly different from that of the absent condition. Thus, the blanked visual reference could have been used as a reference point, or at least to a certain extent.

The present study was designed to further investigate effects of blanked saccadic targets on post-saccadic remapping of pre-saccadic visual space. The present study included Forward and Backward conditions, in which saccadic targets reappeared at a displaced position after blanking, to see if the blanked post-saccadic targets could be used as a reference point for remapping pre-saccadic visual space.

5.2. Methods

5.2.1. Participants

Eight right-handed and one left-handed observers, three males and six females, with normal or corrected vision participated in the study. Their mean age was 25.8 (range: 21 ~ 28).

5.2.2. Apparatus/Materials

Apparatus and Materials utilised were the same as those explained in Chapter 2 except for a change in a screen refresh rate from 60 Hz (16.7 ms) to 75Hz (13.3 ms).

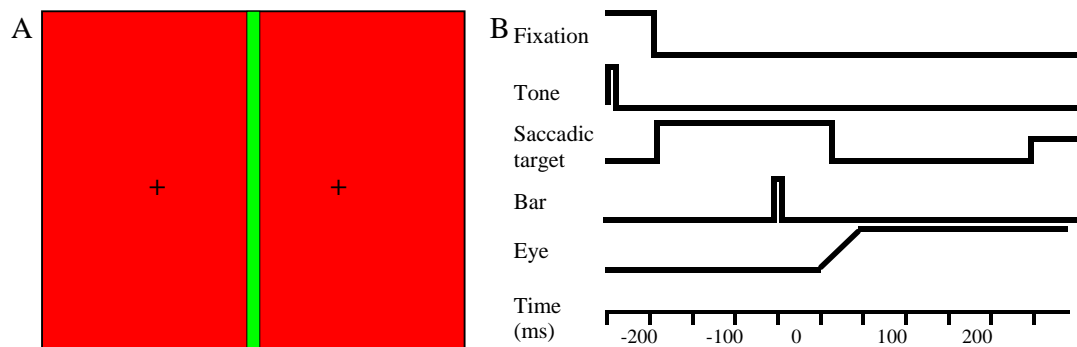


Figure 5.1: Stimuli (A) and time course for the spatial localisation task with a saccadic target blanking and displacement paradigm (B). In this paradigm, the saccadic target disappeared during saccades and was displaced 1° forward or backward 200ms after the offset of saccades.

5.2.3. Design

A three-way (4 x 3 x 2) repeated measures design was utilised. There were three independent variables, Condition, Location and Time. The Condition variable represented four different conditions of the present experiment: Control, Blanking, Forward, Backward. Control referred to a spatial localisation task with no manipulation. Blanking referred to a spatial localisation task with a saccadic target blanking for 200 ms after the offset of saccades. The saccadic target blanking began during saccades. Forward and Backward referred to a spatial localisation task with a saccadic target blanking and displacement. The saccadic target disappeared during saccades and was displaced 1° forward or backward 200ms after the offset of saccades.

The Location variable represented the positions of the probing bar and consisted of three levels: Before, Middle, After. The positions of the probing bar were collapsed to simplify the analysis and the collapsed location could represent the whole spatial area. Before referred to two positions (-10.5° and -14° for the left-to-right trials and 10.5° and 14° for the right-to-left trials) before the fixation cross. Middle referred to three positions (-3.5°, 0° and 3.5° for both the left-to-right trials and the right-to-left trials) between the fixation cross and the saccadic target. After referred to two positions (10.5° and 14° for the left-to-right trials and -10.5° and -14° for the right-to-left trials) beyond the saccadic target. The Time variable represented intervals between time of a probing bar presented and the initiation of saccades and consisted of two levels: -100 to -50 ms and -50 to 0 ms. -100 to -50 ms represented an interval between -100 and -51 ms before saccadic onset and -50 to 0 ms represented an interval between -50 and 0 ms before saccadic onset. The dependent variable was a

mislocalisation error (measured in degrees) between the veridical bar position and the apparent bar position.

5.2.4 Procedure

The procedure was the same as that described in Chapter 4 except for a saccadic target blanking and displacement 200 ms after the offset of saccades. The saccadic target disappeared when a saccadic velocity exceeded 200 °/sec after the onset of saccades. It was displaced 1° forward or backward 200 ms after the offset of saccades, which was detected when the saccadic velocity decreased to less than 100 °/sec. It was emphasised that participants had to fixate the saccadic target before they responded.

Each block consisted of 72 trials (half left-to-right trials and half right-to-left trials). After 36 trials, participants had a break and completed each block following the same calibration procedure. Observers performed three sessions on a different day. Each session was composed of two practice blocks and 7 experimental blocks.

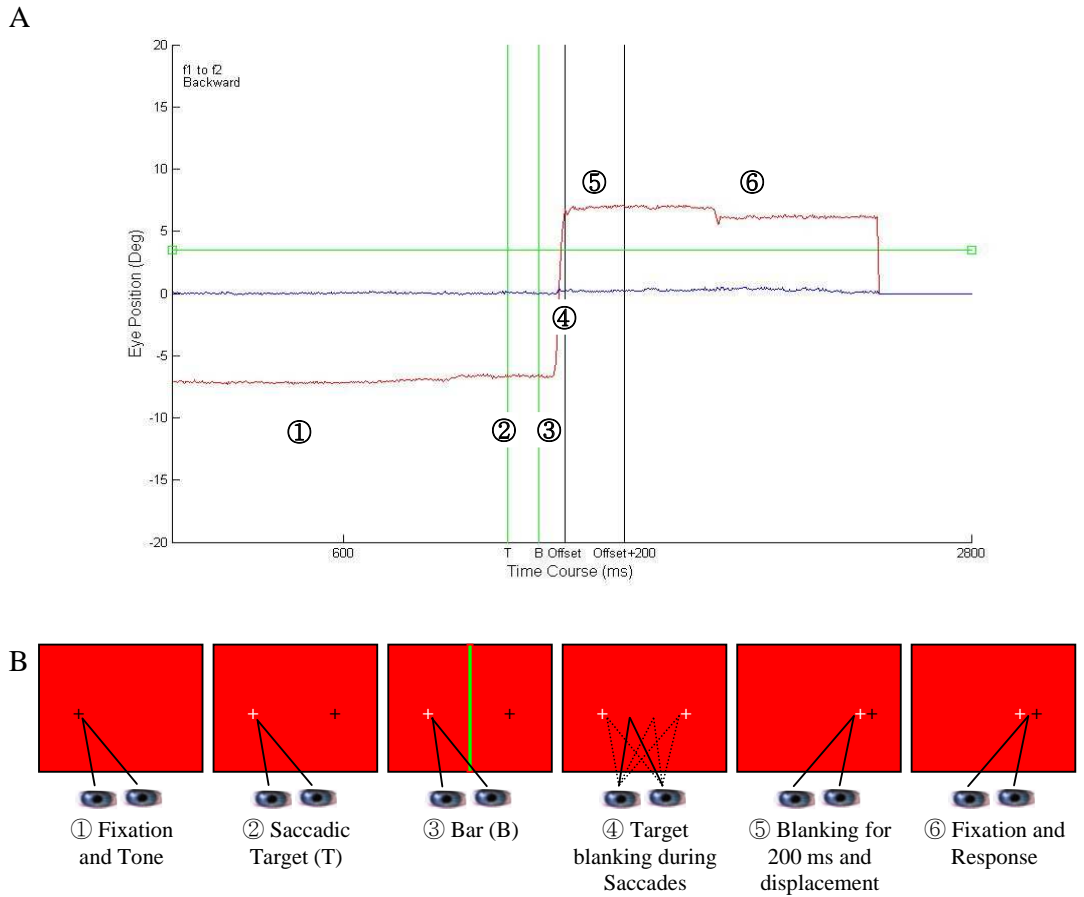


Figure 5.2: Plot of eye movement trace (A) and Schematic illustration of experimental procedure with a saccadic target blanking and displacement paradigm (B).

The plot was used to analyse each trial. The red trace represents horizontal eye movements (x coordinate) and the blue trace represents vertical eye movements (y coordinate). The two solid vertical green lines represent a saccadic target time (T) and a probing bar time (B). The two solid vertical black lines represent the offset of saccades (Offset) and a saccadic target displacement 200 ms after the offset of saccades (Offset+200). The horizontal solid green line represents the position of the probing bar presented on the screen. The numbers on the plot correspond to the time course of the experimental procedure. In each trial, a tone went off when participants fixated a black cross (①). After an interval, a saccadic target was presented on the other side of the screen (②). A vertical green bar was presented (③) before they made an eye movement to the saccadic target. During the saccade, the saccadic target disappeared (④). The saccadic target was blanked for 200 ms after the offset of saccades and displaced 1° forward or backward (⑤). They indicated a perceived position of the bar

using their index finger while fixating the saccadic target (⑥). The white crosses represent traces of the fixation cross and the saccadic target.

5.3. Results

Data analysis for the present study was the same as one described in Chapter 2.

Figure 5.3 shows a data analysis procedure for the Backward condition. Control, Blanking and Forward conditions were analysed using the same procedure.

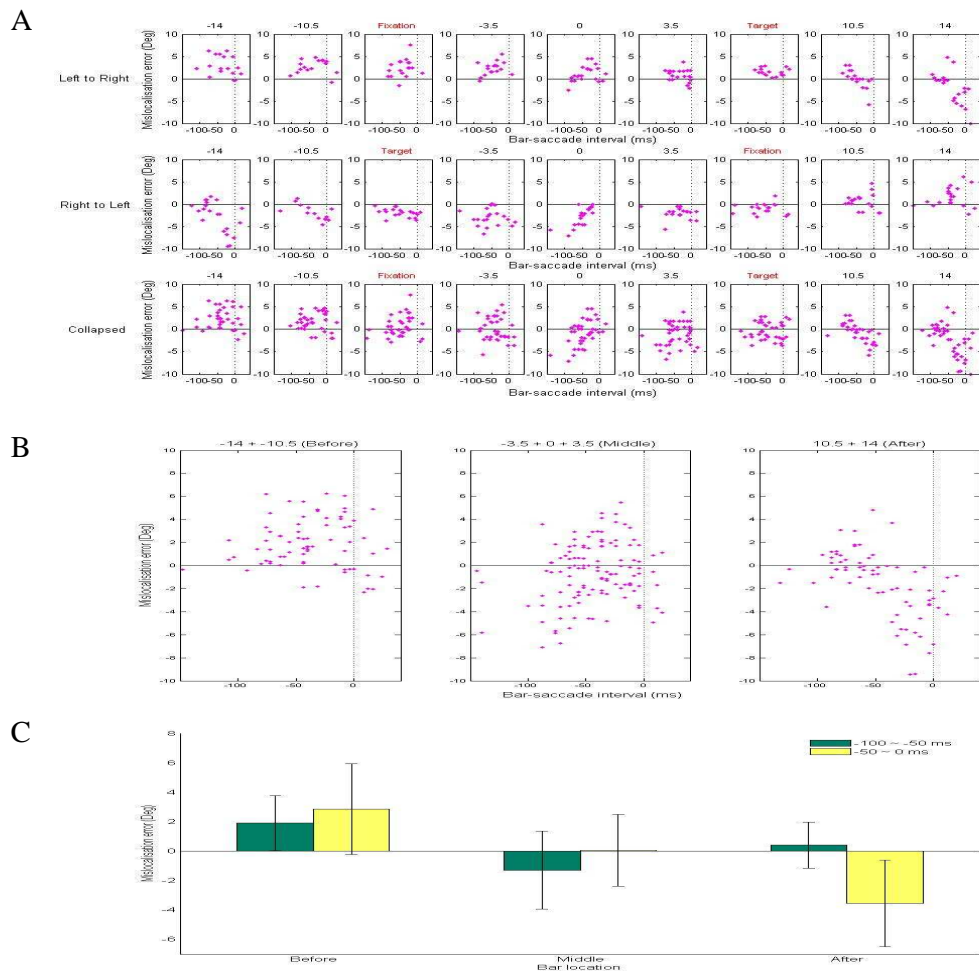


Figure 5.3: Procedure of data analysis for the Backward condition of a participant.

A three-way 4 (Condition: Control, Blanking, Forward, Backward) x 3 (Location: Before, Middle, After) x 2 (Time: -100 to -50 ms, -50 to 0 ms) repeated measures ANOVA was carried out on mean mislocalisation errors of nine observers (see Figure 5.4). There was no significant main effect of Condition, $F(3, 24) = 1.82$, $p = .171$, $\eta_p^2 = 0.19$. There was a significant main effect of Location, $F(1.07, 8.59) = 21.98$, $p = .001$, $\eta_p^2 = 0.73$. Since Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(2) = 13.93$, $p = .001$, corrected values of degrees of freedom were calculated using Greenhouse-Geisser estimates of sphericity ($\epsilon = 0.54$).

Post-hoc tests using a Bonferroni adjustment showed that there was a significant difference in mean mislocalisation errors between Before ($M = 3.38$, $SEM = 0.58$) and Middle ($M = -0.36$, $SEM = 0.20$) locations; $F(1, 8) = 64.95$, $p < .001$, $\eta_p^2 = 0.89$ and between Before ($M = 3.38$, $SEM = 0.58$) and After ($M = -0.51$, $SEM = 0.39$) locations; $F(1, 8) = 17.76$, $p = .003$, $\eta_p^2 = 0.69$. However, there was no significant difference in mean mislocalisation errors between Middle ($M = -0.36$, $SEM = 0.20$) and After ($M = -0.51$, $SEM = 0.39$) locations; $F(1, 8) = 0.09$, $p = .776$, $\eta_p^2 = 0.01$. There was no significant main effect of Time, $F(1, 8) = 2.05$, $p = .190$, $\eta_p^2 = 0.20$.

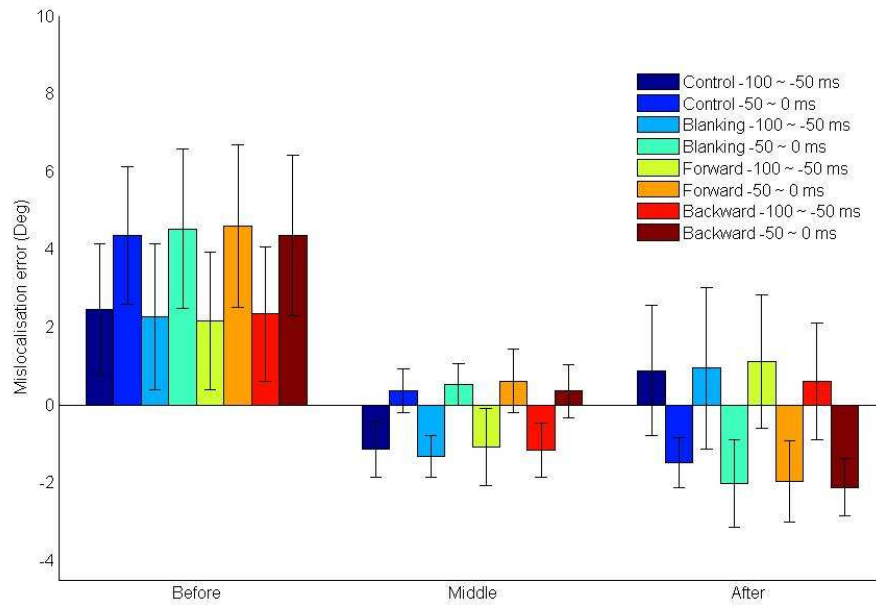


Figure 5.4: Mean mislocalisation errors of nine observers.

Mean mislocalisation errors of four conditions are presented with regard to two separate intervals (-100 to -50 ms and -50 to 0 ms) of three different locations (Before, Middle, After). Error bars represent standard deviations.

The results illustrated that there was no significant interaction between Condition and Location, $F(6, 48) = 1.17$, $p = .336$, $\eta_p^2 = 0.13$. There was no significant interaction between Condition and Time, $F(3, 24) = 0.23$, $p = .875$, $\eta_p^2 = 0.03$. However, there was a significant interaction between Location and Time, $F(2, 16) = 77.59$, $p < .001$, $\eta_p^2 = .91$ (see Figure 5.5).

A simple main effects analysis illustrated that there was a significant effect of Time in Before ($F(1, 8) = 30.76$, $p = .001$, $\eta_p^2 = 0.79$), Middle ($F(1, 8) = 82.44$, $p < .001$, $\eta_p^2 = 0.91$) and After ($F(1, 8) = 45.12$, $p < .001$, $\eta_p^2 = 0.85$) locations.

One-sample t-tests illustrated that in the Before location, mean mislocalisation errors were positive and significant for both -100 to -50 ms ($M = 2.30$, $SEM = 0.58$, $t(8) = 3.99$, $p = .004$) and -50 to 0 ms ($M = 4.46$, $SEM = 0.64$, $t(8) = 6.94$, $p < .001$) intervals. In the Middle location, the mean mislocalisation error for the -100 to -50 ms interval was negative and significant ($M = -1.18$, $SEM = 0.23$, $t(8) = -5.24$, $p = .001$), but that for the -50 to 0 ms interval was not significant ($M = 0.47$, $SEM = 0.21$, $t(8) = 2.26$, $p = .054$). In the After location, the mean mislocalisation error for the -100 to -50 ms interval was not significant ($M = 0.89$, $SEM = 0.57$, $t(8) = 1.57$, $p = .156$), but that for the -50 to 0 ms interval was negative and significant ($M = -1.90$, $SEM = 0.27$, $t(8) = -6.96$, $p < .001$). There was no significant interaction among three factors, $F(6, 48) = 1.51$, $p = .194$, $\eta_p^2 = 0.16$.

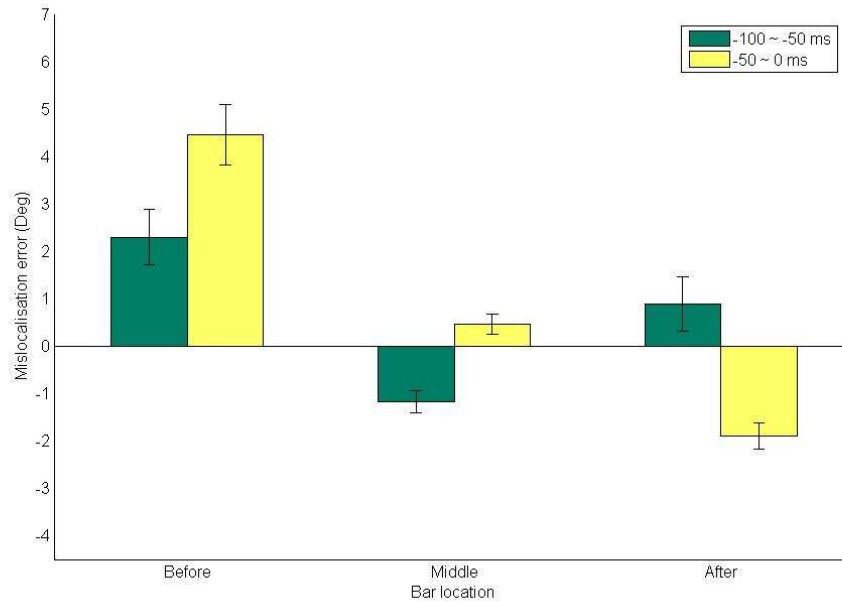


Figure 5.5: Graph for simple effects analysis between Location and Time.

5.4. Discussion

There was no significant difference among four conditions. The significant interaction between Location and Time and the significant effects of Time in three locations indicate that two different remapping mechanisms are involved in the two intervals. At the interval of -50 to 0 ms, the mean mislocalisation error in the Before location was in the direction of saccades, but that in the After location was in the opposite direction of saccades. They together show a pattern of spatial compression towards the saccadic target. At the interval of -100 to -50 ms, the mean mislocalisation error in the Before was in the direction of saccades, but that in the Middle location was in the opposite direction of saccades. The mean mislocalisation errors in the Before and Middle locations show a pattern of spatial compression towards the initial fixation cross. The four conditions showed the same pattern of interactions between Location and Time.

When a saccadic target is not present immediately after the eyes lands and appears in a different location other than the location of the pre-saccadic target, information about the location of the post-saccadic target relative to the pre-saccadic target is available as the location of the pre-saccadic target is remapped using precise efference copy (Deubel et al., 1996). Thus, it was expected that either the location of a pre-saccadic target remapped using efference copy or the blanked post-saccadic target would be used to remap pre-saccadic stimuli after saccades. The results showed that the pre-saccadic stimuli were not remapped relative to the blanked post-saccadic target, but to the location of the pre-saccadic target remapped using precise efference copy.

A blanking paradigm was utilised to investigate how a post-saccadic target is localised relative to a pre-saccadic target across saccades (Collins et al., 2009). Probes were disappeared with the onset of saccades and reappeared about 200 ms after the offset of saccades. Participants reported the location of the post-saccadic target relative to the pre-saccadic target. The perceptual null location (PNL) of the displacement judgments for the location of the post-saccadic target relative to the location of the pre-saccadic target was measured. In the pre-adaptation block, the average PNL was close to 0 and the displacement judgments were based on the distance between the remapped target and the post-saccadic target rather than on the distance between the saccadic landing site and the post-saccadic target. Thus, it was suggested that an efference copy vector contains an oculomotor error of each saccade and this efference copy vector is used to remap the location of a pre-saccadic target after saccades. As the oculomotor error varies in each eye movement, the remapped target location is often not foveal. However, it is consistent and accurate. In the present study, the pre-saccadic stimuli predictively remapped before saccades appeared to be anchored to the location of the pre-saccadic target remapped using accurate efference copy including the oculomotor error of each saccade.

The focus of spatial compression can be shifted from the saccadic target, which elicits the saccade, to the new location of the target induced by saccadic adaptation (Awater et al., 2005). Spatial localisation of objects briefly flashed during saccadic adaptation was investigated. During saccadic adaptation, the initial target moved to a new position. As the saccadic amplitude adapted, the endpoint of the first saccade fell closer to the new position of the target. In the unadapted condition, the bar presented around the saccadic eye movement was mislocalised towards the saccadic

target. However, in the adapted condition, the focus of compression was not towards the initial target, but towards the new position of the target. Interestingly, the compression closer towards the new location of the target was not induced by the physical presence of the target. In the control experiment, the initial saccadic target disappeared and did not reappear in the new position. The focus of compression was still towards the new location of the target without its presence. It seems that visual stimuli presented around saccades were anchored relative to the location remapped using a signal which carries the magnitude of saccadic adaptation.

Such a signal is used to align pre- and post-saccadic targets rather than a signal which elicits the initial saccade (Bahcall & Kowler, 1999). Perceptual mislocalisations were induced by saccadic adaptation. A blanking interval was inserted between the pre-saccadic target and the probe. The results showed that the perceptual mislocalisations were in the same direction as the target displacements in the adaptation trials. During forward adaptation sessions, the post-saccadic probes had to be displaced forward to be perceived as in the same location as the pre-saccadic target. During backward adaptation sessions, the post-saccadic probes had to be displaced backward to be perceived as in the same location as the pre-saccadic target. This perceptual mislocalisation was found even when the location of the pre-saccadic target was displaced to the probe location during saccades. The perceptual mislocalisations of the post-saccadic probe relative to the pre-saccadic target following saccadic adaptation point out that a signal which elicits the actual saccade is not used to align the pre-saccadic target and post-saccadic probe. Thus, the alignments of the pre-saccadic target and the post-saccadic probe were carried out

using a high level efference copy which is created by adapted saccadic command and contains information about the forward or backward adaptation of the target.

There is another evidence that the visual stimuli presented around saccades can be mislocalised towards the location of the target remapped using precise efference copy carrying metric information about adaptation (Collins et al., 2009). In the study of localising the post-saccadic target relative to the pre-saccadic target using a blanking paradigm, after the adaptation session the eyes landed short of the saccadic goal. There was a significant shift of the post-adaptation PNL from the pre-adaptation PNL and the average PNL was significantly less than 0. As a result, stationary targets were perceived as displaced forward and backward displaced targets were perceived as stationary. Although adaptation shifted the saccadic landing site, the displacement judgments did not rely on the saccadic landing site. The shift of the post-adaptation PNL suggests that the remapped location of the pre-saccadic target was modified by saccadic adaptation. In other words, the location of the pre-saccadic target was remapped using efference copy carrying metric information modified by adaptation.

Thus, it can be suggested that the pre-saccadic stimuli predictively remapped before the onset of saccades are anchored to the location of the pre-saccadic target remapped using efference copy carrying accurate metric information about forthcoming saccades.

Chapter 6: An investigation into effects of finger movements on somatosensory perception: A behavioural study

6.1. Introduction

Perceived time of visual stimuli presented before saccades was compressed and temporal order of visual stimuli flashed just before saccades was reversed (Morrone et al., 2005). The perceived duration of a tactile stimulus delivered at the end of an arm movement was overestimated (Yarrow & Rothwell, 2003) just as temporal perception of a saccadic target was distorted (Yarrow et al., 2001). It is not only sensory stimuli that are misperceived, but anticipatory awareness of voluntary movements was also observed (Haggard et al., 1999).

The pre-motor theory put forward that the preparation to make an eye movement should improve capacity to process sensory information presented the location of the target (Rizzolatti et al., 1994). A shift of visual attention prior to eye movements was shown by enhanced detectability of visual stimuli presented at the location of saccades (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995). Tactile attention shifted by saccadic eye movements can also facilitate processing of tactile stimuli (Juravle & Deubel, 2009; Rorden et al., 2002). According to pre-motor theory, different motor tasks can activate different cortical circuit for spatial attention (Rizzolatti et al., 1994). The theory proposed that preparation to reach a target improves capacity to process sensory information presented the location of the target. It was demonstrated that discrimination of mirror image symbols is better when a

discrimination symbol is a target for reaching movements than when a discrimination symbol and a pointing target are different (Deubel & Schneider, 1998) and action preparation can improve processing of tactile stimuli (Juravle & Deubel, 2009).

Just as retinal displacements by eye movements were adjusted by efference copy of a motor command (von Holst, 1954) or a corollary discharge (Sperry, 1950), according to the internal forward model, sensory prediction can be used to cancel the sensory consequences of self-generated movements (Wolpert & Flanagan, 2001). Consequently, self-administered tactile stimuli were rated as less ticklish, intense and pleasant than when they were externally administered by a robot (Blakemore et al., 1999) and self-generated forces could not match externally-generated forces of the same magnitude (Shergill et al., 2003). However, studies illustrated that externally delivered sensory stimuli were also attenuated. Cutaneous sensory thresholds were elevated during movements (Angel & Malenka, 1982) and muscular sense was significantly attenuated by the fast movement condition compared to the slow movement, passive movement and static conditions (Collins et al., 1998). Dependency of sensory attenuation on central signals generated during motor preparation was also demonstrated by applying transcranial magnetic stimulation to the primary motor cortex (Voss et al., 2006).

The present study was designed to further investigate effects of manual movements on perception of externally-administered tactile stimuli as the previous studies contradict. They showed that perception of externally generated tactile stimuli applied around manual movements was either suppressed or enhanced. In the Motor/Tactile tasks of the present study, participants were cued to press a push

button of the response box either with their left or with right index finger and a pneumatic tap was delivered to either to their left or right middle finger. A Moving condition represented a condition in which stimulated finger was on the same hand as the responded finger and a Non-Moving condition represented a condition in which the stimulated finger was not on the same hand as the responded finger. In the analysis, the Moving condition and the Non-Moving condition were compared.

6.2. Methods

6.2.1. Participants

Nine healthy participants, five female and four male, aged 24–35 (mean age 27.7) gave informed consent and took part in the study. They were all right-handed and had normal or corrected to normal vision.

6.2.2. Material & Apparatus

A rectangular response box with two air holes at the top and two push buttons at the bottom was located on a table in front of the participants. The dimensions of the response box measured 20cm x 10cm x 5cm and the distance between two holes and two push buttons was 15.5cm. The distance between the air hole and the push button measured 4 cm. The diameters of the air hole and the push button were 7.5 mm and 5 mm respectively. The participants received pneumatic stimulation (125 psi) on their middle fingers through the holes and they responded to a visual cue presented on the 17” monitor located 30 cm in front of them by pressing the buttons. The response box and the monitor were located in line with their mid-sagittal axis. A control board

was connected to the response box to deliver the pneumatic stimulation and a compressor (JUN-AIR compressor, 6-25 model, 230V/50Hz) was connected to the control board which was operated by a computer. The participants' temporal order judgements were recorded using foot pedals. The positions of the pedals were adjusted for the participants so that they could put their foot comfortably on the separate pedals. The participants were listening to classical music with earphones throughout the experiment (see Figure 6.1). The experiment was written in Matlab and the visual stimuli were generated utilising Cogent Graphics (developed by John Romaya at the Laboratory of Neurobiology, Wellcome Department of Imaging Neuroscience, UCL, UK) and Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).



A. Response box

B. Control board

C. Compressor

Figure 6.1: Photos of the apparatus used in the experiment. Participants located their middle finger on the air hole (a) and pressed the push button (b) with their index finger.

6.2.3. Design

The present study used a within participants design. Participants performed Motor/Tactile tasks, in which they were cued to press the push button with their left

or right index finger and a pneumatic tap was delivered to their left or right middle finger. Four types of trials were involved in this task. Participants were cued to press the button with their left index finger and received the tap either on their left middle finger (the Moving Left condition) or on their right middle finger (the Non Moving Right condition). Participants were cued to press the button with their right index finger and received the tap either on their right middle finger (the Moving Right condition) or on their left middle finger (the Non Moving Left condition). The terms 'Left' and 'Right' represented stimulated fingers. The term 'Moving' implied that the stimulated finger and responded finger were on the same hand. The term 'Non Moving' implied that the stimulated finger and responded finger were not on the same hand. The present study categorised the trials into two conditions: the Moving condition and the Non Moving condition.

6.2.4. Procedure

At the beginning of the experiment, the participants were instructed to sit close to a table and to position both hands on the rectangular response box with their middle fingers on the air holes and their index fingers on the push buttons. Each trial began with a white fixation cross at the centre of the 17" monitor. After a random interval (mean = 500 ms, variance = 1500 ms) a blue or yellow square was presented. The participants were instructed to respond to the stimulus either by pressing the left button when a blue square was presented or by pressing the right button when a yellow square was presented. A pneumatic tap was delivered for 100 ms randomly to a left or right middle finger at a random interval (mean = mean response time – 108 ms, variance = 3000 ms) after the stimulus presentation. The mean response time was obtained by calculating the median of five previous response times. 108 ms was deducted from the mean response time because there was a delay between triggering

the tap and actual delivery of the tap to the finger. The screen went blank 500 ms after the tap was delivered. After 1000 ms the participants were asked whether the tap was delivered before or after their movement onset. The participants responded by pressing the left foot pedal if it was delivered before the onset of their finger movement or by pressing the right foot pedal if it was delivered after the onset of their finger movement located on the floor. They performed two practice blocks (on average 50 trials) before they carried out two experimental blocks (on average 320 trials).

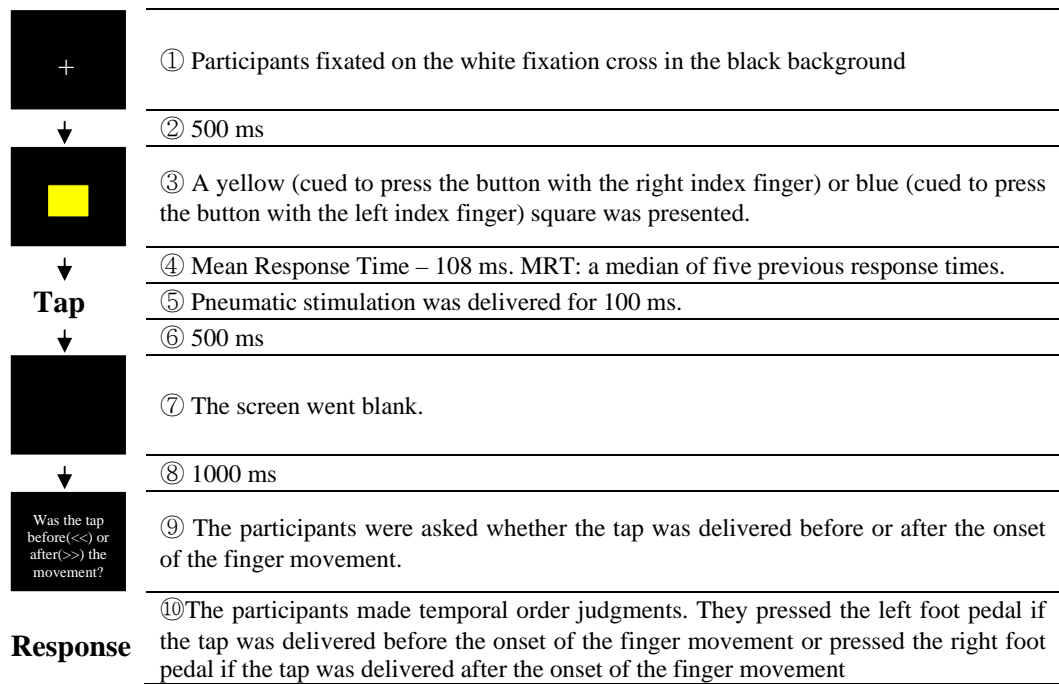


Figure 6.2: Chronological order of experimental procedure.

6.3. Results

For each trial, Stimulus-Movement Interval (SMI) was measured. It is time difference between the pneumatic tap and the finger movement. Positive SMIs

indicate that the tap was delivered after the onset of the finger movement and negative SMIs indicate that the tap was delivered before the onset of the finger movement. The range of SMI in the present study was between -300ms and 300ms. This range was divided into 14 time bins in a step of 40 ms from 0 SMI. The proportion of 'after' responses was calculated for each bin. Psychometric functions were fitted using the `psignifit` toolbox version 2.5.6 for Matlab (see <http://bootstrap-software.org/psignifit/>) which implements the maximum-likelihood method described by Wichmann and Hill (2001). The point of subjective simultaneity (PSS) and the just noticeable difference (JND) were estimated for the Moving condition and the Non Moving condition for each participant (see Table 6.1). The PSS is the SMI at which the participants perceived the pneumatic stimulation and the onset of the finger movement to be simultaneous and was obtained from the interpolated 50% crossover point, that is, the SMI at which the participants responded 'after' and 'before' equally often. The JND is the smallest detectable difference between the tactile stimulation and the finger movement. The JND was obtained by subtracting the SMI at which the proportion of 'after' responses was 50 % from the SMI at which the proportion of 'after' responses was 75%.

Participant	PSS		JND	
	Moving	Non Moving	Moving	Non Moving
1	165.50	12.37	133.5789	75.75067
2	-0.64	-20.64	82.74048	88.28267
3	-75.65	-63.17	81.58926	105.8576
4	169.44	-89.72	95.97348	145.962
5	19.88	-9.87	79.1299	44.96324
6	48.29	-9.97	85.49391	73.03763
7	-25.66	-129.10	124.4488	252.9836
8	8.70	-11.61	76.33748	36.83312
9	160.35	122.11	79.18456	89.79994
Mean	52.25	-22.18	93.16	101.50
SD	91.12	70.80	21.20	65.29
SEM	30.38	23.60	7.07	21.76

Table 6.1: Individual PSS and JND for the Moving and Non Moving conditions.

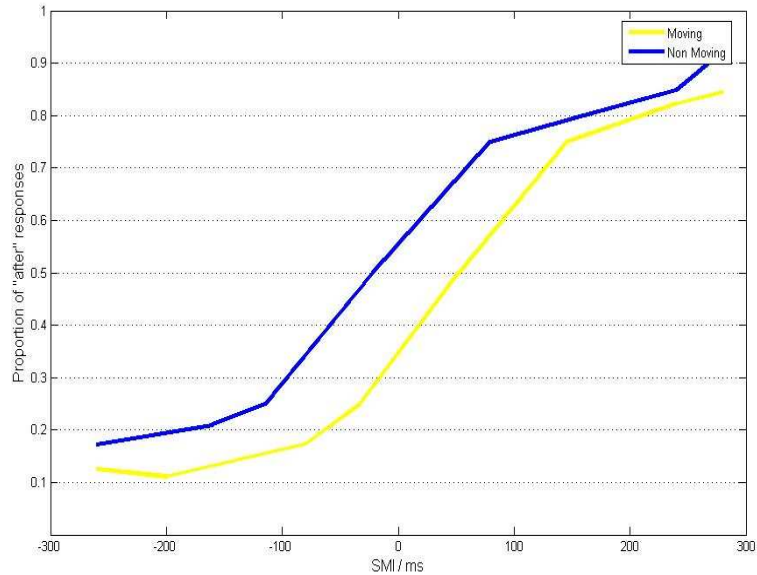


Figure 6.3: Mean proportion of 'after' responses as a function of SMI (ms) for the Moving and Non Moving conditions. The positive SMIs indicate that the tactile stimulation followed the finger movement and the negative SMIs indicate that the tactile stimulation preceded the tactile stimulation.

Although the mean PSS for the Non Moving condition shows that the tactile stimulation has to precede the finger movement by 22.18 ms in order for them to be perceived as synchronous and the mean PSS for the Moving condition shows that the tactile stimulation has to follow the finger movement by 52.25 ms in order for them to be perceived as synchronous (see Figure 6.4), one sample t-test illustrates that the PSSs for the Moving condition ($t(8) = 1.720$, $p = .124$) and the Non Moving condition ($t(8) = -0.940$, $p = .375$) are not significantly different from 0 ms SMI. However, a paired samples t-test illustrates that the difference between the PSS for the Moving condition (M: 52.25, SEM: 30.38) and the PSS for the Non Moving condition (M: -22.18, SEM: 23.60) is significant ($t(8) = 2.618$, $p = .031$).

A paired samples t-test illustrates that the difference between the JND for the Moving condition (M: 93.16, SEM: 7.07) and the JND for the Non Moving condition (M: 101.50, SEM: 21.76) is not significant ($t(8) = -0.444$, $p = .669$, see Figure 6.4).

6.4. Discussion

Participants carried out Motor/Tactile tasks, in which they were cued to press the push button with their left or right index finger and a pneumatic tap was delivered to their left or right middle finger. The Moving condition represented a condition in which the stimulated finger was on the same hand as the responded finger. The Non Moving condition represented a condition in which the stimulated finger was not on the same hand as the responded finger. The results showed that participants' sensitivity to the temporal order of the finger movement and the tactile stimulation was not affected by the finger movement as the JNDs between the Moving and Non moving conditions were not significantly different. In the Non Moving condition, the

tactile stimulation had to lead the finger movement by 22.18 ms in order for synchrony to be perceived and in the Moving condition, tactile stimulation had to follow the finger movement by 52.25 in order for synchrony to be perceived. However, the statistical analysis showed that their perceptual synchrony was accurate. When the PSSs for both conditions were compared, the result indicated that the tactile stimulation in the Non Moving condition had to lead the tactile stimulation in the Moving condition by 74.43 ms in order for synchrony to be perceived.

The results showed that the tactile stimuli in the Moving condition were processed 74.43 ms faster than those in the Non Moving condition. Juravle and Deubel (2009) demonstrated a link between tactile attention and motor preparation. They suggested that action preparation can facilitate the processing of tactile stimuli. In Experiment 2, an auditory cue, either low or high, prepared participants to lift either the right or left index finger while fixating on a central fixation cross. The offset of the auditory cue prompted the participant to execute finger-lifting movement and a tactile stimulus was presented to one of the fingers for 100 ms. The tactile stimulus was an increase in the vibration intensity from the base vibration intensity which was presented with the auditory cue from the beginning of each trial. Participants were requested to respond to the tactile stimulus by pressing the foot pedal. The results showed that tactile stimuli presented at the finger of the planned movement were detected faster than those presented on the opposite finger of the planned movement. Thus, the shift of covert tactile attention to the location of the planned movement improved the processing of tactile stimuli.

As the location of the index finger and the goal of the finger movement were identical, the centre of the attention shifted by the preparation of the finger movement in the present study was the location of the cued finger. As a result, the tactile stimuli in the Moving condition were processed faster than those in the Non Moving condition. Action can selectively allocate attention to the location which is relevant to the action (Tipper et al., 1992). The participant made a reaching movement towards a target located in the middle row. A distractor was located either in the front row or in the back row. When the starting position of the hand was at the bottom of the stimulus board, participants made forward reaching movements towards the target crossing the front row, whereas when the starting position was at the top of the board they made backward reaching movements towards the target crossing the back row. The results illustrated that front-row distractors induced more interference when the starting position of the hand was at the bottom, but the interference effect was induced by the back row distractor when the starting position of hand was changed to the top of the stimulus board. Selective attention was allocated to a distractor in the movement related location and consequently, the distractor induced greater interference than a detractor out of the trajectory of the movement. Thus, the study illustrates that attention operates in the action-centred coordinate.

It seems that in the visual frame of reference a visual mapping affects processing of tactile stimuli as attention shifts to the location of saccades in the action-centred coordinate. Eye movements shift tactile attention to the location of forthcoming saccades (Rorden et al., 2002). Participants made an eye movement from a central fixation point to the left or right yellow LED located near the hand. A tactile stimulus

was delivered to the proximal or distal location of either index finger either 200 or 500 ms after the central saccade cue. Participants gave verbal responses whether the tactile stimulus was 'down' (proximal) or 'up' (distal) location of the index finger. It was found that participants responded significantly faster when the tactile stimulus was delivered near the location of forthcoming saccades rather than when it was delivered to the opposite location. With their hands crossed participants responded faster for the tactile stimuli delivered to the location near the forthcoming saccades than for those delivered to the opposite location. This crossed-hands experiment shows that in visual modality attention shifts in the visual frame of reference and a visual mapping have an important effect on facilitation of tactile stimuli.

The pre-motor theory of attention claimed that when a goal-directed movement is prepared, the shared cortical circuits are activated for spatial attention and different motor tasks can activate different cortical circuit for spatial attention (Rizzolatti et al., 1994). The theory also suggested that the preparation to reach a target should improve capacity to process sensory information presented the location of the target in the same way as the preparation to make an eye movement does. An event-related potential (ERP) study illustrated that attention shifts can be induced by the covert preparation of unimanual responses (Eimer et al., 2005). ERPs were recorded during the interval between a response-hand selection cue and a subsequent action cue (Go/Nogo signal) while participants were preparing to lift their left or right index finger. Somatosensory ERP components were boosted when task-irrelevant tactile stimuli were delivered to the prepared finger early (520 ms after the hand-selection cue) or late (920 ms after the hand-selection cue) during the response preparation period. When the tactile stimuli were delivered early, the N140 component was

increased for tactile stimuli delivered to the cued index finger compared to those delivered to the uncued index finger in both contralateral and ipsilateral hemispheres (F3/4 and C3/4) to the stimulated hand. When the tactile stimuli were delivered late, the N140 component was also increased for the tactile stimuli delivered to the cued finger in the contralateral hemisphere (F3/4 and C3/4) to the stimulated finger. During this late period, the P90 component was boosted for the stimuli delivered to the cued finger in the ipsilateral hemisphere (F3/4 and C3/4) to the stimulated finger. The study provides evidence that tactile attention shifted by the preparation to lift a finger can enhance capacity to process tactile stimuli.

The effects of covert shifts of attention and saccade preparation on somatosensory processing were also investigated (Gherri & Eimer, 2008). In the Covert attention task, an auditory cue was used to direct participants' attention to the side of a tactile target and a tactile target or non-target was presented to either the cued index finger or the uncued index finger. The non-target stimuli were relevant for the ERP analysis. In the saccade task, an auditory cue indicated the side of saccades and either the participants made a saccade with a central auditory cue (Go signal) or a tactile target (Nogo signal) was delivered to the left or right index finger. The results showed that for both tasks somatosensory N140 components (130-170 ms post-stimulus) were increased for tactile stimuli delivered to the cued finger compared to the uncued finger in the ipsilateral hemisphere (FC5/6, C3/4 and CP5/6) to the stimulated hand. Thus, both covert shifts of tactile attention and attention shifts by saccade preparation facilitated the processing of somatosensory stimuli and that they have a shared effect on somatosensory processing.

While tactile attention was shown to be shifted to the location of the forthcoming saccades, a manual response preparation shifts tactile attention to the effector rather than to the final location of the manual movement (Forster & Eimer, 2007). Participants were instructed to touch the index finger of either hand with the index finger of the other hand. Task-irrelevant tactile stimuli were presented to the effector or the goal finger of the forthcoming movement during covert response preparation. There were two different task instructions in the experiment. The response cues at the beginning of each trial indicated either the effector or the movement goal of the manual responses. Early somatosensory N140 component was boosted over the hemisphere (C3/4) contralateral to the stimulated finger with both instructions when tactile stimuli were delivered to the effector rather than the goal finger of the forthcoming movement.

The present study showed that tactile stimuli delivered to the middle finger which was not on the same hand as the cued index finger had to precede those delivered to the middle finger which was on the same hand as the cued index finger 74.43 ms in order for synchrony to be perceived. That is, the tactile attention induced by the cued index finger facilitated processing of tactile stimuli presented to the middle finger of the responded hand compared that of tactile stimuli presented to the middle finger of the stationary hand. The results of the present study substantiate a claim that a voluntary attention can be directed to a location or part of the body and this attention can improve the processing of subsequent tactile, visual or auditory stimuli presented near or at the attended location (Spence & Gallace, 2007). Action preparation can increase capacity to process tactile stimuli (Juravle & Deubel, 2009). It appears that attention operates in the action-centred coordinate (Tipper et al., 1992). With

reference to eye movements, attention shifts to the goal location of saccades and facilitate the processing of tactile stimuli (Rorden et al., 2002). With regard to manual movements, tactile attention is shifted to the effector rather than the goal of the manual responses (Forster & Eimer, 2007). The pre-motor theory of attention claimed that a goal-directed movement activates the shared cortical circuits for spatial attention (Rizzolatti et al., 1994). ERP studies demonstrated that tactile attention shifted by preparation to lift a finger or to make an eye movement can enhance processing of somatosensory stimuli (Eimer et al., 2005; Gherri & Eimer, 2008).

However, somatosensory evoked potentials (SEP) were decreased during movement or even before the onset of movement (Shimazu et al., 1999; Starr & Cohen, 1985). A relationship between sensory suppression and velocity of movement and attenuation of muscular sense by voluntary movements also supports the gating of SEPs (Angel & Malenka, 1982; Collins et al., 1998). Voss et al. (2006) suggested that sensory attenuation during voluntary movement is caused by an efferent signal from upstream of primary motor cortex. Therefore, it would be of interest to carry out an imaging study to investigate modulations of cortical processing of somatosensory stimuli adopting Motor/Tactile tasks used in the present study.

Chapter 7: An investigation into effects of finger movements on somatosensory perception: An fMRI study

7.1. Introduction

The results in the previous study revealed that the tactile stimulation in the Non Moving condition had to lead the tactile stimulation in the Moving condition by 74.43 ms in order for synchrony to be perceived. In other words, the tactile stimuli in the Moving condition were processed 74.43 ms faster than those in the Non Moving condition. Thus, the behavioural study provided evidence in favour of the pre-motor theory of attention since the tactile attention induced by the cued index finger facilitated processing of tactile stimuli. An event-related potential (ERP) study also illustrated that somatosensory ERP components were boosted when task-irrelevant tactile stimuli were delivered to the prepared finger during a response preparation period (Eimer et al., 2005) and that manual response preparation shifted tactile attention to the effector rather than to the final location of the manual movements (Forster & Eimer, 2007). However, studies reported suppression of somatosensory evoked potentials (SEPs) prior to the onset of movements (Angel & Malenka, 1982; Collins et al., 1998; Shimazu et al., 1999; Starr & Cohen, 1985).

The present study was designed to further investigate effects of manual movements on perception of externally-administered tactile stimuli using the experimental design used for the behavioural study and a functional magnetic resonance imaging (fMRI) method. The study was carried out to find modulations of somatosensory processing in both somatosensory areas such as SI and SII and cortical areas. A separate run was

conducted to identify somatosensory areas and participants continued to carry out Motor/Tactile tasks just as they did in the behavioural study.

7.2. Methods

7.2.1. Participants

Twelve healthy participants, seven female and five male, aged 21–35 (mean age 26.7) gave informed consent and took part in the study. They were all right-handed and had normal or corrected to normal vision.

7.2.2. Material & Apparatus

Apparatus and Materials utilised were the same as those explained in Chapter 6. Some changes had to be made as tasks were performed in the scanner. Participants wore ear plugs and ear protection in the scanner and their right and left middle fingers were taped onto the corresponding air holes using microporous tape. A visual cue (yellow or blue square) was presented through in-scanner goggles (Silent Vision, Avotec, Inc).

7.2.3. Design

The present study used a within participants design. First, participants underwent the Tap Alone condition, in which they only received pneumatic taps without making any movement, to identify somatosensory areas for region of interest (ROI) analysis. Next, they performed Motor/Tactile tasks, in which they were cued to press the

button with their left or right index finger and a pneumatic tap was delivered to their left or right middle finger. Four types of trials involved in the task were described in Chapter 6 (Moving Left, Non Moving Left, Moving Right and Non Moving Right). Incidentally, the Moving condition included the Moving Right and Moving Left conditions and represented a condition in which the stimulated finger was on the same hand as the responded finger. The Non Moving condition included the Non Moving Right and Non Moving Left conditions and represented a condition in which the stimulated finger was not on the same hand as the responded finger. The Left condition included the Moving Left and Non Moving Left conditions and represented a condition in which the left fingers were stimulated. The Right condition included the Moving Right and Non Moving Right conditions and represented a condition in which the right fingers were stimulated.

7.2.4. Procedure

7.2.4.1. Motor/Tactile tasks:

Participants lay in a head first supine position in the scanner and the response box was located on their abdomen. The in-scanner goggles were adjusted for their visual clarity. They underwent one Tap Alone run and three Motor/Tactile runs.

In the Air Alone run, the participants only received pneumatic taps without any movement response while looking at the screen. Each trial began with a white fixation cross at the centre of the screen. After a random interval (mean = 1500 ms, variance = 1500 ms), a white square was presented. The screen went blank for 2000 ms after a random interval (mean = 500 ms, variance = 3000 ms). Then, three

consecutive pneumatic taps were delivered to either the left or right middle finger. Each tap lasted for 100ms. After a random interval (mean = 500 ms, variance = 3000 ms), a new trial began. After every ten trials there was a 15-seconds break before a new trial began. The Tap Alone run lasted for five minutes.

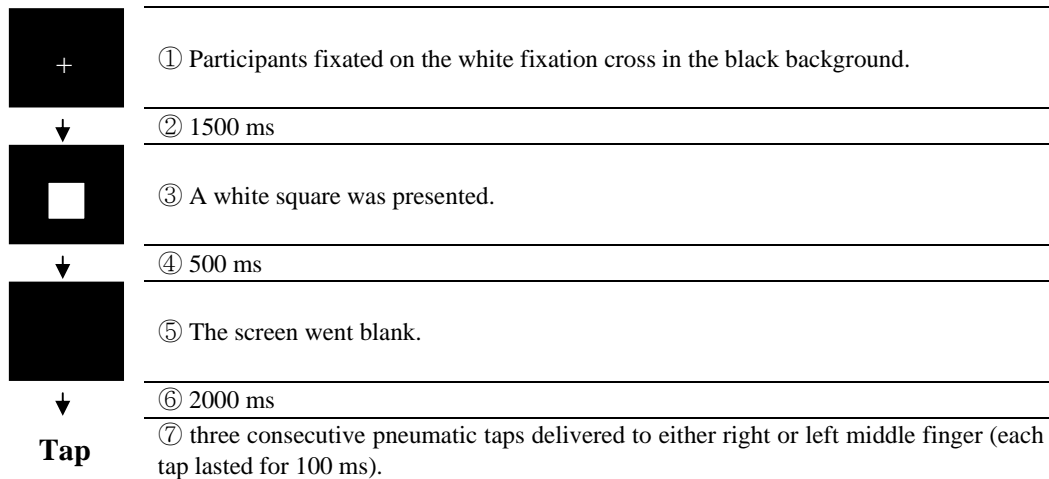


Figure 7.1: Chronological order of the Tap Alone condition.

In the Motor/Tactile run, each trial began with a white fixation cross at the centre of the screen. After a random interval (mean = 1500 ms, variance = 1500 ms), a blue or yellow square was presented. The participants were instructed to respond to the stimulus either by pressing the left button when a blue square was presented or by pressing the right button when a yellow square was presented. A pneumatic tap was delivered for 100ms randomly to the left or right middle finger at a random interval (mean = mean response time - 75ms, variance = 4000ms) after the visual stimulus presentation. The mean response time was obtained by calculating the median of five previous response times. The screen went blank 500ms after the tap was delivered. The participants waited for a random interval (mean = 3500ms, variance =

300000ms) before a new trial started. Each Motor/Tactile run lasted for approximately twelve and a half minutes.

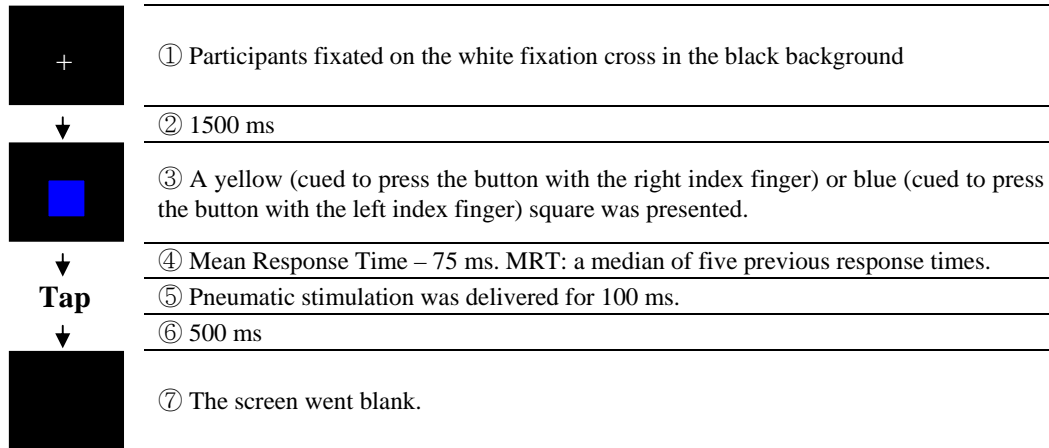


Figure 7.2: Chronological order of the Motor/Tactile tasks.

7.2.4.2. Data acquisition and preprocessing:

fMRI data was obtained at the Sir Peter Mansfield Magnetic Resonance Centre (University of Nottingham), using a Philips 3Tesla MR scanner equipped with a Sense Head 8 channel RF coil. Foam pads were used to prevent head motion. For the functional images 30 contiguous axial slices parallel to AC-PC plane were obtained in a descending order using the whole brain gradient-echo Echo Planar Imaging (EPI) sequence (192 mm FOV, 96 x 96 matrix, 3 mm slice thickness, 2 x 2 x 3 m³ voxel size, TE = 40 ms, TR = 2400 ms, flip angle = 80 degrees). High resolution T1-weighted structural images were acquired for each participant (160 sagittal slices at a resolution of 1 x 1 x 1 m³). For the Tap Alone run, two dummy volumes and 120 volumes were obtained for approximately five minutes. For each Motor/Tactile run, two dummy volumes and 310 volumes were obtained for approximately twelve and a

half minutes. (FOV = field of view; TR = repetition time; TE = echo time, AC = anterior commissure; PC = posterior commissure).

The functional and anatomical data (PAR format) were analysed using BrainVoyager QX 1.10 software package. The anatomical data was translated and rotated into the AC-PC plane by identifying the bottom-most anterior commissure point and the top-most posterior commissure points. It was then transformed into Talairach standard space by specifying coordinates of the eight points (anterior commissure, posterior commissure, and the most anterior, posterior, superior, inferior, right and left points of the cerebrum). The functional data of each participant underwent the following preprocessing steps. Slice scan time correction was carried out using cubic spline interpolation based on the descending order of slice scanning. Corrections for small head movements (3-D motion correction) were carried out using trilinear interpolation. After applying a linear trend removal, FFT-based high-pass filter with a cut-off of 3 cycles (0.006 Hz) per time course was applied.

To normalise the functional data, the preprocessed functional data was coregistered with the participant's non-Talairach, non-ACPC-ised anatomical data before it was transformed into Talairach space employing the transformation matrix used for the transformation of the anatomical data into Talairach standard space. Consequently, a normalised volume time course (VTC) data was created for each run of the session. Four normalised VTC data were obtained from each participant. One data was obtained from the Tap Alone run and three data from the Motor/Tactile runs. These normalised functional data were used for multi-subject and single-subject General Linear Model (GLM) analyses.

7.2.4.3. Data analysis:

Random effects analysis (RFX) was initially carried out to obtain somatosensory areas for ROI analysis from the Tap Alone run. Statistical significance was set to a threshold of $p < 0.05$ (uncorrected for multiple comparisons, $t = 2.3$, a minimum cluster size of 4 voxels). As the left and right middle fingers were stimulated, only bilaterally activated somatosensory areas were defined as regions of interest. Subsequently, four contrasts were carried out in each ROI to ascertain whether there were any modulations of somatosensory processing by manual movements: Moving vs Non Moving, Left vs Right, Moving Left vs Non Moving Left and Moving Right vs Non Moving Right. As four comparisons were made for each ROI, the significance level was set at 0.0125 (0.05/4, Bonferroni adjustment). A single-subject GLM analysis was also carried out to identify how many ROIs identified from RFX were shown at the individual level. Although the significance level was set to a threshold of $p < 0.05$ (uncorrected for multiple comparisons), different t-values were used to identify the ROIs for different participants as individuals showed different levels of activation. Even for the same participant different t-values were adopted to identify the ROIs and to separate overlapping ROIs in some cases, for example, while one area was identified at a lower threshold, other two areas were overlapped at this threshold.

A priori RFX (Moving vs Non Moving) was conducted to find cortical areas which showed modulations of somatosensory processing by manual movements. The significance level was set to a threshold of $p < .05$ (uncorrected for multiple comparisons, $t = 2.4$, a minimum cluster size of 4 voxels). Within the cortical areas

identified from the RFX further two contrasts (Moving Left vs Non Moving Left and Moving Right vs Non Moving Right) were carried out to ensure that both Moving conditions (Moving Left and Moving Right) were significantly different from the corresponding Non Moving conditions (Non Moving Left and Non Moving Right) since one contrast could dominantly affected the overall effect. For example, the effect of a contrast (Moving Left vs Non Moving Left) could determine the overall effect (Moving vs Non Moving) if the magnitude of the effect of a contrast (Moving Left vs Non Moving Left) is much larger than that of the effect of a contrast (Moving Right vs Non Moving Right) and the direction of their effects are opposite. As two comparisons were made for the cortical areas, the significance level was set at 0.025 (0.05/2, Bonferroni adjustment).

Labelling for the ROIs was performed based on sulci and gyri of anatomical data in Talairach space. For the group analysis Participant 4's normalised anatomical data was used to label activated areas and for the single-subject analysis each individual's own normalised anatomical data was used. To clarify the localisation and labelling of each ROI, sagittal, coronal and axial views and Talairach coordinates of each ROI were presented in figures and tables.

7.3. Results

Only two Motor/Tactile runs of Participant 1 were included in the analysis as data from the first run could not be analysed. The functional data of the Tap Alone run of Participant 2 was acquired in a separate session as the initial data showed large head movements.

7.3.1. Modulation of somatosensory processing within the somatosensory areas:

Random effects analysis (RFX) conducted for the Tap Alone condition identified somatosensory ROIs. In the right hemisphere, secondary sensory area (SII), two locations in the primary sensory area (SI, SI-2 is located superior to SI-1), , inferior parietal lobe (IPL, close to postcentral sulcus), premotor cortex (PM), insula, supplementary motor area (SMA) and posterior rostral cingulate zone (RCZp) showed significant activation ($p < 0.05$, $t = 2.3$, uncorrected for multiple comparisons). In the left hemisphere, SII, SI-1, SI-2, IPL, PM, insula, middle frontal gyrus (MFG) showed significant activation ($p < 0.05$, $t = 2.3$, uncorrected for multiple comparisons). As the left and right middle fingers were stimulated, only bilaterally activated somatosensory areas were defined as ROIs. Thus, the ROIs defined for further analyses are SII, SI-1, SI-2, IPL, PM and insula in both hemispheres (see Figure 7.3). The number of participants who showed significant activation in each ROI was shown in Table 7.1.

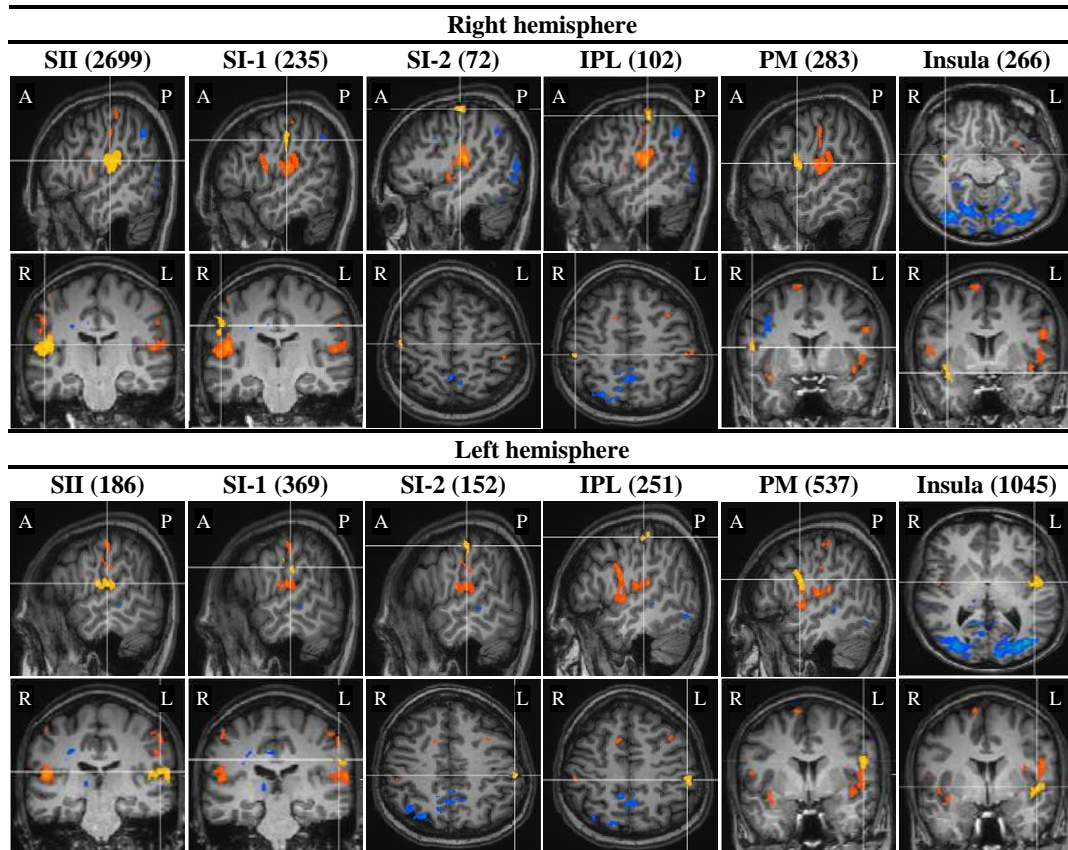


Figure 7.3: Sagittal, coronal and axial views of ROIs obtained from random effects analysis of the Tap Alone condition ($p < 0.05$, $t = 2.3$, uncorrected for multiple comparisons). ROIs are indicated by a white cross and highlighted in yellow. The number in brackets shows the number of voxels in the ROI. (SII, secondary somatosensory area; SI, primary somatosensory area; IPL, inferior parietal lobe; PM, premotor cortex; Insula, insular cortex).

Right hemisphere						
Participant	SII(11)	SI_1(11)	SI_2(11)	IPL(9)	PM(10)	Insula(10)
1	t = 4.0 56_-26_15	t = 4.0 60_-22_28	t = 4.0 54_-22_46	t = 4.0 45_-34_53	t = 4.0 57_2_18	t = 3.0 40_-6_-5
2	t = 3.0 45_-18_14	t = 3.0 43_-17_27	t = 3.0 49_-8_40	t = 2.3 44_-35_43	t = 2.3 54_3_13	t = 2.0 38_-2_-1
3	t = 2.5 63_-21_20	t = 2.5 53_-22_32	t = 2.5 55_-23_42	t = 2.5 42_-35_42	t = 3.0 51_-2_39	t = 2.5 35_-5_13
4		t = 2.3 51_-19_31	t = 2.3 46_-20_39	t = 2.3 36_-38_56		
5	t = 2.2 47_-16_22	t = 2.2 46_-15_43	t = 2.2 46_-22_53	t = 2.1 36_-33_47	t = 2.5 47_2_8	t = 2.1 32_9_11
6	t = 3.0 55_-27_25	t = 3.0 53_-23_35	t = 3.0 54_-23_43	t = 3.0 49_-33_49	t = 2.7 46_4_19	t = 2.7 43_-3_-2
7	t = 2.3 46_-15_16	t = 2.3 58_-14_38	t = 2.3 41_-23_58		t = 2.3 59_12_22	t = 2.2 43_-2_-3
8	t = 3.0 47_-23_29	t = 2.3 57_-13_31	t = 2.3 51_-26_48		t = 2.3 51_6_19	t = 2.3 34_3_-5
9	t = 2.0 48_-19_15					
10	t = 3.5 52_-22_18	t = 2.5 56_-19_33	t = 2.5 44_-20_48	t = 2.5 42_-22_36	t = 2.5 51_4_16	t = 3.0 37_-4_12
11	t = 3.5 54_-21_19	t = 3.5 57_-20_34	t = 3.0 39_-23_57	t = 4.0 49_-34_41	t = 2.5 52_4_16	t = 3.0 32_12_9
12	t = 2.5 49_-18_17	t = 2.5 53_-23_47	t = 2.4 39_-34_54	t = 2.5 45_-28_48	t = 2.1 41_-1_56	t = 2.5 43_-14_11
Left hemisphere						
Participant	SII(9)	SI_1(10)	SI_2(10)	IPL(8)	PM(12)	Insula(10)
1	t = 4.0 -50_-25_18	t = 4.0 -52_-26_31	t = 4.0 -52_-25_43	t = 4.0 -48_-45_44	t = 4.0 -47_1_18	t = 3.0 -40_-10_-2
2	t = 2.3 -57_-7_21	t = 2.3 -56_-8_37	t = 2.3 -54_-10_44		t = 3.0 -52_3_39	
3	t = 3.0 -56_-24_18	t = 3.0 -51_-19_37	t = 3.0 -53_-24_47	t = 3.0 -45_-30_39	t = 3.0 -41_-10_42	t = 2.5 -34_-5_5
4	t = 2.3 -43_-26_17	t = 2.3 -44_-21_46	t = 2.3 -36_-28_56	t = 2.3 -52_-24_39	t = 2.2 -50_-8_15	t = 2.2 -34_-6_12
5					t = 2.5 -47_3_10	t = 2.1 -36_10_4
6	t = 2.6 -60_-33_22	t = 3.0 -62_-28_30	t = 3.0 -56_-25_42	t = 2.7 -62_-40_29	t = 2.7 -49_-8_35	t = 2.7 -36_13_1
7		t = 2.3 -53_-20_35	t = 2.3 -54_-25_42	t = 2.2 -52_-30_46	t = 2.0 -45_0_37	t = 2.2 -40_-3_-4
8	t = 3.0 -47_-18_24	t = 2.3 -42_-27_46	t = 2.3 -44_-29_56	t = 2.3 -46_-36_52	t = 2.2 -49_5_34	t = 2.3 -37_7_1
9					t = 2.0 -62_6_15	
10	t = 3.5 -56_-18_14	t = 3.5 -57_-14_26	t = 2.1 -49_-17_46	t = 2.1 -38_-28_32	t = 2.5 -52_2_28	t = 2.5 -35_4_16
11	t = 4.5 -57_-21_11	t = 3.5 -54_-19_29	t = 2.1 -43_-25_47	t = 4.0 -46_-36_45	t = 2.5 -50_1_25	t = 3.0 -36_-9_9
12	t = 3.0 -55_-25_13	t = 2.5 -50_-25_38	t = 3.0 -43_-31_56		t = 3.0 -49_-1_28	t = 4.0 -40_-10_12

Table 7.1: The number of participants who showed significant activation ($p < 0.05$, uncorrected for multiple comparisons) in each ROI is shown in brackets. Somatosensory areas were identified from single-subject GLM analysis of the Tap Alone condition. ROIs of each participant were found at t-value shown in the table and their Talairach coordinates (x_y_z) are also shown.

Four contrasts (significance level $\alpha = 0.0125$ ($0.05/4$)) within the ROIs demonstrated that in the right hemisphere SI-1 ($t = 6.042$, $p < .0001$) and IPL ($t = 4.597$, $p < .001$) were significantly more activated by contralateral stimulation (the Left condition) than ipsilateral stimulation (the Right condition), while in the left hemisphere SII ($t = -3.260$, $p = .008$), SI-2 ($t = -3.642$, $p = .004$), IPL ($t = -4.592$, $p < .001$), insula ($t = -3.036$, $p = .011$) were significantly more activated by contralateral stimulation (the Right condition) than ipsilateral stimulation (the Left condition). Additionally, IPL ($t = 3.728$, $p = .003$) in the left hemisphere was significantly more activated by stimulation on the contralateral finger of the moving hand (the Moving Right condition) than stimulation on the contralateral finger of the non-moving hand (the Non Moving Right condition). No more significant results were observed from the contrasts carried out in the somatosensory ROIs. Table 7.2 shows the results of all the contrasts performed in the ROIs obtained from the multi-subject random effect analysis of the Tap Alone condition.

Right Hemisphere						
Contrast	SII (49_-20_15)	SI-1 (52_-19_35)	SI-2 (46_-16_55)	IPL (49_-26_48)	PM (52_2_15)	Insula (37_0_-7)
Moving >	t = 2.153	t = -1.080	t = -0.540	t = -1.049	t = .080	t = -0.001
Non Moving	p = .054	p = .303	p = .600	p = .317	p = .938	p = .999
Left >	t = 2.560	t = 6.042	t = 2.881	t = 4.597	t = 2.093	t = .505
Right	p = .027	p < .0001	p = .015	p < .001	p = .060	p = .624
Moving Left >	t = 1.809	t = .222	t = .518	t = -0.017	t = -0.483	t = -0.702
Non Moving Left	p = .098	p = .828	p = .614	p = .987	p = .639	p = .497
Moving Right >	t = .259	t = -1.384	t = -0.792	t = -1.215	t = .808	t = .347
Non Moving Right	p = .801	p = .194	p = .445	p = .250	p = .436	p = .735

Left Hemisphere						
Contrast	SII (-55_-23_16)	SI-1 (-56_-25_29)	SI-2 (-54_-23_44)	IPL (-48_-26_50)	PM (-49_-1_23)	Insula (-44_-2_3)
Moving >	t = -1.197	t = -1.178	t = .503	t = 1.025	t = 1.157	t = .091
Non Moving	p = .256	p = .264	p = .625	p = .378	p = .272	p = .929
Left >	t = -3.260	t = -2.118	t = -3.642	t = -4.592	t = -2.317	t = -3.036
Right	p = .008	p = .058	p = .004	p < .001	p = .041	p = .011
Moving Left >	t = -2.220	t = -0.421	t = -1.012	t = -2.093	t = -0.088	t = -0.137
Non Moving Left	p = .048	p = .682	p = .333	p = .060	p = .932	p = .893
Moving Right >	t = 1.428	t = 2.757	t = 2.053	t = 3.728	t = 1.638	t = .698
Non Moving Right	p = .181	p = .019	p = .065	p = .003	p = .130	p = .500

Table 7.2: Results of four contrasts carried out in the somatosensory ROIs identified from multi-subjects GLM analysis of the Tap Alone condition. Talairach coordinates (x_y_z) of the ROIs are shown in brackets. As four comparisons were performed for each ROI, the significance level was set at 0.0125 (0.05/4, Bonferroni adjustment). t-value and p-value for the contrasts are shown. Values in bold indicate statistical significance for the contrast. The Moving condition includes the Moving Left and Moving Right conditions. The Non Moving condition includes the Non Moving Left and Non Moving Right conditions. The Left condition includes the Moving Left and Non Moving Left conditions. The Right condition includes the Moving Right and Non Moving Right conditions. (SII, secondary somatosensory area; SI, primary somatosensory area; IPL, inferior parietal lobe; PM, premotor cortex; Insula, insular cortex).

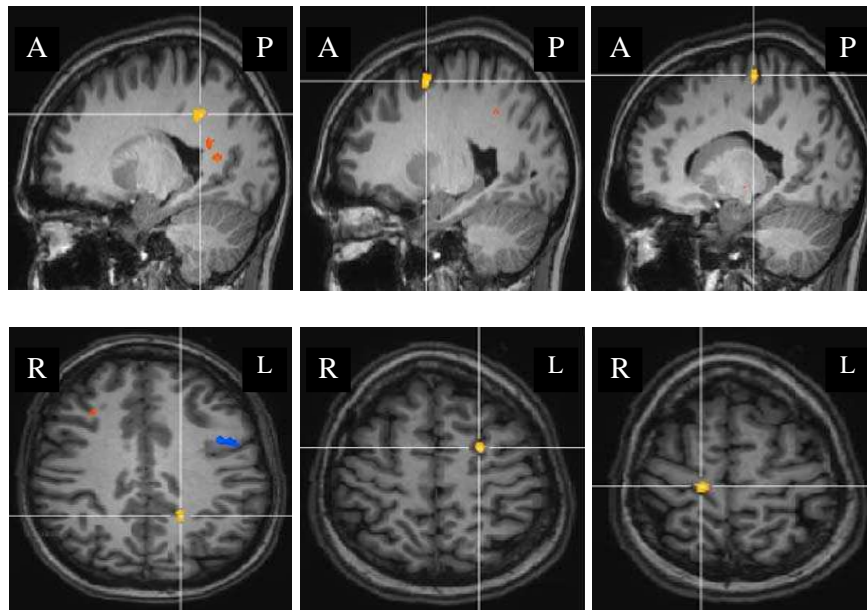
7.3.2. Modulation of somatosensory processing in the cortical areas:

Random effects analysis (Moving vs Non Moving) carried out to ascertain cortical areas showing modulations of somatosensory processing by manual movements illustrated several areas in both hemispheres. In the right hemisphere, middle frontal gyrus (MFG), caudal cingulate zone (CCZ), primary motor cortex (M1), superior occipital gyrus (SOG) and two locations in parahippocampal gyrus (PHG-1 and

PHG-2) were significantly more activated by the Moving condition than the Non Moving condition. In the left hemisphere, two locations in middle frontal gyrus (MFG-1 and MFG-2) showed statistical significance. MFG-1, precuneus (PreC), posterior cingulate gyrus (PCG), caudal cingulate zone (CCZ), superior temporal gyrus (STG) were significantly more activated by the Moving condition than the Non Moving condition whereas MFG-2 and middle temporal gyrus (MTG) were significantly more activated by the Non Moving condition than the Moving condition.

Further two contrasts (Moving Left vs Non Moving Left and Moving Right vs Non Moving Right, significance level $\alpha = 0.025$ ($0.05/2$)) were carried out within the significantly activated areas to ensure that the overall significant effect was not dominantly influenced by one contrast. The results illustrate that in the right hemisphere only M1 (Moving Left > Non Moving Left: $t = 5.600$, $p < .001$, Moving Right > Non Moving Right: $t = 2.842$, $p = .016$) was significantly more activated by both Moving conditions compared to the corresponding Non Moving conditions while in the left hemisphere MFG-1 (Moving Left > Non Moving Left: $t = 2.338$, $p = .039$, Moving Right > Non Moving Right: $t = 2.688$, $p = .021$) and PreC (Moving Left > Non Moving Left: $t = 2.235$, $p = .047$, Moving Right > Non Moving Right: $t = 4.270$, $p < .001$) were significantly more activated by both Moving conditions compared to the corresponding Non Moving conditions. Thus, right primary motor cortex (right M1), left precuneus (left PreC) and left middle frontal gyrus (left MFG) were the cortical areas which showed significant modulations of somatosensory processing by the Moving conditions relative to the Non Moving conditions (see Figure 7.4). Table 7.3 shows the results of the contrasts performed in the cortical

areas obtained from the multi-subject random effect analysis contrasting the Moving condition with the Non Moving condition.



Left Precuneus (111) Left MFG (173) Right M1 (150)

Figure 7.4: Sagittal and axial views of cortical areas showing significant modulations of somatosensory processing by the Moving conditions relative to the Non Moving conditions ($p < 0.05$, $t = 2.4$, uncorrected for multiple comparisons). They are indicated by a white cross and highlighted in yellow. The number in brackets shows the number of voxels in the activated area. (Left, left hemisphere; Right, right hemisphere; MFG, middle frontal gyrus; M1, primary motor cortex)

Right Hemisphere							
Contrast	MFG (32_26_39)	CCZ (4_-18_41)	M1 (16_-23_59)	SOG (27_-74_23)	PHG-1 (25_-29_-9)	PHG-2 (28_-38_-12)	
Moving Left >	t = 2.338	t = 2.235	t = 5.600	t = 2.622	t = 1.135	t = 1.915	
Non Moving Left	p = .039	p = .047	p < .001	p = .024	p = .280	p = .082	
Moving Right >	t = 2.688	t = 4.270	t = 2.842	t = -1.516	t = 4.981	t = 3.645	
Non Moving Right	p = .021	p = .001	p = .016	p = .158	p = .001	p = .004	

Left Hemisphere							
Contrast	MFG-1 (-21_2_54)	Precuneus (-18_-45_37)	PCG (-16_-55_17)	CCZ (-3_-16_46)	STG (-50_-6_-4)	MFG-2 (-42_5_38)	MTG (-51_-58_0)
Moving Left >	t = 3.375	t = 2.958	t = 4.055	t = 1.299	t = 1.503	t = -3.339	t = -3.584
Non Moving Left	p = .006	p = .013	p = .002	p = .221	p = .161	p = .007	p = .004
Moving Right >	t = 2.962	t = 3.232	t = 2.547	t = 3.829	t = 10.549	t = -1.927	t = -1.859
Non Moving Right	p = .013	p = .008	p = .027	p = .003	p < .001	p = .080	p = .090

Table 7.3: Results of the contrasts conducted in the cortical areas identified from multi-subject GLM analysis contrasting the Moving condition with the Non Moving condition ($p < 0.05$, $t = 2.4$, uncorrected for multiple comparisons). Talairach coordinates (x_y_z) of the cortical areas are shown in brackets. As two comparisons were carried out for each activated area, the significance level was set at 0.025 (0.05/2, Bonferroni adjustment). t-value and p-value for the contrasts are shown. Values in bold indicate statistical significance for the contrast. (MFG, middle frontal gyrus; CCZ, caudal cingulate zone; M1, primary motor cortex; SOG, superior occipital gyrus; PHG, parahippocampal gyrus; PCG, posterior cingulate gyrus; STG, superior temporal gyrus; MTG, middle temporal gyrus)

7.4. Discussion

The behavioural study in the previous chapter showed that the tactile attention induced by the cued index finger facilitated processing of tactile stimuli presented to the middle finger of the same hand compared to the middle finger of the opposite hand. The present study was carried out to investigate modulations of cortical processing of somatosensory stimuli adopting Motor/Tactile tasks used in the previous study.

7.4.1. Modulation of somatosensory processing within the somatosensory areas:

Random effects analysis (RFX) conducted for the Tap Alone condition identified six bilateral somatosensory ROIs (SII, SI-1, SI-2, IPL (located close to postcentral

sulcus), PM and insula, $p < 0.05$, $t = 2.3$, uncorrected for multiple comparisons). SI-2 is located superior to SI-1. Four contrasts (significance level $\alpha = 0.0125$ ($0.05/4$)) within the ROIs showed that in the right hemisphere SI-1 and IPL were significantly more activated by contralateral stimulation (the Left condition) than ipsilateral stimulation (the Right condition), while in the left hemisphere SII, SI-2, IPL, insula were significantly more activated by contralateral stimulation (the Right condition) than ipsilateral stimulation (the Left condition). Only IPL in the left hemisphere was significantly more activated by stimulation on the contralateral finger of the moving hand (the Moving Right condition) than stimulation on the contralateral finger of the non-moving hand (the Non Moving Right condition).

The somatosensory ROIs identified in the present study mainly showed a bias towards contralateral tactile stimulation in comparison with ipsilateral tactile stimulation. A few studies showed attentional modulations of tactile processing in both SII and SI (Burton et al., 1999; Hämäläinen et al., 2002). However, SII and SI in the present study did not show modulations of somatosensory processing by tactile attention shifted by manual movements. It is possible that there was high variation in functional anatomy among individual brains (Johansen-Berg et al., 2000). They found that only SII showed attentional modulation of tactile processing after a random effects group analysis. However, with a subject regions of interest analysis attention-related modulation was also illustrated in SI. Another possibility is that task difficulty can influence attentional modulation in SII and SI. It was reported that with a low task difficulty, that is, with a low demand of attention there was no attentional modulation in both SII and SI (Galazky et al., 2009). The reason why there was no attentional modulation in SII and SI may be that they are sensitive to any type of

tactile stimulation. They can be readily activated by a paradigm which is not related to attention tasks (Francis et al., 2000). A study showed that pain and vibration conditions induced similar regional cerebral blood flow (rCBF) changes in several cortical areas including SII and SI (Coghill et al., 1994). However, comparison between two conditions illustrated no difference in rCBF in SII and SI.

Attentional modulation was found only in IPL of the left hemisphere. The difference between the Moving right condition and the Non Moving right condition in the left hemisphere qualifies the bias towards contralateral tactile stimulation in the somatosensory area. As this somatosensory area is a part of the supramarginal gyrus which is known to be involved in motor attention (Rushworth, Krams et al., 2001; Rushworth, Ellison et al., 2001; Rushworth et al., 1997; Rushworth, Paus et al., 2001), attentional modulation in this region may indicate a link between tactile attention and motor attention. Effects of repetitive transcranial magnetic stimulation (rTMS) on orienting and motor attention tasks were investigated (Rushworth, Ellison et al., 2001). In the visuospatial orienting task, the disruptive effects of rTMS were noticeable when the right angular gyrus was interfered on invalid trials in which the target appeared in the opposite side of the pre-cue. In the motor attention task, the disruptive effects were found when rTMS was applied to the left supramarginal gyrus on invalid trials. Thus, modality-specific lateralised attentional processes were observed. While the right angular gyrus is crucial for covert orienting attention, the left supramarginal gyrus is crucial for covert motor attention. The disruptive effects on invalid trials suggest that these regions are essential for disengaging and redirecting attention to a new centre of attention. With reference to tactile attention, the attentional modulation of somatosensory processing in left IPL in the present

study may be related to facilitation of redirecting motor attention from one movement to another. As attentional modulation in the left IPL in the present study was showed by contralateral tactile stimulation, it only shows a possible link between tactile attention and motor attention. However, further analysis in the cortical area substantiates the link between them.

7.4.2. Modulation of somatosensory processing in the cortical areas:

Random effects analysis (Moving vs Non Moving) performed to find out cortical areas showing attentional modulations of somatosensory processing by manual movements and further two contrasts (Moving Left vs Non Moving Left and Moving Right vs Non Moving Right, significance level $\alpha = 0.025$ ($0.05/2$)) were performed within each significantly activated area to ensure that the overall significant effect was not dominantly influenced by one contrast. The results demonstrated that left precuneus (left PreC) and left middle frontal gyrus (left MFG) and right primary motor cortex (right M1) were significantly more activated by both Moving conditions compared to the corresponding Non Moving conditions.

Tactile attention shifted by manual movements modulated tactile processing in right primary motor cortex (M1), left precuneus (PreC) and left middle frontal gyrus (MFG). Attentional modulation of somatosensory processing in M1 might have a different functional role of tactile attention in comparison with attentional modulation in left PreC and left MFG. Movement preparation and anticipatory activity of M1 prior to intended movements were demonstrated (Riehle & Requin,

1989; Schluter et al., 1998; Tanji & Evarts, 1976). TMS was delivered during movement preparation period between the movement instruction signal and the movement execution signal (Schluter et al., 1998). TMS delivered over both premotor and motor cortices induced slow reaction time of subsequent movements, that is, the disruption of movement preparation in those regions. M1 is not just involved in motor preparation or execution, but it also showed modulation by attention (Binkofski et al., 2002). Functional magnetic resonance imaging in healthy volunteers showed that a posterior part of M1 was modulated by different levels of attention to finger movements. Thus, tactile attention shifted by manual movements might have an effect during movement preparation. Attentional modulation of tactile processing could have two facilitatory effects. One effect is a faster detection of tactile stimuli presented to an effector that is planned to move (Juravle & Deubel, 2009). The other is a faster movement initiation of an effector that is prepared to move (Eimer et al., 2005; Juravle & Deubel, 2009; Juravle et al., 2010). In a task where tactile stimuli were response-irrelevant, manual response times to visual 'Go' signal were faster when tactile stimuli were delivered to the cued hand compared to when they were delivered to the uncued hand (Eimer et al., 2005). The reaction times were slowest on trials in which no tactile stimuli were delivered. This alerting facilitation effect was suggested in a study of attentional modulation of tactile events (Galazky et al., 2009). Participants were asked to count tactile stimuli delivered to the index and fifth finger of an attended hand (the attended condition) and to ignore stimuli delivered to the index and fifth finger of the other hand (the unattended condition). Attentional modulation was found in the primary motor cortex and the supplementary motor area (SMA) in the bilateral hemisphere. Bilateral activations of M1 were found even when attention was drawn only to either right or left fingers.

Galazky et al. (2009) suggested that modulation in regions related to the motor preparation and execution may indicate the involvement of tactile attention in preparation and facilitation for motor action. Bilateral attentional modulations in the motor related areas without any motor responses in the task might also suggest a general role of tactile attention in facilitation of motor action. Lateralised attentional modulation of tactile processing of the right M1 in the present study might indicate its role in facilitating attended action (Diederich et al., 2003). Further experiments are needed to investigate the role of the right M1 in attended action.

As mentioned earlier, attentional modulation of tactile processing in the left PreC and the left MFG can support a link between tactile attention shifted by manual movements and redirecting of motor attention from one movement to another. Parts of the parietal cortex equivalent to the left PreC in the present study were identified in a study adopting attention switching paradigms (Rushworth, Paus et al., 2001). Two attention-switching paradigms were used to investigate activity in the human parietal cortex. In the visual switching paradigm (VS), participants were asked to attend to one of two stimuli according to a rule indicating either colour or shape. One of the two stimuli was always red and the other was green. One of the two stimuli was always a triangle and the other was a square. Every 9 – 11 trials, a white cue shape (+ or x) instructed participants to stay with a current rule or to switch to the other rule. The participant's task was to detect a rare target (V) embedded in the shape and respond with a key press. In the response switching paradigm (RS), participants were presented with a series of stimuli, either a triangle or a square. Participants switched between two response rules, either triangle-left-hand and square-right-hand or triangle-right-hand and square-left-hand. Every 9 – 11 trials, a

white cue shape (+ or x) instructed participants to stay with a current rule or to switch to the other rule. The results showed that while VS activations (switch – stay) were recorded in the posterior lateral intraparietal sulcus and the parieto-occipital region, RS activations (switch – stay) were recorded in the medial intraparietal sulcus (MIP), adjacent dorsomedial surface (PEp) in the posterior superior parietal lobule (SPL), the supramarginal gyrus and the adjacent anterior lateral intraparietal sulcus (AIP). Rushworth et al. (2001) suggested that complementary activations of LIP and AIP in VS and RS tasks show their roles in visual attention and visuomotor intention respectively. They also proposed that activations in MIP and PEp in RS tasks are related to an intentional switch from one visuomotor transformation to another, which is distinct from the role for the supramarginal gyrus and AIP in redirecting motor attention from one movement to another. However, with reference to tactile attention shifted by manual movements, attentional modulation of tactile processing in the left PreC can be merely related to facilitation of redirecting motor attention from one movement to a new, most recent one in the process of a visuomotor transformation as tactile attention can not be involved in the cognitive process of switching a visuomotor transformation rule.

Involvement of the left parietal cortex in motor attention was illustrated in a study with a patient who lived without the left parietal lobe as a consequence of a perinatal insult (Castiello & Paine, 2002). The patient was able to perform both detection and pointing tasks as fast as the control participant after valid precues. The costs after invalid cues in the detection task were also similar between the patient and the control participant. However, the patient showed a greater cost after invalid precues in the pointing task. Castiello and Paine (2002) suggested that the patient had

difficulty in disengaging attention from a precued position and initiating and executing action to a new position. As this study involved using one dominant hand, the functional role played by the left parietal lobe may be more relevant to disengaging and engaging motor attention from one movement to another rather than disengaging and engaging attention for action from one location to another. Attentional modulation of tactile processing in the left parietal lobe in the present study shows that shifts of tactile attention by manual movements can be related to minimising costs associated with disengaging and redirecting motor attention from an invalid movement to a new valid movement.

In addition to the lateralised role of the left parietal cortex in motor attention, a lateralised role of the left prefrontal cortex in motor attention can substantiate a link between tactile attention shifted by manual movements and its facilitatory effect on motor attention as the present study found attentional modulation of somatosensory processing in the left MFG. Rounis et al. (2007) found that repetitive transcranial magnetic stimulation (rTMS) applied over either side of the dorsolateral prefrontal cortex (DLPFC) did not have a significant effect on the costs between the validly and invalidly cued trials in a visual attention task. However, rTMS over the left DLPFC induced an increase in the reaction times of invalidly cued trials in a motor attention task. Thus, attention related modulation of tactile processing in the left MFG in the present study suggests a facilitatory effect of tactile attention on redirecting motor attention from one movement to another. It is not clear at what stage the facilitatory effect of tactile attention might operate. Tactile attention can be operating either in disengaging invalidly cued motor responses or in engaging new motor responses. If the increased reaction times of invalidly cued trials in the motor attention task were

induced due to failure in activating a new motor response (Rounis et al., 2007) since the left frontal lesions led to a global deficit in activating a currently relevant task set (Mayr et al., 2006), attentional modulation of somatosensory processing could have a facilitatory effect on engaging motor attention with a new, most recent motor response.

The present study only showed facilitatory modulation of tactile processing in the cortical areas when tactile stimuli were delivered to the fingers of tactile attention shifted by manual movements. It has been reported that tactile sensitivity were suppressed during the movement execution period (Juravle et al., 2010) while attentional facilitation of somatosensory processing of tactile stimuli was found when they were presented during the movement preparation period (Eimer et al., 2005; Juravle & Deubel, 2009). As the present study involved responding to a visual cue by pressing a small response button with an index finger, the number of tactile stimuli delivered during the movement execution period had been minimised. As tactile stimuli were delivered to the middle fingers rather than the index finger, sensory suppression that otherwise would have been present in the index finger during the movement execution period had also been minimised in the present study. Thus, the present study showed attentional facilitation of somatosensory processing of tactile stimuli delivered to the fingers of tactile attention shifted by manual movements.

The present study investigated modulation of somatosensory processing in the cortical areas by tactile attention shifted by manual movements. Attentional modulation of somatosensory processing found in the right M1 implies the involvement of tactile attention in facilitating attended action. Attentional

modulation in the somatosensory (left IPL) and the cortical (left PreC and left MFG) areas can support a link between tactile attention and motor attention. Tactile attention shifted by movements may have a facilitatory effect on redirecting motor attention from one movement to another. Further investigations are needed to be carried out to disentangle sensory suppression and facilitation effects by manual movements on cortical processing of somatosensory stimuli. It would also be interesting to investigate into the involvement of the right M1 in attended action and effects of tactile attention on redirecting motor attention in apraxic patients who show deficit in tasks requiring sequences of movements (Rushworth et al., 2003).

Chapter 8: Summary and general discussion

8.1. Modulations of visual perception by eye movements

The first four experiments of the thesis were carried out to investigate effects of eye movements on modulations of visual perception and to find out theoretical relevance of the modulations to previous findings and suggestions of studies of peri-saccadic localisation. They focused on how perceptual stability is maintained across saccades.

Stable perception of visual space is a natural phenomenon which human beings experience just as they breathe in and out. It was suggested that retinal displacements by eye movements are compensated by efference copy of a motor command (von Holst, 1954) or a corollary discharge (Sperry, 1950) and the stable perception of the surroundings is maintained by this compensation. However, Martin & Pearce (1965) found that retinal displacements of visual stimuli were not compensated. When visual stimuli presented around saccades were mislocalised in the direction of saccades (Dassonville et al., 1992; Honda, 1997; Schlag & Schlag-Rey, 1995), they suggested that the mislocalisation reflects a difference between inaccurate hypothetical eye position signal (EPS) and the actual eye position. The EPS theory of the peri-saccadic mislocalisation could not explain a peri-saccadic mislocalisation when participants made mislocalisation errors towards a saccadic target (Ross et al., 1997). Ross et al. (1997) argued that visual space appeared to be compressed towards a saccadic target before, during and after eye movements. Lappe et al. (2000) found that visual information after saccades is a significant factor for the perception of spatial compression towards a saccadic goal, but compression of visual space was

also shown without post-saccadic visual references (Awater & Lappe, 2006; Morrone et al., 2005).

Experiment 1 adopted a pointing paradigm (Burr et al., 2001) to study peri-saccadic localisation of visual stimuli. The results showed that when the probing bars were briefly presented at the interval of -50 to 0 ms, they were mislocalised towards the saccadic target. This pattern of mislocalisation is consistent with previous studies of peri-saccadic localisation which showed compression of visual space before, during and after saccades (Burr et al., 2001; Jackson et al., 2005; Kaiser & Lappe, 2004; Morrone et al., 1997; Ross et al., 1997). However, when the probing bars were presented at the interval of -100 to -50 ms, the pattern of mislocalisation was towards the initial fixation. Sheth & Shimojo (2001) found a near-identical pattern of mislocalisation errors in studies of visual memory, in which flashed visual stimuli were mislocalised towards the centre of gaze. Thus, the results of Experiment 1 could suggest that there was a shift of centre of gaze before the onset of eye movements. That is, the centre of gaze was the initial fixation at the interval of -100 to -50 ms and the centre of gaze was shifted to the saccadic target at the interval of -50 to 0 ms.

A study of a temporal illusion termed as saccadic chronostasis suggested a mechanism of a post-saccadic remapping of pre-saccadic visual space (Yarrow et al., 2001). They argued that backward extension of perception of a saccadic goal to a moment around 50 ms before the onset of saccades may be related to filling a perceptual gap during saccadic suppression to maintain perceptual continuity. However, when positional stability of a saccadic target was broken by a saccadic target displacement during saccades, saccadic chronostasis disappeared whether

participants perceived the displacement or not. Thus, Experiment 2 adopted a target displacement paradigm, in which a saccadic target was displaced during saccades. It was hypothesised that if the target displacement paradigm disrupted bridging a perceptual gap during saccadic suppression, it would increase uncertainty of visual stimuli and consequently, the magnitude of mislocalisation errors for visual stimuli presented during the interval of -50 to 0 ms would rise since less visible stimuli induced larger mislocalisation errors (Georg et al., 2008; Michels & Lappe, 2004). The results of Experiment 2 showed that the magnitude of mislocalisation errors did not change when the saccadic target was displaced during saccades. Hence, Experiment 2 provides no evidence that the temporal illusion of saccadic chronostasis is related to perceived compression of visual space. However, the results of Experiment 2 suggested that when the saccadic target was displaced during saccades, pre-saccadic visual information was updated relative to the initial location of the saccadic target. As a consequent, Experiment 3 and 4 were carried out to investigate how pre-saccadic visual information is maintained across saccades.

Visual information coded before the onset of saccades was updated after the end of saccades (Duhamel et al., 1992). The memory trace of stimuli flashed long or immediately before saccade was remapped after saccades. Gottlieb (2007) suggested that post-saccadic remapping of pre-saccadic visual space plays a part in linking information about a stable object across saccades. Thus, Experiment 3 and 4 was carried out to find out what reference point might be used to update pre-saccadic visual information after saccades. A target blanking paradigm was adopted as Deubel et al. (1996) proposed that the absence of a saccadic target immediately after saccades destabilises the visual system and the system has to employ other available

information such as efference copy or remembered target location. They showed that a precise extraretinal signal about the location of a saccadic target and its displacement are available when a saccadic target is not available after saccades.

The target blanking paradigm can also be useful to check if saccadic landing sites are used for updating pre-saccadic visual space since corrective saccade is not made until a saccadic target appears again if it is blanked (Deubel et al., 1982). The results of Experiment 3 and 4 suggested that saccadic landing sites, the location of remembered saccadic targets, and the blanked target location are not used for post-saccadic updating of pre-saccadic visual space, but the location of the saccadic target remapped using accurate efference copy.

The first four studies of modulations of visual perception by eye movements can provide suggestions for issues related to studies of peri-saccadic localisation and remapping of visual space.

8.1.1. Why are visual stimuli flashed before saccades mislocalised towards a saccadic target?

The four experiments of visual perception showed exactly the same pattern of peri-saccadic mislocalisation errors for visual stimuli presented within 100 ms before the onset of saccades. In particular, when the probing bars were briefly presented at the interval of -50 to 0 ms, they were mislocalised towards the saccadic target. This pattern of mislocalisation errors was shown by previous studies (Burr et al., 2001; Jackson et al., 2005; Kaiser & Lappe, 2004; Morrone et al., 1997; Ross et al., 1997), but the explanation for the mislocalisation was based on the perceived pattern of the mislocalisation. Consequently, Ross et al. (1997) claimed that visual space is

perceived to be compressed before, during and after saccades. Lappe et al. (2000) proposed that visual space appears to be compressed towards a saccadic goal is because pre-saccadic visual stimuli are integrated into the post-saccadic coordinate system formed by visual information available after saccades. However, the perception of compressed visual space was illustrated without post-saccadic visual references (Awater & Lappe, 2006; Morrone et al., 2005). Experiment 2, 3 and 4 in the present study also provide evidence that changes in a post-saccadic target does not affect integration of pre-saccadic visual space into the post-saccadic coordinate system as they showed that the magnitude of mislocalisation errors was not influenced by changes in the saccadic target.

Differently from previous studies of peri-saccadic localisation, the present study found a different pattern of mislocalisation errors which might provide possible explanation for peri-saccadic mislocalisation errors towards a saccadic target. When the probing bars were presented at the interval of -100 to -50 ms, the pattern of mislocalisation was towards the initial fixation. In a study of visual memory, a near-identical pattern of mislocalisation errors was observed (Sheth & Shimojo, 2001). Observers showed a tendency to mislocalise a briefly presented visual stimulus closer towards the centre of gaze. When observers made an eye movement to another fixation point and remained fixated while responding, the pre-saccadic visual stimulus presented at least 500 ms before the onset of saccades was still mislocalised towards the initial fixation point. Thus, the two patterns of mislocalisation errors could indicate two separate representations of the coordinate system before the onset of eye movements. Visual stimuli presented at the interval of -100 to -50 ms are represented in the coordinate system with the initial fixation point as a centre and the

stimuli presented at the interval of -50 to 0 ms are represented in the coordinate system with the saccadic goal as a centre. Thus, present study provides empirical evidence of an effortless transition of the coordinate system from one fixation to another (Burr et al., 2001; Ross et al., 2001). As this shift of the coordinate system occurs before the onset of eye movements, it is indicative of predictive remapping of visual space.

Although studies of peri-saccadic localisation did not link mislocalisation errors to distortion of visual memory, there is growing evidence that studies of visual memory are closely related to studies of spatial compression towards a saccadic goal.

Characteristics of their mislocalisation errors are very similar. For example, the four studies showed that the magnitude of mislocalisation errors in the location to the left of the initial fixation was larger compared to that in the location between the initial fixation and the saccadic target. Likewise, peripherally presented flashed stimuli were mislocalised towards a fixation cross and the magnitude of foveal mislocalisation was enlarged as a function of eccentricity of presentation (Musseler et al., 1999; Osaka, 1977; Sheth & Shimojo, 2001; van der Heijden et al., 1999).

Stimulus contrasts affect perception and visual memory. Low-contrast random visual stimuli were more difficult to process than high contrast stimuli (Harley et al., 2004).

Less obvious stimuli can cause larger mislocalisation errors. Thus, stimulus contrast can have a strong effect on compression of visual space as low contrast probes induced greater compression than high contrast probes (Michels & Lappe, 2004).

Similarly, when stimuli with near-threshold or above-threshold luminance were presented in the dark-adapted or light-adapted conditions, near-threshold stimuli with low visibility showed larger mislocalisation errors than more conspicuous above-

threshold stimuli (Georg et al., 2008). In a dark room, visual stimuli presented in the retinal periphery were mislocalised towards a fixation point (Osaka, 1977; Sheth & Shimojo, 2001). Morrone et al. (2005) also demonstrated that post-saccadic visual references are not essential to induce perceived compression of visual space towards a saccadic target.

In conclusion, peri-saccadic mislocalisation errors towards a saccadic target provides evidence for predictive shifts of the coordinate system before saccades and the mislocalisation errors does not indicate actual compression of visual space, but a distortion of visual memory of flashed stimuli.

8.1.2. Is mislocalisation errors towards a saccadic target evidence of predictive remapping or post hoc reconstruction of visual space?

Yarrow et al. (2001) claimed that backward extension of perception of a saccadic goal to a moment around 50 ms before the onset of saccade may be related to filling a perceptual gap during saccadic suppression to maintain perceptual continuity. As the time course of saccadic suppression and perception of spatial compression is similar to saccadic chronostasis, they contended that three phenomena are closely related. This suggestion is contrary to a predictive shift of the coordinate system as saccadic chronostasis implies a mechanism of a post-saccadic reconstruction of pre-saccadic visual space.

One interesting characteristic of saccadic chronostasis is that the temporal illusion disappears when positional stability of a saccadic target was broken by a saccadic target displacement during saccades (Yarrow et al., 2001). As a result, Experiment 2

was carried out adopting a target displacement paradigm. It was expected that if the target displacement paradigm disrupted bridging a perceptual gap during saccadic suppression, it would increase uncertainty of visual stimuli. Consequently, the magnitude of mislocalisation errors for visual stimuli presented during the interval of -50 to 0 ms would rise. However, the results did not support the relevance of saccadic chronostasis to peri-saccadic mislocalisation towards a saccadic target as the magnitude of mislocalisation errors did not change with the target displacement paradigm. The results of Experiment 3 and 4 also did not show any change in the magnitude of mislocalisation errors even when a saccadic target was blanked for 200 ms after the offset of saccades.

Saccadic chronostasis does not seem to serve as a mechanism that reconstructs visual stimuli presented during saccadic suppression. Georg and Lappe (2007) illustrated that the typical chronostasis phenomenon occurred at the location of the saccadic target, but not at the location halfway between the initial fixation point and the saccadic target. In other words, saccadic chronostasis does not take place in the entire visual field. However, mislocalisation errors towards a saccadic target occurred in the entire visual field in the present study as well as previous studies of peri-saccadic localisation (Burr et al., 2001; Jackson et al., 2005; Lappe et al., 2000; Ross et al., 1997).

Hunt and Cavanagh (2009) found that observers experience fixating a saccadic target before their eyes have actually landed on it. This observer experience could be explained the predictive shift of the coordinate system in the present study shown by mislocalisation errors of visual stimuli towards a saccadic target when they were

presented at the interval of -50 to 0 ms before the onset of saccades. Previous electrophysiological studies ascertained anticipatory shifts of receptive fields of neurons (Duhamel et al., 1992; Umeno & Goldberg, 2001). Melcher (2007) found that tilt adaptation was transferred from the initial fixation position to the future fixation position before saccades. A predictive interhemispheric remapping before saccades was also demonstrated using event-related potentials (Parks & Corballis, 2008).

Thus, mislocalisation errors towards a saccadic target just before saccades provide evidence of predictive remapping of visual space.

8.1.3. What reference point is used to integrate pre-saccadic visual information into the post-saccadic coordinate system?

Electrophysiological studies support accurate remapping of pre-saccadic visual stimuli after saccades (Duhamel et al., 1992; Umeno & Goldberg, 2001). Almost all parietal neurons (96%) responded when the location of a transient pre-saccadic stimulus was brought into the receptive field by saccades. The memory trace of brief stimuli (less than 50 ms) or stimuli presented long or just before saccades was remapped after saccades (Duhamel et al., 1992). 58 % of the visuomovement cells in the frontal eye field also discharged for a vanished stimulus after saccades (Umeno & Goldberg, 2001). Gottlieb (2007) argued that the remapping of pre-saccadic visual space after saccades plays a role in linking information about a stable object across saccades.

In the first four studies of peri-saccadic localisation, the participants localised the probing bars presented before saccades while fixating on the saccadic target after saccades. It appears that the visual system possesses an accurate memory of which coordinate system the pre-saccadic visual stimuli belong to. The results of Experiment 1 showed that after saccades visual stimuli presented at the interval of -100 to -50 are anchored to the pre-saccadic coordinate system with the initial fixation as a centre and visual stimuli presented at the interval of -50 to 0 are anchored to the post-saccadic coordinate system with the saccadic target as a centre. It can be assumed that the visual stimuli presented at the interval of -50 to 0 are remapped relative to the centre of gaze after saccades. However, the results of Experiment 2 showed that the displaced target was not used as a reference point for post-saccadic remapping of pre-saccadic visual stimuli as the magnitude of mislocalisation errors did not change when the participants fixated on displaced targets.

According to the reference object theory, it is not clear what information was used as a reference point when pre-saccadic visual stimuli was remapped in the post-saccade visual space in Experiment 2 since the theory predicts that spatial information about pre- and post-saccadic locations of a saccadic target is neither available nor compared if the saccadic target is available after saccades (Deubel et al., 1998). Thus, Experiment 3 and 4 was carried out adopting a target blanking paradigm to test whether saccadic landing sites, the location of remembered saccadic targets, the blanked target location or the location of the saccadic target remapped using accurate efference copy are used for post-saccadic updating of pre-saccadic visual space. It was expected that if saccadic landing sites, the location of remembered saccadic targets or the location of blanked target location was used as a reference point for

post-saccadic remapping of pre-saccadic visual stimuli, there would be changes in the magnitude of mislocalisation errors for visual stimuli presented at the interval of -50 to 0. However, the results of Experiment 3 and 4 showed there was not any change in the magnitude of mislocalisation errors. Thus, the results of Experiment 3 and 4 suggests that the location of the saccadic target remapped using accurate efference copy is used for a reference point for the post-saccadic remapping of pre-saccadic visual stimuli.

When a saccadic target is not present immediately after the eyes lands and appears in a different location other than the location of the pre-saccadic target, information about the location of the post-saccadic target relative to the pre-saccadic target is available as the location of the pre-saccadic target is remapped using precise efference copy (Deubel et al., 1996). Efference copy seems to carry about information about an oculomotor error of each saccade (Collins et al., 2009) and a magnitude of saccadic adaptation (Awater et al., 2005; Bahcall & Kowler, 1999; Collins et al., 2009). For example, the focus of spatial compression can be shifted from the saccadic target, which elicits saccades, to the new location of the target induced by saccadic adaptation (Awater et al., 2005). Collins et al. (2009) suggested that an efference copy vector contains an oculomotor error of each saccade and this efference copy vector is used to remap the location of a pre-saccadic target after saccades. As the oculomotor error varies in each eye movement, the remapped target location is often not foveal. However, it is consistent and accurate. Thus, it can be suggested that in Experiment 2, 3 and 4, the pre-saccadic stimuli predictively remapped before saccades are anchored to the location of the pre-saccadic target

remapped using accurate efference copy including the oculomotor error of each saccade.

In conclusion, when pre-saccadic visual information is integrated into the post-saccadic coordinate system, visual stimuli, which are presented before saccadic suppression, are updated relative to the initial fixation and visual stimuli presented during saccadic suppression are updated relative to the location of a pre-saccadic target remapped using accurate efference copy.

8.2. Modulations of somatosensory perception by finger movements

Experiment 5 and 6 were carried out to investigate effects of finger movements on perception of externally-administered tactile stimuli. They focused on how and why motor intention affects perception of sensory events.

According to pre-motor theory, different motor tasks can activate different cortical circuit for spatial attention (Rizzolatti et al., 1994). The theory proposed that preparation to reach a target improves capacity to process sensory information presented the location of the target. It was demonstrated that discrimination performance of mirror image symbols is better when a discrimination symbol is a target for reaching movements than when a discrimination symbol and a pointing target are different (Deubel & Schneider, 1998) and action preparation can improve processing of tactile stimuli (Juravle & Deubel, 2009). However, studies illustrated that externally delivered sensory stimuli were attenuated. Cutaneous sensory

thresholds were elevated during movements (Angel & Malenka, 1982) and muscular sense was significantly attenuated by the fast movement condition compared to the slow movement, passive movement and static conditions (Collins et al., 1998).

Dependency of sensory attenuation on central signals generated during motor preparation was also demonstrated by applying transcranial magnetic stimulation to the primary motor cortex (Voss et al., 2006).

In Experiment 5, participants were cued to press the push button with their left or right index finger and a pneumatic tap was delivered to their left or right middle finger. In the Moving condition, the stimulated finger and the responded finger were on the same hand. In the Non Moving condition, the stimulated finger and the responded finger was not on the same hand. The results showed that participants' sensitivity to the temporal order of the finger movement and the tactile stimulation was not affected by the finger movement as the JNDs between the Moving and Non moving conditions were not significantly different. However, when the PSSs for both conditions were compared the tactile stimulation in the Non Moving condition had to lead the tactile stimulation in the Moving condition by 74.43 ms in order for synchrony to be perceived. In other words, tactile stimuli in the Moving condition were processed 74.43 ms faster than those in the Non Moving condition. The results of Experiment 5 provide evidence to support facilitation of tactile processing by attention shifts induced by manual movements (Juravle & Deubel, 2009; Rizzolatti et al., 1994). Juravle and Deubel (2009) suggested that action preparation can facilitate the processing of tactile stimuli.

In Experiment 6, an fMRI study was carried out to find modulations of somatosensory processing in both somatosensory areas such as SI and SII and cortical areas. Participants carried out Motor/Tactile tasks just as they did in Experiment 5. The results showed that there were no modulations of tactile processing in the somatosensory areas, especially in SII and SI, although previous studies found attentional modulations of tactile processing in both SII and SI (Burton et al., 1999; Hämäläinen et al., 2002).

Why were attentional modulations of tactile stimuli not found in SII and SI in Experiment 6? First, it is possible that there was high variation in functional anatomy among individual brains (Johansen-Berg et al., 2000). Only SII showed an attentional modulation of tactile processing after a random effects group analysis. However, with a subject regions of interest analysis, an attention-related modulation in SI was also illustrated. Second, task difficulty can influence attentional modulation in SII and SI (Galazky et al., 2009). With a low task difficulty, that is, with a low demand of attention there was no attentional modulation in both SII and SI. Third, SII and SI are sensitive to any type of tactile stimulation (Francis et al., 2000). They can be readily activated by a paradigm which is not related to attention tasks. Pain and vibration conditions induced similar regional cerebral blood flow (rCBF) changes in several cortical areas including SII and SI. However, comparison between two conditions illustrated no difference in rCBF in SII and SI (Coghill et al., 1994). Finally, timing of tactile stimuli delivered to effectors may be an important factor. Tactile sensitivity were suppressed during the movement execution period (Juravle et al., 2010). Attentional facilitation of somatosensory processing of tactile stimuli was found when they were presented during the movement preparation period (Eimer et

al., 2005; Juravle & Deubel, 2009). If the data in Experiment 6 were analysed with reference to these two separate periods, facilitation or attenuation of tactile processing could be found in SII and SI.

8.3. Efference copy, corollary discharge, pre-motor theory and internal model in modulations of visual and somatosensory perception by action

Efference copy and corollary discharge are implied in compensation of retinal displacements by eye movements for stable perception of the surroundings (Sperry, 1950; von Holst, 1954). However, Martin & Pearce (1965) found that retinal displacements of visual stimuli were not compensated. Visual stimuli presented around saccades were mislocalised in the direction of saccades (Dassonville et al., 1992; Honda, 1997; Schlag & Schlag-Rey, 1995) or towards a saccadic target (Ross et al., 1997). Efference copy and corollary discharge do not seem to play a part in cancelling out retinal displacement. However, the first part of the thesis suggests that efference copy and corollary discharge are used for predictive shifts of the coordinate system.

Experiment 1, 2, 3 and 4 in the thesis illustrated that visual stimuli presented at the interval of -100 to -50 ms are represented in the coordinate system with the initial fixation point as a centre and the stimuli presented at the interval of -50 to 0 ms are represented in the coordinate system with the saccadic goal as a centre. Thus, there is an effortless shift of the coordinate system from one fixation to another (Burr et al., 2001; Ross et al., 2001). As this shift of the coordinate system occurs before the

onset of eye movements, this indicates predictive remapping of visual space. Previous electrophysiological studies ascertained anticipatory shifts (corollary discharge) of receptive fields of neurons (Duhamel et al., 1992; Umeno & Goldberg, 2001). Receptive fields of the parietal neurons shifted about 80 ms before the onset of saccades to remap a stimulus in the post-saccadic location of the receptive field (Duhamel et al., 1992). Visual cells in the frontal eye field discharged for both a flashed stimulus and a continuously present stimulus before saccades (Umeno & Goldberg, 2001).

The results of Experiment 2 illustrated that the displaced target was not used as a reference point for post-saccadic remapping of pre-saccadic visual stimuli and the results of Experiment 3 and 4 proposed that saccadic landing sites, the location of remembered saccadic targets, the blanked target location were not used for post-saccadic updating of pre-saccadic visual stimuli presented during saccadic suppression. Consequently, Experiment 2, 3 and 4 concluded that the location of the saccadic target remapped using accurate efference copy is used for a reference point for the post-saccadic remapping of pre-saccadic visual stimuli. In other words, efference copy is used to remap a reference point to localise a pre-saccadic target across saccades.

According to an internal model, sensory prediction is utilised to cancel the sensory consequences of movements (Wolpert & Flanagan, 2001). Sensory consequences of self-generated movements can be attenuated by efference copy of a motor command according to forward models (Blakemore et al., 1999; Shergill et al., 2003).

Externally-generated tactile stimuli are also attenuated prior to, during and after movements (Collins et al., 1998; Shimazu et al., 1999; Starr & Cohen, 1985; Voss et al., 2006). On the contrary, the pre-motor theory suggested that the preparation to reach a target should improve capacity to process sensory information presented the location of the target in the same way as the preparation to make an eye movement does (Rizzolatti et al., 1994). Accordingly, studies shows enhanced tactile processing during action preparation (Deubel & Schneider, 1998; Eimer et al., 2005; Juravle & Deubel, 2009).

The results of Experiment 5 support the pre-motor theory as the processing of tactile stimuli was facilitated by attention shifts induced by manual movements. However, in Experiment 6 there were no modulations of tactile processing in the somatosensory areas. The results of Experiment 6 might suggest that both the pre-motor theory and an internal model are involved in processing of externally-administered tactile stimuli. Recent studies found that time of the presentation of tactile stimuli is an important factor for the processing of externally-generated tactile stimuli (Juravle & Deubel, 2009; Juravle et al., 2010). Tactile sensitivity were suppressed during the movement execution period (Juravle et al., 2010). Attentional facilitation of somatosensory processing of tactile stimuli was found when they were presented during the movement preparation period (Eimer et al., 2005; Juravle & Deubel, 2009). In Experiment 5, the PSS in the Moving condition was not significant and this might also indicate the difference in tactile processing during these two periods since data from the two periods were analysed together in the analysis. Further investigations should be carried out to clarify different processing of tactile stimuli during the movement execution and preparation periods.

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