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MECHANISMS INVOLVED IN AGENCY ATTRIBUTION AND THEIR CONTRIBUTIONS TO NORMAL AND ABNORMAL EXPERIENCE OF AGENCY

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

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Dedication

I would like to dedicate this thesis to all past, present and future members of Headway Leicestershire and Rutland.

Abstract

Agency attribution is the ability to distinguish between events that occur as a result of our own actions and events that occur as a result of the actions of other people. Previous accounts of agency attribution have been mainly divided into two camps, either explaining agency in terms of high-level conscious processes (Stephens and Graham, 2000) or low-level Comparator Model (CM) processes (Frith et al. 2000). Recently, however, theorists have begun to incorporate these two approaches, but as the bulk of previous experiments fail to specify which aspects of agency are investigated, little empirical evidence exists to inform us about how these different mechanisms interact.

The aim of the current thesis was to tease apart these processes by examining high-level self/other judgments and low-level motor responses to actual and perturbed visual feedback of self-generated actions. Results from Chapters 3, 4 and 5 suggest that low-level (CM) agency mechanisms are situated in right hemisphere regions, disruption of which can reduce high-level self-judgments (Chapter 5). Proprioception was also found to negatively inform high-level judgments, as reducing proprioceptive signals increased self-judgments and visual-proprioceptive incongruence increased other judgments (Chapters 6 and 7). In terms of low-level agency mechanisms, however, visual-proprioceptive congruence was found to enhance low-level correction of visual perturbations (Chapter 8). Results from Chapter 8 and Chapter 9 provide evidence for a lack of high-level conscious awareness of low-level motor responses, as participants failed to notice their own low-level corrections (Chapter 8) and as a result failed to recognise their own actions (Chapter 9). Therefore, the current body of research provides evidence for a visual-proprioceptive comparison as an integral component of low-level (CM) agency mechanisms, and that these CM processes do not produce feelings of agency per se, but identify mismatches that inform and are then interpreted by conscious awareness.

Publications

The results of Chapters 3 and 5 have been accepted for publication

Preston, C. & Newport, R. (in press). Was That Me? The Right Hemisphere and the Sense of Agency: Embodiment of Others and Misattribution of Self-Generated Action. In B. Hardy-Vallee, & N. Payette (Eds.), Beyond the Brain: Embodied, Situated and Distributed Cognition. Newcastle, U.K: Cambridge Scholars Publishing.

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Contents

SECTION 1: Agency Attribution and the Right Hemisphere

SECTION 2: Proprioceptive Contributions to Agency

7a: Evidence from a Patient with Somatosensory Impairment

7b: Evidence from Healthy Controls using Tendon Vibration

List of Figures

were presented in incremental steps (with an unperturbed trial embedded with in each step) than when all perturbations (including 0-degree perturbations) were presented randomly. Small to medium sized perturbations for both conditions produced a high percentage of self-judgments, whilst for the larger perturbations a greater number of self-judgments were produced for the incrementally presented perturbations compared to when randomly presented. Error bars represent standard error and asterisks denote significant differences (*= p<0.05, **=p<0.001).

Chapter 1
General Introduction

Agency is the sense that you yourself are the cause of an action or event. For example, knowing that you touched your own arm, rather than your arm being touched by someone else or knowing that the image of an object moving across your retina is the result of your own head or eye movement rather than the object itself moving. Agency attribution is the ability to identify the source of an event as either yourself or an external agent and is crucial to the survival of every biological being. Attribution of movement agency is also crucial for normal human social interaction, as before we can attribute intentions and desires to other people, we must first be able to determine whether a perceived action or event has been caused by ourselves or by another person.

1.1: Recognising the Self Through Action and the Experience of Agency

There is a great similarity between our own actions and those of other people, not only in terms of the movement's characteristics, but also in the way that the movements are processed in the brain. For example, research in monkeys has identified neurons in the brain that respond to both performed and observed actions (e.g. Rizzolatti, et al. 1996). Similar neurons have also been identified in humans. Georgieff and Jeannerod (1998) highlighted these common areas, which are frontal parietal networks, including the ventral premotor area, part of the supplementary motor area (SMA) and the inferior parietal lobe. They interpreted these overlapping areas of activation to reflect shared representations of actions. That is, action representations that are shared between several individuals. Such shared action representations allow for interpretation and prediction of other people’s actions and social phenomena such as empathy. However, before we can do this we need to be able to distinguish the movements that are made by ourselves from those produced by other people. The ability to correctly identify our own actions from those produced by others (agency attribution) is therefore a fundamental component of human social interaction and while ambiguity of this experience is rare, the process can become compromised in specific presentations of psychosis or following brain injury if mechanisms associated with self-awareness and agency attribution become disrupted.

Gallagher (2000) defined a sense of agency as the sense that I am causing an action. Such feelings are likely to depend strongly on the actor’s intentions. The way that humans process observed actions of other people has been found to change dependent on the observer’s intentions. Grézes et al. (1999) conducted a Positron emission tomography (PET) study in which the participants observed video clips of meaningless hand actions. In one group the participants were instructed to pay attention to the movements for a later recognition task, whilst others were told they would later be required to imitate the actions. Although there were many common networks activated between the two groups the intention to imitate group demonstrated bilateral increases in regional cerebral blood flow of the dorsal pathway including premotor and prefrontal areas when compared to the recognition group. All such activations, although bilateral, were more pronounced in the right hemisphere and in addition the inferior parietal lobe demonstrated greater activation only on the right side. Such a change in processing between the groups indicates that high-level intentions can have a direct effect on how the observed action is processed within the brain. Notably, this effect of intentions seems to have greatest impact on right hemisphere structures particularly the right inferior parietal lobe.

1.2: Agency Attribution and the Right Hemisphere

There is significant evidence in the literature implicating the right hemisphere, specifically frontal parietal networks (Decety and Chaminade, 2003), with self-awareness and other aspects of self-processing including self and self-body representations. For example, Fink et al. (1996) conducted a PET study in which participants were exposed to sentences that were either describing their own autobiographical experiences or those of another person. When the sentences were of their own experiences an increase in blood flow was found in right hemisphere structures compared to ‘at rest’ and exposure to descriptions of others experiences. These structures included the right prefrontal and posterior cingulate areas and the right insula. It was suggested that this activity could correspond to representations of the self embedded in such memories.

In a further demonstration of self-representations being situated in the right hemisphere, direct cortical stimulation of the right angular gyrus of a 43 year-old female epileptic patient was found to induce out-of-body experiences. In these experiences the patient felt as though she was floating above the bed and could see herself from outside of her body. At higher-level stimulations

she then reported feeling as though her limbs were shrinking and when her legs were bent at the knee she felt as though her legs were moving towards her face (Blanke et al., 2002). These illusions produced by the cortical stimulation were confined only to the patient's own body parts and as such implicates the right angular gyrus to be specifically involved in self-body representation. In addition to these examples, neurological deficits characterised by deficits in own-body perception are predominantly associated with damage to the right hemisphere (e.g. anosognosia, discussed below).

In terms of the feeling of agency the right hemisphere has been found to correspond with making self/other attributions of observed actions. For example, Farrer and Frith (2002) conducted an fMRI experiment in which the participants had to guide a cursor along a T-shaped path. When the cursor reached the junction of the path, at which one branch went to the left and the other to the right, the participants then guided the cursor down one of the branches as indicated by the spatial position of a cross (which had appeared at the beginning of the trial). However, the movements of the cursor were not always controlled by the participant. In these conditions the cursor was controlled by the computer and travelled down the opposite branch to that indicated by the cross.

It was found that when the cursor was controlled by the computer (other) there was increased activation in the right inferior parietal lobe and when the participant was in control, greater activity was observed in the anterior insula. In a similar follow up study using PET, Farrer et al. (2003a) were able to replicate these findings. In this study the other movements were produced by applying varying degrees of angular perturbation between

physically coincident actual and virtual feedback and the activity observed in the rIPL was found to increase with the increasing size of perturbation. A PET study by Spence et al. (1997) associated schizophrenic delusions of control (discussed below) with the rIPL. These patients lay in the scanner and performed random movements with a joystick. The movements made did not differ from movements made by controls and were performed as instructed (matched intentions) yet the patients reported feeling that they were under external control. Whilst this was happening, the PET results recorded hyperactivity in the right inferior parietal lobe. Additionally, Maruff et al. (2005) found reduced cortical volume in the rIPL of such patients. (Note that the insula and particularly the right inferior parietal lobe have been associated in many studies investigating different elements of self-processing).

However, high-level self-awareness (Morin, 2002) and agency experiences have been related to inner speech (Stephens and Graham, 2000), which is associated with left hemisphere regions (McGuire et al., 1996). In addition to this, other studies have implicated agency attribution with the left inferior parietal lobe, using patients with left parietal damage (Sirigu et al., 1999) and rTMS on neurologically intact participants (MacDonald and Paus 2003). However, because of left inferior parietal lobe's associations with movement production, its contribution to experiences of agency may be more associated with issuing the appropriate motor commands as opposed to feelings of agency per se. This highlights an inherent problem with agency attribution research as the experience of agency may be influenced by many mechanisms, which are likely to account for the conflicting results.

1.4: Current Perspectives in Agency Attribution

Current theories on agency attribution disagree about the extent to which the sense of agency is a result of bottom-up or top-down processes or a mixture of the two. Outlined below are two perspectives on agency attribution, one centred on high-level processes, and one on low-level processes.

The Narrative Approach to Agency

A high-level explanation of agency relies on the human narrative, an action occurs and feelings of agency are implied retrospectively, rationalised by the actor to fit in with their beliefs and prior knowledge about themselves. This approach has been advocated by Stephens and Graham (2000), who described the way in which we feel a sense of agency over our actions to be similar in principle to how we infer the attitudes and intentions of others. They stated that our perception of intentional movement is based on inferences from the knowledge about ourselves with important reference to inner speech. It was suggested that inferences of our intentions based on our inner dialogue are formed in much the same way as inferences based on the overt dialogue of other people. If the actions we perform fit in with our previous knowledge of ourselves then intention, and thus wilful causality and agency, is inferred.

The results of a study by Libet et al. (1983) support the narrative explanation of agency. Participants were required to make finger movements, the frequency and exact timing of which, were to be decided by the individual, with the instructions placing a specific emphasis on spontaneity. The perceived intention to act, measured by the exact position of a second hand on the clock (actual time corresponding to far less than a second) as reported by the

participant when they experienced the urge to move, was compared to the cerebral readiness to act, measured by EEG readiness-potentials from the cortex. It was found that the cortical readiness-potentials preceded the reported urge to move by a mean time of 350ms. This suggests by the time we feel the urge to move, the decision to move has already been made by the motor system.

The narrative definition of agency draws parallels to utilisation syndrome (see below) in which patients perform actions in direct response to visual cues and then appear to justify their behaviour based on retrospectively implied intentions (confabulation). However, Bayne and Pacherie, (2007) criticised this approach by highlighting that patients who have suffered sever amnesia, and so lack this prior knowledge of their beliefs, do not seem to have deficits of agency. Similarly, many examples of patients with disrupted experiences of agency (excluding schizophrenic patients), do not appear to have problems with internal narrative. For example, the apparent lucidity of the

anosognosia patients described by Ramachandran, (1995, 1996), who, despite having a good knowledge of their personal history, including other medical conditions, deny their left sided paralysis.

The Comparator Model

A different standpoint is based on low-level comparator mechanisms of motor control. The comparator model explanation of agency as described by Frith et al. (2000) (see Figure 1.1) consists of an inverse loop, which executes the action, and a forward model that predicts the consequences of that action (based on efference copy of the original motor commands).

Figure 1.1: Starting from the top left of the diagram and working down the left hand side: the intended goal of an action is necessary to specify the desired (next) state of

the limb and also the movement required to achieve that state. At this stage a motor command is generated to execute the necessary movements and a parallel efference copy is sent to the predictor in order to calculate the consequences of that particular motor command. In addition to this, and following on from the motor command, there is the (estimated) actual state of the motor system based on the outgoing motor commands and sensory feedback. This is an iterative loop and is constantly active both before and throughout the movement and as the movement unfolds there are a number of comparisons that can be made in order to monitor and update it. Comparisons (represented by crossed circles) can be made between the desired state and the predicted state, between the desired state and the actual state and between the actual state and the predicted state. Any discrepancies can be used to modify and correct the motor command on-line during the movement and so make it as accurate as possible. Thus, feelings of agency are apparent when the comparisons match, but if the discrepancies between any of the comparisons become too large then the CNS may treat any observed or internally monitored self movement as belonging to, or being under the influence of, an external agent. When the system dysfunctions, therefore, perhaps through brain abnormality or lesion, misperceptions of agency can occur.
Adapted from Frith et al. (2000)

In this account feelings of agency are derived from matching the actual movement with the predicted consequences. Small mismatches of the comparator are also used for motor learning purposes, adapting the motor commands in order to successfully achieve the intended outcome. Larger mismatches, however, are interpreted as being the action of another agent. Frith et al. (2000) related the predicted representations of actions (predicted state representation) to the action representations of imagined movements because they share similar properties and are processes in similar places within the brain (e.g. Decety et al., 1994). The comparator model was also used to explain schizophrenic delusions of control in which a specific deficit with the predicted state representation was described.

1.3: Abnormal Experience of Agency

Under normal circumstances humans have little difficulty in discriminating between the actions produced by ourselves from those produced by other people. However, certain pathological conditions can disrupt self-awareness and self/other attribution in numerous and variable ways. In the current section an outline will be given of some of the most documented of these pathologies.

Schizophrenic Delusions of Control

Delusions of control, otherwise known as passivity is one of the first order positive symptoms of schizophrenia. This particular type of symptom is characterised by the patient feeling as though they are not in control (the agent) of their actions. Although passivity can also present for thoughts and/or emotions, for the relevance of the current research the description here will relate only to delusions of control for actions. Such patients appear to have no significant deficit in action production and interestingly the ‘alien’ actions appear to successfully comply with the initial intentions, yet feelings of agency are absent (Frith, 2002).

The comparator model explanation of schizophrenic delusions of control describes a malfunctioning predicted state representation. By lesioning the comparator model at this area (see Figure 1.2) so that the comparator no longer produces an accurate prediction of the next state of the motor system means that a mismatch would be detected between the predicted state representation and the estimated actual state, even when the action is self-produced and conforms to prior intentions.

Figure 1.2: Schematic representation of comparator model lesions for schizophrenic delusions of control. An impaired predicted state representation leads to false mismatches with the estimated actual state.

Frith et al. (2000) connected the predicted state representation with motor imagery due to the similarities found between real and imagined actions.

For example, imaginary movements can affect motor learning in a similar way to actual movements (Mendoza and Wichman, 1978). Similarities are observed in timing of actual and imagined movements (Decety and Michel, 1989) and similar neural activity is also shared between the two (Decety et al., 1994) (Jeannerod, 1994 for review). Wilson et al. (2003) even documented patient C.W., a 67 year-old man who, following bilateral parietal damage from two separate strokes, was found to accidentally act out his imagined movements.

Schizophrenic patients have been found to have deficits with mental imagery of body parts and motor imagery of self-produced movements. For example, de Vignemont et al. (2006) found that schizophrenic patients were impaired in comparison to controls in a mental rotation task. Although they found the same pattern in reaction time (increases in reaction time correlated with increases in image rotation), overall reaction time and error rate was greater for schizophrenic patients when identifying if a rotated image was of a left or right hand. Similarly, imagined movements are restricted by the same constraints as actual movements (Decety and Michel, 1989). This is not the case, however, with schizophrenic patients suffering from passivity whose movements have been found to be unaffected by factors such as distance and target size (Maruff et al., 2003). In addition, these patients also had difficulty in answering questions that required them to imagine performing simple gestures (e.g., when using a pair of scissors what is nearer to the floor, your index finger or your thumb?). If the imagined movements are representative of the predicted state representation these findings support the idea that it is impaired in this specific patient group.

However, schizophrenic patients also have delusional beliefs, which may indicate a deficit in high-level processing and crucially for Stephen and Graham’s (2000) narrative approach to agency, schizophrenic delusions of control often co-occurs with auditory hallucinations (Jones and Fernhough, 2007). In addition to this, other studies have found schizophrenic patients to be able to successfully control their movements suggesting low-level mechanisms to be intact. For example, Soud at al. (2000) found that reaching movements of schizophrenic patients exhibited the same speed/ accuracy trade off as found with non-schizophrenics, demonstrating that they are taking into account the external contextual cues. Similarly an experiment conducted by Fourneret et al. (2001) required participants to direct a visually presented cursor towards a target. The experimenters applied an angular perturbation to the visual feedback so that the participants had to deviate the trajectory of their actual movements (hidden from view) to one side, in order to accurately guide the visual feedback towards the target. Both schizophrenic patients and controls were successfully able to adjust their movements in this way, the difference between the two groups only becoming apparent after the movement was completed. At the end of each movement participants were presented with feedback of their actual hand position in relation to the target, which was inaccurate due to compensating for the perturbation. The control group recognised that the inaccuracy was due to manipulations by the computer, whilst the schizophrenic patients attributed the inaccuracy to themselves (blaming tiredness etc). This experiment clearly shows that the schizophrenic patients can successfully make online adjustments to their movements in accordance with visual feedback, suggesting that the actual deficit may only involve higher-level attribution.

Further experiments, however, have revealed that in the absence of vision, error correction of movements is impaired in schizophrenic patients (Frith and Done 1989). For example, Mlakar et al. (1994) found that when drawing geometric shapes in the absence of vision schizophrenic patients performed worse than controls. These results suggest schizophrenic patients do have a deficit in low-level control of action, specifically in proprioceptive monitoring of self-produced actions (explaining why the aforementioned studies using visually guided movements found no impairment). In addition to this, schizophrenic patients appear to lack some of the implicit advantages of self-producing a movement. For example, the enactment effect describes the advantage of remembering phrases describing previously performed actions in comparison to recall of action phrases that were not performed. Daprati et al. (2005) compared the free recall of performed action phrases in comparison to non-performed action phrases in schizophrenic patients and in a non-schizophrenic control group. Each group was exposed to 30 phrases all of which were presented aurally and visually (video clip of an actor performing the action). In half of the trials the participants were also required to act out the movements themselves, whilst in the remaining trials they made no movements. The control group demonstrated an enactment effect, remembering significantly more of the action phrases that were also performed. However, the schizophrenic group did not have this advantage, demonstrating no difference in recall of acted or non-acted phrases. The authors argued that this was not a result of a general memory impairment as there was no difference between the control and schizophrenic groups for the non-performed phrases and there was also no difference in an additional recognition task (same phrases used). Therefore, it was suggested that the schizophrenic patients failed to gain the benefit of enactment due to a failure to correctly bind representations of the action with the self.

Similarly, schizophrenic patients have also been found to rate the intensity and ticklishness of self-produced stimuli to be in line with that which is externally produced (stroking the left palm with a piece of foam either controlled by the right hand -self-produced, or the experimenter -externally produced) whilst control participants rated self-produced stimuli as less intense and ticklish (Blakemore et al. 2003). The interesting finding from these studies is that the reduced sense of agency felt by the schizophrenic patients appears to be also affecting low-level processes. That is, not only do the high-level beliefs of the patients fail to feel a sense of agency but the low-level processes of the motor system also interpret the actions as externally produced.

Another example of Schizophrenic patients demonstrating a deficit in low-level agency processes, directly associates their deficits with action prediction mechanisms (predicted state representation). Bulot et al. (2007) conducted an experiment in which the participants were required to stop the movements of a swinging pendulum by applying sufficient grip force onto a load cell. The participants were instructed to be as efficient as possible applying only the minimum grip force required, whilst not letting it slip through their fingers. The experiment was completed both when the pendulum was released by the participant's free hand and when it was released by the experimenter. The non-schizophrenic control group showed an advantage in the trials in which the pendulum was released by themselves, in that they were able to stop the pendulum whilst applying less grip force than when the pendulum was released by the experimenter. The schizophrenic patients, however, failed to show this advantage, demonstrating a similar degree of grip force in the self releasing trials as in the experimenter releasing trials. These findings suggest that although schizophrenic patients have abnormal beliefs that may contribute to delusions of control, they also have a deficit in low-level processing of self-generated movement.

Anarchic Limbs

A disorder in which patients are recorded to deny agency over their own limb movements is alien or anarchic limb syndrome. This is described as a motor phenomenon in which the actions of the affected hand are not under voluntary control. Although patients with an anarchic limb are generally under no illusion that the limb is their own, they often refer to it in the third person, and as such movements are distressing to the individuals, there is often negative feelings towards the limb (Muangpaisan et al., 2005). Anarchic limbs are most commonly a result of damage to either the supplementary motor area (SMA) or the corpus callosum (Della Sala, 2005). Interestingly, these two anatomical locations have been differentiated in terms of the nature of the alien movements. Anarchic limbs following frontal lesions incorporating the SMA, have been described as performing stereotyped actions in direct response to visual stimuli grasping and groping at objects. Following lesions to the corpus callosum, however, the involuntary movements are more often described mirroring movements of, or making movements that are the opposite to, those performed by the unaffected limb. For example, doing up buttons with the unaffected hand whilst immediately undoing them with the anarchic hand (Geschwind et al. 1995)

Crucially the reduced sense of agency evident in patients with alien limb syndrome demonstrates a key difference from the lack of agency experienced in schizophrenic delusions of control (described above). Patients with alien limbs carry out unintended movements with the affected limb for which they fail to feel agency towards, whilst schizophrenic patients with delusions of control claim absence of feelings of agency for movements that were intended. Due to this important distinction it is stated by Frith et al. (2000) that whilst delusions of control reflect a deficit with the experience agency, the presence of an alien limb does not. When the motor system initiates a movement an efference copy of the issued motor commands is used to form the predicted state representation. However, afferent signals from the movement and the environment help to fine-tune the motor commands in order to make a successful and accurate reach. One example of such influences on the motor commands is affordances (e.g. graspable objects) in the surrounding visual environment. It was claimed by Frith et al. (2000) that patients with alien limb

syndrome make actions with the affected limb that are no longer controlled by their intentions but are instead initiated by affordances in their environment, thus producing discrepancies between their actions and intentions.

However, since there is no deficit in feelings of agency these patients are aware of the discrepancies as well as being aware that it is their own limb i.e.

they have no deficit in either agency attribution or in the sense of ownership (Figure 1.3a). This point is used as an explanation for why alien limb syndrome

is associated with the SMA and the corpus callosum opposed to parietal areas. The SMA being linked to motor selection processes (Leuthold and Jentzsch, 2001) and damage to the corpus callosum is suggested to prevent inhibition of the affected limb from initiating movements already completed by the unaffected limb (Frith et al., 2000).

Another disorder in which the patients actions appear to be initiated by visual affordances, is utilisation disorder. These patients produce stereotyped behaviours that were not intended but if questioned about their actions they attempt to rationalise them as if they were intended. For example, Lhermitte (1983) described a 62 year-old woman, who following a ruptured aneurysm, showed utilisation behaviour towards numerous objects including picking up a knife and fork and making cutting movements (nothing to cut). This can be explained within the framework of the comparator model in a similar way to that of alien limb syndrome. The utilisation behaviour is triggered by environmental affordances as opposed to being produced in accordance with prior intentions. However, unlike alien limb syndrome, these patients are not aware of their lack of agency as they retrospectively devise intention. This is explained by a failure to form intentions, so that no discrepancies of the comparator are detected because there were no intentions for the actions to be discrepant against. Hence, in absence of any information to the contrary, the patient assumes agency (see Figure 1.3b).

Figure 1.3: a) Schematic representation of comparator model lesions for alien limb syndrome.
The patient’s movements are no longer controlled by intentions but by visual affordances.
Patients are completely aware of the discrepancies present between intentions and actions
because they have no deficit in feelings of agency. b) Schematic representation of lesions of
the comparator model for utilisation disorders. No intentions are formed so that movements are
initiated based on visual affordances only. No discrepancies are present between actions and
intentions as there were no intentions to begin with.

This latter example is interesting as it suggests a role for the internal narrative in the attribution of agency. Frith et al. (2000) admitted that in most
cases people are largely unaware of their actions, as is shown by experiments in which participants make significant alterations to their movements without it

reaching awareness (Fourneret et al, 2001). In fact in most cases it is likely that humans only become aware of their actions when a discrepancy is detected. Whilst utilisation disorder appears a prime example of the narrative explanation of agency in which it is claimed that intentions are retrospectively inferred to our actions (see above), such behaviour seems to also rely upon

output from the comparator. Stephens and Graham (2000) claimed that our own intentions (and hence agency) are inferred in a similar manner to inferring the intentions of other people, based on prior behaviour. Utilisation behaviours, however, are by nature out of character and often inappropriate, yet the patients presenting with such symptoms are often lucid with good past and recent autobiographical memory from which such inferences are said to be made (Lhermitte 1983). Therefore, although these patients appear to confabulate intentions for their actions subsequent to the event, it is unlikely to be due to inferences based on prior behaviour but instead due the comparator not detecting a discrepancy and thus not alerting the patient to their otherwise unconscious intentions.

Anosognosia

Anosognosia has been described in conjunction with several disabilities (e.g. anorexia -Vandereycken, 2006, hemianopia and aphasia -Bisiach et al., 1986), but for the current purposes this description will focus on anosognosia for hemiplegia (one sided paralysis). Anosognosia for hemiplegia can occur in varying severities from indifference towards the paralysis to consistent denial despite being presented with irrefutable evidence to the contrary. The disorder is most frequent following right hemisphere damage predominantly including the parietal area (Pia et al., 2004). The denial of disability can occur despite normal intelligence and lucidity of the patient and can be specific to one form of illness whilst awareness of other conditions is unaffected. For example, Ramachandran (1995) described a patient B.M., a 76 year-old woman who, following a right hemisphere stroke, denied her left sided paralysis yet

admitted that she was in hospital due to a stroke and who also was in no denial of her additional diabetic condition.

One previous explanation given for anosognosia is that because it often presents alongside hemispatial neglect (see below), in which the patient is not aware of the contralesional (left) side of space, the hemiplegia, like most on the left, is ignored. However, double dissociations between neglect and anosognosia are common, suggesting that, although in some cases neglect might contribute to the lack of awareness of hemiplegia, anosognosia is a functionally separate disorder (Bisiach et al., 1986). A further explanation is that because such patients do not attempt to move their limb they never receive information confirming the paralysis (Heilman, 1998). Often when asked to move their paralysed limb patients attempt to talk their way out of the question. For example, Ramachandran (1995) described patient O.S. a 65 year-old woman, who, when asked whether she could move her left, hand responded “did you know my farther was left handed?...” to deflect from the emphasis away from the question. In other examples patients have claimed tiredness or additional ailments that would excuse them from using their paralysed hand. For example, patient L.R., a 77 year-old woman described by Ramachandran (1996) who, when asked to point with her left hand and failed to do so, claimed it was because she had arthritis in her left shoulder.

However, some patients claim agency over movements of their paralysed hand that were never made. The following examples are taken from Ramachandran (1996) who described the anosognosia symptoms patient F.D., a 77 year-old woman who, despite being highly lucid and intelligent, claimed to be moving her left arm that lay paralysed in front of her.

Experimenter: Mrs D can you clap?
F.D.: of course I can clap
Experimenter: can you clap for me?
F.D.: (she proceeded to make clapping movements with her right hand as if clapping with an imaginary hand near the midline).
Experimenter: Are you clapping?
F.D.: Yes, I’m clapping. Ramachandran (1996)

In a further example;

Experimenter: Can you point to my nose with your right hand?
F.D.: (she followed his instructions and pointed to the experimenters nose).
Experimenter: Mrs. D, point to me with your left hand.
F.D.: (her hand lay paralysed in front of her).
Experimenter: Mrs. D, are you pointing to my nose?
F.D.: yes.
Experimenter: Can you clearly see it pointing?
F.D.: yes it’s about two inches from your nose. Ramachandran (1996)

Patient F.D. had no problems with vision and no hemispatial neglect, yet in both instances she was claiming agency over movements she did not make and in the latter example even claimed to see her limb pointing. These descriptions do not follow the assumption that the paralysis is not realised because movement is not attempted and suggest that the patient, on at least some level, had the experience of her limb moving. In addition to this, some patients with anosognosia have been found not only to be unaware of their own disabilities but also those of other patients (Ramachandran and Rogers-Ramachandran, 1996), suggesting that in some patients at least the disturbed body representation also extends to other peoples bodies.

Frith et al. (2000) stated that the urge to move is a result of forming a representation of the intended next position of the limb (desired state representation). Following this, the individual then perceives the initiation of that movement, which is distinct from actual movement initiation and occurs as a result of forming a representation of the predicted next state of the motor system that is based on the efference copy of the motor commands (predicted state representation). This was supported by a study conducted by Haggard and Magno (1999), in which they found that by applying TMS to the motor cortex they could delay the actual initiation of the movement whilst having little affect on the perceived initiation, demonstrating that the two are dissociable. Thus, if a patient successfully plans a movement and forms a predicted state representation, then even with paralysis, the experience of initiating the movement would be obtained. However, following perceived movement initiation the patient continues to believe that the movement is occurring despite making no actual movement. Therefore, the discrepancies between the estimated actual state and both the predicted and the desired state representations, are ignored (see Figure 1.4).

Somatosensory impairment and neglect of the paretic side, which commonly occur in conjunction with anosognosia, are likely to contribute to the patient’s lack of awareness of these discrepancies. However, not all patients

present with all three deficits (patient F.D. described above being an example) so Frith et al. (2000) claimed that anosognosic patients are likely to have an additional deficit resulting in the poor conscious self-monitoring of movements that is already apparent in neurologically intact individuals (Fourneret et al, 2001) becoming exaggerated. Therefore, the deficit with anosognosia is not within the comparator itself, but in high-level conscious awareness of comparator output.

Figure 1.4: Schematic representation of comparator model lesions explaining anosognosia.
Movement intentions and predicted state representation formed as normal. However, no movements are actually performed and discrepancies between the estimated actual state and predicted and desired state are ignored.

Hemispatial Neglect

Hemispatial neglect is a disorder affecting self-awareness that shows close association with anosognosia as both disorders often occur in conjunction with one another and are associated with similar lesion locations (Pia et al., 2004).

This disorder is characterised by the patient’s failure to acknowledge objects on, or orient towards, the contralesional side. The anatomical location most associated with neglect syndrome is generally the right hemisphere with lesions particularly involving the parietal lobe (Driver and Mattingley, 1998). As such, the neglected side of space is usually the left side. Although in most cases neglect symptoms do not persist more than a few weeks (Cassidy et al., 1998), in some patients it is a more permanent condition and can be a predictor of general poor prognosis and resistance to rehabilitation (Denes et al., 1982).

Classic neuropsychological tests for neglect include line bisection (Figure 1.5a) in which a patient is presented with horizontal lines and asked to mark each one at the centre. In this test a patient with neglect will mark the line significantly over towards the ipsilesional side (most often towards the right side). Another classic test is star cancellation (Figure 1.5b) in which a patient is presented with an array of small and large stars that are evenly distributed across the page. The patient is then asked to mark all the small stars they see. A typical neglect patient will only cancel out stars to the right (ipsilesional) overlooking ones on the far left (contralesional) of the page. This right-sided bias even occurs when producing images from memory. For example, when asked to draw a clock face, a neglect patient is likely to either miss the detail off the left side of the image (e.g. only include numbers 12 – 6, (for example see Figure 1.5c) or attempt to fit all the numbers on the right hand side.

Figure 1.5: Classic neglect tests completed by patient L.S., an 81 year-old male neglect patient tested at the University of Nottingham. a) Line bisection task. When asked to mark the middle of the line L.S.’s responses were heavily biased towards the right. b) Star cancellation task.

When asked to cancel out all the small stars, L.S. only marked the stars to the right of centre. c) Picture of a clock drawn from memory: detail clearly lacking on the left side of the picture.

In relation to self-awareness, many neglect patients fail to acknowledge or use body parts on the contralesional side. For example, patients described as having motor-neglect will use their contralesional limb when prompted but without prompting they will ignore it and favour using the ipsilesional limb even if the ignored limb if fully dextrous (Punt et al., 2005). An example of self/other attribution deficits in neglect comes from observations during rehabilitation. Neglect symptoms have been found to be reduced following prism adaptation, in which the individual's visual field is shifted resulting in

objects in their visual world appearing to one side of their actual physical location. Therefore, in order to interact with this optically shifted world, the individual has to realign their visual and proprioceptive representations. For example, a participant wearing prism goggles with a 10-degree rightward optical shift, when reaching towards a visual target will misreach to the right by an almost equivalent amount (some online correction). After several trials, however, the participant will become accurate with their reaches. Following removal of the prisms, the participant will again misreach, this time in the opposite direction; this second misreach is known as the negative aftereffect. For neurologically intact individuals the aftereffect lasts only a few minutes. With neglect patients, however, (using rightward prisms so that the aftereffect shifts them towards their neglected side – e.g. Luaute et al. 2006) the aftereffect has been found to last for up to four days, reducing their rightward bias on numerous neglect tests such as the ones mentioned above (Pisella et al., 2002). The size of the aftereffect of neglect patients has also been found to be greater in magnitude than found with controls (Rossetti et al., 1998).

Interestingly, in relation to agency, the neglect patients do not appear to be aware of the perturbations and exhibit what has been described as hypernosognosia, which refers to a self-attribution of the prismatically induced errors (Michel et al., 2007). With neurologically intact participants, Michel et al. (2007) have been able to increase the magnitude of the prism-induced aftereffects by incrementally increasing the size of the prismatic perturbation over a series of trials. This mimicked the hypernosognoisa seen with neglect patients, as the participants awareness of the perturbations was reduced. Therefore, the exaggerated prismatic aftereffect observed with neglect patients

may be due to underlying problems with self/other attribution and, furthermore such deficits are unlikely to be centred in low-level mechanisms due to the ability of these patients to adapt to prisms. Therefore, the reduced awareness seen with these patients may be due to a decreased self-monitoring of action, such as that described above for anosognosia.

1.3: The role of Proprioception in Agency

A recent criticism of the comparator model is that it underestimates the role of proprioceptive signals (Synofzik et al., 2007) the main role of which is restricted to formation of the estimated actual state rather than contributing directly to experiences of agency. Some previous studies have found deafferented patients to be impaired in self/other attribution of action (Farrer et al., 2003b and Balslev et al., 2006), which may suggest that proprioception plays a greater role. In addition to this, the previously discussed experiments examining schizophrenics with delusions of control suggest that they have a deficit in monitoring the proprioceptive feedback of their own movements. However, as well as high and low-level agency mechanisms there are also further aspects of self-awareness that are likely to be intrinsically linked to agency whilst remaining fundamentally distinct, such as the sense of ownership. This was defined by Gallagher (2000) as the sense that my body is moving and, unlike with agency, ownership does not require intentions and the active planning of a movement. For this reason, a feeling of ownership cannot depend on efference signals from the motor commands but is more likely to be informed by sensory feedback from the actual movements such as proprioceptive signals and visual-proprioceptive congruence.

Tsakiris et al. (2005) criticised many of the previous agency experiments as not controlling for feelings of ownership and so overemphasising the role of proprioception. In their study they compared the self/other responses of active movements, for which intentions and motor commands are formed in the usual way, to passive movements with no intentions or motor commands so that responses were based on the matching of visual and proprioceptive signals only. The participant's right index finger was lifted on a level that was controlled by either their own left hand (active) or the experimenter (passive). Visual feedback was provided of a video image of either the participant's right index finger moving (self) or the experimenter's finger undergoing the same movement (other) and over which they had to make a self/other judgment. It was found that accuracy of self/other judgments were greatly reduced with passive movements reaffirming the emphasis on efferent signals for determining agency. However, due to the nature of the task (the moving finger being lifted by a lever) it is most likely that judgments were made primarily on temporal differences between movement onset of the visual feedback and the actual movement (movements were small and unlikely to have additional spatial deviations due to being passively moved on a lever).

Frith et al.'s (2000) claimed that awareness of initiating a movement precedes actual movement initiation, before any sensory input is received, therefore such judgments cannot involve proprioception. This was supported by results from Haggard and Magno (1999) (see above) who found that TMS over the primary motor cortex delayed button press reaction times in response to a tone (go signal), with little affect on their perceived reaction times. This finding suggests that awareness of initiating a movement does not come from

sensory feedback, as this would occur after the movement onset, and so perceived reaction time would be delayed to the same extent as the actual reaction time. Although feelings of agency are heavily based upon feelings of movement initiation, it follows on that feelings of control over the entire trajectory are of equal importance, for which proprioception is likely to play a larger role.

De Vignemont and Fourneret (2004) differentiated these two aspects of agency suggesting that movement initiation is accomplished by matching the intended state with the predicted state whilst a sense of ones own movement is accomplished by matching the predicted state with the sensory feedback (see Figure 1.6). However, despite such a distinction it does not necessarily follow that the role of proprioception should extend beyond forming the estimated actual state. Therefore, one of the main aims addressed throughout the current thesis was to investigate to what extent proprioception contributes to the experience of agency and how it might inform both high and low-level agency mechanisms.

Figure 1.6: Schematic representation of the proposed two aspects of agency, a sense of movement initiation and a sense of a movement being one’s own. Adapted from de Vignemont and Fourneret (2004).

1.4: Conscious Awareness of Action

Most of the evidence discussed thus far is compatible with a low-level account of agency opposed to high-level processes. However, our day-to-day experiences of agency are high-level conscious judgments and it is exactly this, that is measured in the majority of previous agency experiments. There is a lot of evidence to suggest that humans are not consciously aware of precise low-level mechanisms of their movements, which may present a problem with low-level explanations of agency, in how low-level mechanisms inform higher-level conscious awareness.

A paper by Georgieff and Jeannerod (1998) highlighted the important differences between automatic actions, which are performed in response to environmental cues and for which the agent has no conscious awareness of the intentions, and voluntary actions that are purposeful and deliberated based firmly on conscious intentions. This dissociation produces a clear distinction between action awareness and the sense of agency as latter can be experienced over movements for which the former is absent. Frith et al. (2000) stated that for the most part, individuals are in fact not consciously aware of their actions until their awareness is captured by unexpected consequences (e.g. a disruption to the sense of agency). This idea is supported by numerous experiments in which participants made alterations to their movements yet remained unaware of them. For example, Goodale et al. (1986) conducted an experiment in which participants had to reach towards targets whilst vision of the reaching arm was occluded. Part way through the reach the target location was shifted. The participants were successfully able to adjust their movement trajectory in order to accurately reach the target without the aid of vision, whilst remaining

unaware of either the target movement or the adjustments made to their own reach.

Further experiments have been completed also demonstrating a lack of conscious monitoring of our movements. In a study by Fourneret and Jeannerod (1998) participants were asked to draw straight lines with a stylus on a graphics tablet, the visual feedback for which was presented so that it appeared in the same spatial location as their actual movements. During the experiment angular perturbations were applied to the visual feedback (the size of which was variable between trials) so that in order to produce a straight line with the visual feedback, participants would have to make angular deviations (away from a straight line trajectory) to their actual movement. Following each trial the participants were then asked to indicate the direction of their actual reach. In one condition this was done verbally by reading out the number of a line from a response card that was perceived to correspond most accurately to the movement they actually made. In an additional condition the participants were required to indicate the trajectory of their movement by making a motor response (recreating their movement with eyes closed). Not only were the participants successfully able to make the motor adjustments so that perturbed visual feedback closely followed the sagittal line, but they were also largely unaware of these alterations, underestimating the angle of their hand deviation, with one group even perceiving their movement to be in the opposite direction. This lack of conscious awareness of actual movements was evident even with motor responses, participants tending to favour a straighter trajectory (closer to visual feedback) than the one actually generated.

In another similar experiment by Slachevsky et al. (2001) it was found that participants were unaware of the changes made to the direction of their reaches up to approximately 14-degrees angular deviation following the application of perturbations that increased in size over consecutive trials. These instances show us that we can have a full sense of agency over an action and yet not be fully aware of what that action entails. This implies that feelings of agency may, in part at least, derive from higher processes than those directly involved in the updating of the motor commands.

1.5: Thesis Aims

Previous experiments in agency attribution often reveal contradictory results, which may be explained by differing paradigms investigating differing aspects of agency. Although recently, theorists have identified a distinction between high and low-level processes, it is as yet unclear how they may interact to produce the experience of agency as we know it. The main aim of this thesis was to investigate interactions between high and low-level agency mechanisms in terms of experience of agency during a movement. To examine this effectively the current thesis is divided into three sections, the first of which (Section 1) examined the relationship between agency attribution and the right hemisphere. This was achieved by testing a patient with callosal agenesis (Chapter 3), determining the reliability of the spatial perturbation paradigm for agency (Chapter 4) and using single pulse TMS over the right inferior parietal lobe (Chapter 5). Section 2 specifically investigated the role of proprioceptive feedback in the experience of agency, by comparing self/other judgments of active and passive movements (Chapters 6), and with reduced proprioceptive

feedback by testing a patient with somatosensory loss (Chapter 7a) and healthy controls with tendon vibration (Chapter 7b). Finally, Section 3 related these findings in terms of high and low-level mechanisms by measuring low-level motor responses as well as high-level self/other judgments in response to both visual and physical perturbations to reaching movements (Chapter 8). This was also investigated by examining self/other judgments during covert adaptation of the motor system (Chapter 9a), and finally relating these findings to a patient with hemispatial neglect (Chapter 9b).

Chapter 2
General Methods Section

2.1: MiniBIRD

The miniBIRD 800 is a motion-tracking device with six degrees of freedom. It consists of up to four sensors each 8.1mm x 8.1mm x 8.1mm which are connected via a 4mm diameter 3m cable to an electronics unit (transmitter). The miniBIRD uses electro magnetic principles to measure the position and orientation of the sensors respective to the transmitter. It has a static position accuracy of 0.05mm RMS and position resolution of 0.18mm RMS and is able to determine position and orientation by pulsing a DC magnetic field from the transmitter, the characteristics of which are interpreted by the sensors. The centre of transmitter is the origin and reference point for X, Y and Z coordinates, which radiate orthogonally out from it in the standard manner. As with any electromagnetic recording device the workspace is required to be devoid of materials that conduct electricity (metal) as it would interfere with the magnetic field and so alter the recordings. The miniBIRD has a useful recoding range of up to 760mm from the centre of the transmitter.

Within the current thesis the miniBIRD is only used for the experiment in Chapter 3 in which X and Y position coordinates of one sensor were measured in order to reproduce accurate online visual feedback of reaching movements. The accuracy and reliability of the miniBIRD was analysed with the following procedures: Two sensors were attached to a rigid body at three different distances apart (50mm, 100mm and 150mm). The distance between

the two sensors was recorded at 20 separate static locations within the workspace that was used for the experiment (800mm x 450mm), which were evenly distributed between lateral and radial orientations. For static marker 95% of the data was found to fall between ±0.26mm of the mean distance between the markers. When a similar procedure was employed with the sensors in motion (using various different velocities) it was found that 95% of the data fell within ±1.23mm of the mean distance between the sensors (using distances of 50mm, 100mm and 150mm).

2.2: Polhemus LIBERTY

The Polhemus LIBERTY 240/8 is a high-resolution, three-dimensional (3df) motion tracking system. The system operates using electro magnetic principles with a sampling rate of up to 240Hz. It consists of a host computer, a systems electronic unit, a magnetic source and up to 8 independent sensors. The systems electronic unit is a stand-alone device, which contains connector ports for the sensors and the source as well as connections to relay data to the host computer. The source is a 5mm cube (approx.) from which the electromagnetic field is transmitted. This is positioned on a non-metallic surface close to the sensors. The sensors themselves are small devices that can be attached to the moving objects (hand or digits of the reaching limb) the position of which is measured relative to the magnetic source. Each sensor is connected to the Systems electronic unit, which can record the coordinates of up to 8 separate sensors each at 120 or 240 Hz. The Polhemus can be connected to the host computer via a USB or COM port and requires either Windows 2000 or Windows XP and to have the Polhemus PiMgr GUI software installed.

The Polhemus records with a latency of 3.5ms and also contains a built-in adaptive filter designed to reduce noise in the data. In order to reduce lag between the requesting and receiving data from the Polhemus, output record length should be kept to a minimum and all non-essential software applications on the host computer need to be disabled. Strength of the signal is indicated via the LED on the front of the systems electronic unit. The Polhemus provides all altitude angular coverage, recording both position (X, Y and Z coordinates) and orientation. It provides a static accuracy of 0.03 inches RMS for X, Y and Z positions and 0.15 degrees RMS for orientation. At a distance of 300mm the Polhemus records at a resolution of 0.038mm for X, Y and Z positions and 0.0012 degrees for orientation. Total recording range is 900mm at the above specifications, with overall useful operation in excess of 1800mm.

Within the current thesis the Polhemus LIBERTY is used to record X and Y co-ordinates from one sensor (240Hz) for the experiments in Chapter 2 , Chapter 4 and Chapter 5. The data was used to provide real time visual feedback of the movements. Reach length was approx. 300mm towards the source, in order to fall well within useful recording range.

2.3: vBOT 2D Robotic Manipuladum

The vBOT 2D is a two-dimensional (2df) robotic manipulandum for motion tracking and force generation, sampling at a rate of 1000Hz. The vBOT consists of a manipulandum, controller and host computer. The manipulandum is the robot arm component of the vBOT, which includes all associated hardware; torque motors, encoders, pulleys and drive belts and the optional force/torque sensor. The robot arm is also the location of the safety switch,

which needs to be closed (along with the controller unit to be started) in order

for the vBOT to be active. The controller unit relays information between the manipulandum and the host computer. It is connected via three ribbon cables attached to a PCI card in the host computer and requires either Windows 2000 or Windows XP, a PCI card interface, 2PCI slots, a graphics adapter and at least a 1GHz processor, 256 MB memory, and 1GB free disk space. All applications for the vBOT need to be written using Microsoft Visual C++, which must also be installed on the host computer.

The encoders attached to the manipuandum monitor the angular rotations of the motors in order to measure the position of the robot arm. All information to and from the manipulandum are analogue signals which are interfaced with the digital signals from the host computer. Digital to analog converters allow the torque levels of the motors to be set and analogue digital converters read the analogue signals from the optional force/torque sensor and relay that information back to the host computer.

In order to safely and accurately apply forces to the handle specific timing is required. Whilst the vBOT is activated, the Forces Function (responsible for applying the forces) is continuously receiving position information of the arm and sending information about the desired forces. These operations are interfaced using a high priority thread running at 1kHz, leaving the main thread for other functions such as graphics, for which exact timing is less crucial.

In the current thesis the vBOT 2D is used to record X and Y coordinates from the manipulatdum (1000Hz) for the experiments in Chapters 6, 7, and 8. The data is used to examine reach accuracy in addition to providing

real time visual feedback of the movements. The vBOT is also used to create passive movements (Chapters 5 and 6) and physical perturbations (Chapter 7) utilising the Forces Function component of the device. In order for the visual feedback to appear in the same location as the actual movements a scaling factor of 1/8 had to be used.

In order to determine the reliability of the vBOT manipulandum, it was programmed to perform 16 passive movements to four separate locations within the workspace. 95% of the data fell within ±0.15mm of the mean endpoint of the X axis and ±0.12mm on the Y axis.

2.4: The Mirage System

The Mirage system consists of a monochrome Basler A601F firewire CCD (charge-couple device) Camera with a Tamron 6mm fixed focal length lens, an iMAC OSX 10.4.1, 2.8GHz computer, two mirrors, one down-facing and one up-facing a short range 8 diode infrared camera with the a disabled light sensor

and a infrared reflective marker.

The CCD camera is positioned on a tabletop at a 75-degree angle with the lens facing towards the horizontal down facing mirror, which enables the camera to pick up movements in the plane of the tabletop. The CCD camera is attached to the iMAC OSX 10.4.1 computer via a standard firewire cable and mounted on the back of the CCD camera is the 8-diode infrared camera. The 8 light emitting diodes reflect of the infrared reflective marker, making it the brightest part of the image. The iMAC OSX 10.4.1 requires windows XP compatibility to run LabVIEW 8.2 IMAQ vision software, which allows tracking of the X and Y co-ordinates for the marker whilst in the image

(brightest point of the image). Therefore, movements of the marker can be tracked within a 225x290mm area sampling at 60Hz at 640 x 480 vga resolution. A crucial component of the Mirage system is that it allows live video feedback of actual reaching movements to be viewed in the same physical location, and from the same perspective, as if viewing the actual hand.

Therefore instead of having a cursor representing the actual limb movements the system allows real time video footage of the actual limb to be presented as visual feedback, which then can be manipulated by the computer.

Within the current thesis the mirage system was used for the experiments in Chapter 9 for which the X and Y position co-ordinates of the marker were recorded in order to examine reach accuracy of the movements and to apply angular perturbations to the movements. Accuracy of the setup was achieved by placing the Mirage ultraviolet marker on top of a sensor from the Polhemus LIBERTY from which calibration algorithms were produced for the workspace.

2.5: Transcranial Magnetic Stimulation

For the experiment in Chapter 5 the Polhemus Liberty (above) was used in conjunction with single pulse transcranial magnetic stimulation (TMS) applied to the right Inferior parietal lobe (rIPL), in order to ascertain the functional

nature of this area in the task. Previous studies showed that activity in the rIPL
is associated with making other judgments to visual feedback of actions in a self/other judgment task. The benefit of TMS is that it allows for a causal association to be established between brain and behaviour and can help

determine specific functional properties of observed neuronal activations. For these reasons a brief account of TMS is given below.

What is TMS?

TMS is a non-invasive technique that involves a brief, high-current pulse produced from a coil of wire. From this a magnetic field is formed that is perpendicular relative to the plane of the coil the strength and which can reach

up to 1.5 Tesla, equivalent to tens of thousands of times the strength of the earth’s own magnetic field (George, 2003). When placed on the scalp the current passes through it and disrupts the underlying neurons inducing a transient lesion in the brain. These time-locked 'virtual lesions' when placed over a specific region of interest on the cortex, can, if essential to the task, alter
the participant's performance (Pascual-Leone et al., 2000).

TMS units are comprised of a stimulation coil, from which the pulse is initiated and a main unit that contains at least one energy storage capacitor, a

charging system, discharge switch and circuits for pulse shaping, energy recovery and control functions (Pascual-Leone, 1999). The stimulation coils are either circular or have a figure 8 shape, the figure 8 coils generate a more focal pulse as the maximal current is localised to the intersection of the two circular components. With circular coil, however, the maximal current is around the coils entire circumference (Hallet, 2000).

The principle of TMS is based upon exciting the neurons in the brain underneath the coil by inducing an electrical field that causes neurons to depolarise and fire, thus disrupting normal brain activity. As such the TMS pulse is taking advantage of the electrical processes already apparent within the

brain (George et al. 2003). Successful stimulation is dependent upon two criteria; a large enough current to produce a magnetic field of suitable intensity and the rate of change of the magnetic field that is kept rapid by using a very short rise time (the time taken for the magnetic field to develop). (Pascual-Leone et al., 1999).

The TMS ‘virtual lesions’ have many advantages over actual lesions observed in brain damage patients. The spatial resolution of TMS is restricted to approximately 1cm. This is much smaller than many lesions found in brain-damaged patients, which can result in additional deficits that can also affect performance on a given task. In addition to this, larger lesions can also make functional assumptions towards anatomical structures more difficult. Similarly due to the transient nature of the pulse effects, there is not time for cortical reorganisation to take place, which is a normal process that occurs following brain damage. For these reasons Walsh and Rushworth (1999) claim TMS has high functional resolution and is useful tool in modern cognitive neuroscience.

Single pulse TMS has the advantage of producing neuronal interference at a precise point in time (Pascual-Leone et al. 2000). This transient nature of the stimulation allows specific processes within a task to be targeted which is important for the use of TMS within this thesis. In addition to this, single pulse TMS is well established for its high safety record when applied to healthy controls (Pascual-Leone et al. 2000). Repetitive TMS (rTMS) on the other hand involves the application of multiple successive pulses, the effects of which are far less transient and although useful for cognitive tasks, can cause seizures with those particularly at risk, such as individuals with a personal or family history of epilepsy. For these reasons The TMS experiment conducted

within this thesis uses single pulse TMS, being a reliably safe method and allowing precise timing of pulse delivery to be achieved.

Exclusion Criteria

Although single pulse TMS is considered completely safe all participants who took part in TMS study (Chapter 5) were screened for contraindications using a self-report questionnaire based on the TMS Adult safety Screen (Keel et al., 2001). Due to the risks of seizures (although unlikely with single pulse TMS) a history of epilepsy in the family is included as exclusion criteria. Additional exclusion criteria includes the presence of pace makers, hearing aids and other mechanical aids, because the strong electrical fields generated with TMS can interfere with these devices as well as metallic materials within them posing a risk due to the conductive properties of metal. For this reason metal implants are also part of the exclusion criteria and all participants were asked to remove any metal jewellery before participating.

Placement of the coil

Many different methods exist to decide which area of the scalp relates to a particular brain area. One method is using a functional BOLD signal from fMRI images for each individual participant (for example, Niyazov et al., 2005). However, this method is both expensive and time consuming, without being infallible as TMS and fMRI maps have been found to be consistently and systematically inaccurate (Herwig et al., 2002). Significant results have been found with other methods such as using an international 10-20 EEG system, which has been found to be mostly accurate between individuals for larger

scale areas (Herwig et al., 2003). The experiment described in Chapter 5 uses co-ordinates from a previous successful study looking at the right parietal area;
Nager et al.(2004) positioned the coil 5cm posterior to the site used to determine the intensity of the TMS (motor hand area). Nager et al. (2004) found that stimulation of this area resulted in reduced detection of somatosensory stimuli on the contralateral side. This should not be a factor in for the TMS experiment, as the participants will only be making reaches with the ipsilateral limb.

2.6: Pilot Study

Introduction

Previous studies investigating self/other attribution have used a variety of techniques to create the other movements. Sirigu et al., (1999) used video images of the experimenter producing actions (forming finger postures) that where either the same or different to those produced by the participant, whilst both were wearing gloves to disguise morphological differences. In this experiment the participants demonstrated a high level of accuracy in self/other judgments over feedback that was either other and incongruent (the experimenters hand performing a different action to that performed by themselves) or self (an accurate representation of their own hand). However, the trials in which they saw the experimenter’s hand conducting the same movements as themselves produced more errors. Tsakiris et al. (2005) only used this more difficult condition for their experiment but expanded on it by ensuring that all seen movements were actually passive. The moving finger being lifted by a lever that was controlled by either, the participant’s other

hand that was hidden from view, or by the experimenter. With this method of producing other visual feedback only small movements can be used otherwise synchronisation of the participant’s and experimenter’s movement is too difficult. In addition, the exact amount by which the self and other movements differ is difficult to ascertain, so that it is almost impossible to establish thresholds for what is accepted as self.

Other studies have used perturbed self-produced movements, providing virtual visual feedback of the participant’s own actions but applying spatial (e.g. Farrer et al., 2003a and Farrer et al., 2003b) or temporal (e.g. Macdonald and Paus, 2003) perturbations to them. With this technique the other refers to the computer and not another person, but it allows greater control over the degree of discrepancy between the actual movement and the visual feedback provided. This therefore allows easier identification of what specific aspects are important for feelings of agency. Moreover, this method allows the use of larger and more complex movements as the other movements are always based on the participant’s actual limb position. However, unlike with the aforementioned technique, which used video footage of the participant’s actual hand, in most cases the visual feedback is not of the actual limb but of a virtual representation of the limb (a notable exception to this is the mirage system see above).
Importantly with this latter method it allows investigation of the separate aspects that may contribute to experiences of agency for example

action initiation can be better examined using temporal perturbations whilst the detection of spatial differences and the importance of endpoint accuracy can be better examined using spatial perturbations. The reason for this is due to the crucial difference between these two types of perturbation, that with temporal perturbation the perturbed action always reaches the desire endpoint of the movement whilst spatial perturbations make the visual feedback inaccurate.

The benefit of the spatial perturbations is that the actual movement may only differ in spatial parameters whilst temporal perturbations, in addition to the temporal differences between the self and other movements there is also a spatial deviation as the visual representation is either just ahead or just behind the actual movement. Therefore spatial perturbations allow the contributions of spatial aspects of reaches, in feelings and judgments of agency, to be closely examined whilst tightly controlling for all other factors.

Within the current thesis spatial perturbations were applied to visual feedback of actual movements in order to produce the other conditions (visual feedback is controlled by the computer). Previous experiments that used spatial perturbations use cursor rotations in order to rotate the trajectory of the visual feedback of the movement away from the actual reach trajectory. For example, with a leftward 4-degree perturbation the trajectory of the visual feedback (cursor) is rotated by 4-degrees from the actual reach trajectory so that after a reach of 220mm the cursor will be approximately 150mm to the left of the actual location of the limb.

Previous studies have used these rotations on small movements. For example, Farrer et al. (2003a) and Farrer et al. (2003b) applied angular perturbation to joystick movements involving the hand a wrist. The sizes of perturbations used varied from 5 -50-degrees. Due to the nature of this type of perturbation the lateral deviation of the visual feedback from the actual limb position increases as movement length increases. Therefore whilst a 50-degree angular perturbation will produce a lateral shift of approximately 60mm over a 50mm movement for a larger movement of 220mm the lateral shift would be 260mm (figure 2.1).

Figure 2.1: Schematic representation of a linear perturbation. The lateral shift increases with distance through the movement. Therefore smaller perturbation sizes are required for large compared to small movements to obtain the same size lateral shift at endpoint. The solid line depicts the actual movement trajectory and the dashed line depicts the cursor trajectory.

Because the current set of experiments uses large reaches (using the full limb) smaller perturbation sizes were required than used by Farrer and colleagues (Farrer et al., 2003a, Farrer et al., 2003b). The purpose of the current experiment is to determine which size perturbations would be most valuable in order to investigate agency attribution and this was achieved by investigating the effects of Gaussian training on self/other judgments to an array of perturbation sizes. The aim of the current experiment was to detect a size of perturbation applied to full arm reaching movements, the responses to which were most sensitive to experimental manipulation. Such perturbations can be used for future experiments, so that any slight alterations to the experience of agency are likely to be detected.

In the current experiment participants were required to take part in a self/other judgment task taken in two separate sessions with an array of randomly presented perturbation sizes. Before each session, however, was a training period in which the participants were asked to make reaching movements that were similar to those used in the main task. In the training period participants were informed that the feedback was always self, however, in one training session the feedback was veridical, (an accurate representation of the actual movements), whilst in the other session noise was introduced to the trajectory of the feedback by applying small perturbations selected from a Gaussian distribution. Planned comparisons were conducted between the two sessions at each perturbation size in order to determine which perturbations were affected by the type of training.

Method

Participants

A sample of six participants was used consisting of five females and one male with a mean age of 25 years (age range 24-26 years). All were right handed and had normal or corrected to normal vision.

Materials

Participants were seated in front of a horizontal mirror (450x300mm) placed on a wooden board 300mm above a 900x900mm table. A projection screen (800x540mm) was suspended horizontally 300mm above the mirror. A Mitsubishi 750 projector was also suspended a further 910mm above the projection screen. Thus, the image projected onto the screen appeared to the participant to be in the same plane as the table surface (see Figure 2.2). Hand movements were recorded at 240Hz by an electromagnetic sensor (Polhemus Liberty) attached to the index finger of the reaching (right) hand. A circular plastic disc (10mm diameter) attached to the leading edge of the table was used to mark the start point and a life-sized projected colour image of the experimenter’s (female) hand positioned in a pointing posture (extended index finger) was used as a representation of the participant’s own hand.

Figure 2.2: Schematic representation of experimental set up. When looking into the mirror, images projected into the upper screen appear to be in the same plane as the table surface. Thus, an unperturbed image of a virtual hand appears to be in the same location as the participant’s actual hand.

Procedure

Participants sat at the table and looked down into the mirror in which they could see a black screen (a reflection of the image from the projector on the projection screen). Participants placed their index finger on the start position with their hand in the same posture as the image that represented their movements (a pointing posture) and were required to return to the same start position at the end of each trial. At the beginning of a trial a red target bar appeared for 500ms (bar: 160x20mm, with the inner edge 40mm from the midline and 300mm from the start point). Immediately following removal of the target bar image a tone indicated to the participant that they should make a unimanual reaching movement with their right hand towards where the target bar had been. In one fifth of the trials the trajectory and velocity of the virtual

hand was an accurate representation of the actual movement (calculated online using position data from the motion tracker on the index finger of the actual hand, delay <10ms). In the remaining fourth fifths of the trials the trajectory of
the virtual hand was perturbed from the actual hand-path by an angular perturbation, either 4, 8, 12 or 16-degrees all of which were presented equally and randomly with the unperturbed trials. These linear perturbations were created using with the following equation:

$Xc = Xa + Ya\tan(P)$

In which Xc refers to the X position of the cursor, Xa refers to the X position of
the actual movement Ya refers to the Y position of the actual movement and P is the perturbation size (0, 4 or 16-degrees).

At the end of each reach the participants were required to make a verbal judgment as to whether the virtual hand trajectory was perturbed (self) or not (other). Each participant took part in two separate experimental sessions, each consisting of 120 trials (24 of each perturbation size – 12 leftward and 12 rightward) conducted one day apart, the order of which was counterbalanced between participants. In both sessions participants took part in an identical agency task, prior to which was a training period. Both training periods

consisted of 40 reaches completed in the same procedure as the reaches in the agency task. In one of the training periods the trajectory of the virtual hand was
always an accurate representation of the actual movement (zero degree perturbation or self). In the other training period, however, noise was added to

the reach in the form of small linear perturbations selected from a Gaussian distribution (mean=0, standard deviation=4). Participants were informed that the training period was to obtain standardised reach trajectories and no self/other judgments were required as there was no manipulation.

Results

Each participant’s results were converted into mean percent self-score (self was

the correct judgment for ZERO but incorrect for all other perturbation sizes) at

each perturbation size for the agency tasks following both perturbed and unperturbed training periods. A 2x5 repeated measures ANOVA was conducted with the factors TRAINING (GAUSSIAN and NON-GAUSSIAN) and PERTURBATION (ZERO, FOUR, EIGHT, TWELVE and SIXTEEN). No significant main effect was found of TRAINING (F(1,5)= 1.62,p=NS). A significant main effect was found of PERTURBATION (F(4,20)=51.91,p<0.001) and no significant interaction was found (F(4,20)=1.98,p=NS).

Planned comparisons were conducted between PERTURBED and UNPERTURBED TRAINING for each PERTURBATION. No significant differences were found at the level of ZERO (F(1)=0.24.p=NS), EIGHT (F(1)=0.21.p=NS), TWELVE (F(1)=0.6.p=NS) or SIXTEEN (F(1)=0.09.p=NS)

degree perturbations. A significant difference was found at the level of the FOUR degree perturbation (F(1)=7.79,p<0.05) with percent self-judgements being greater following the GAUSSIAN (mean=84.83%) than NON-GAUSSIAN (mean=72.22) TRAINING (see Figure 2.3).

Figure 2.3: percent self-judgments for all five perturbation sizes for GAUSSIAN (filled squares)

and NON-GAUSSIAN (open circles) training periods. The larger the perturbation size leads to fewer self-judgments. The asterisk denotes a significant difference revealed by the planned comparisons. Error bars show standard error.

Discussion

The type of training made no difference to the percent self-score for any of the perturbation sizes except for the 4-degree perturbation at which training with Gaussian noise lead to an increase in self-judgments. Therefore, it appears that with this size of perturbation the feelings of agency can be readily influenced by experimental intervention. The reason for this could be because the participants find detection of the 4-degree perturbation difficult even with no Gaussian training. In the no training condition the percentage of self-judgment was in excess of 70% for the 4-degree perturbation so that even in normal

circumstances, a discrepancy of this size is insufficient to consistently produce an other judgment. Following Gaussian training in which self feedback is manipulated to vary from the actual self movement, the detection of the 4degree perturbation is reduced further, with participants giving a correct other judgment less than 20% of the time. However, self-judgments given in response to visual feedback perturbed by 4-degrees are fewer in number in comparison to that of the unperturbed trials demonstrating that detection of such perturbations is not impossible. Therefore, from the current results it could be argued that introduction of such a small perturbation to the visual feedback introduces an element of uncertainty to judgments of agency and as a direct result of this uncertainty that allows such judgments to be easily manipulated.

In relation to findings by Farrer et al. (2003b) who also used several perturbation sizes in a similar self/other judgment task using angular perturbations, the data takes on a similar pattern. The greater the size of perturbation leads to fewer self-judgments. The largest perturbation sizes producing close to 0% self-judgments, whilst the unperturbed trials gave rise to a percentage surpassing 90%. Aside from the 4-degree perturbation the difference in percent self-judgments for all other perturbation sizes following the different training sessions did not approach significance. Therefore, for the following experiments it was decided that in addition to the 4-degree perturbation, for which agency is uncertain, to select the 0-degree perturbations, to which participants responded consistently self and the 16degree perturbation, for which participants responded consistently other.

Section 1

AGENCY ATTRIBUTION AND THE RIGHT HEMISPHERE

Chapter 3

Lateralisation of Agency in a Patient with Callosal Agenesis.

3.1: Introduction

Functional imaging has implicated brain regions in the right hemisphere for the successful discrimination between actions made by the self and those made by other people. For example, Farrer et al. (2003a) tested a sample of neurologically intact participants making joystick movements in a scanner while measuring brain activity using positron emission tomography (PET). Participants were given visual feedback of their movements by the presentation of a virtual hand and joystick on a mirror positioned in front of their moving hand so that the virtual image appeared to be in the same spatial plane as the actual hand and joystick. In some trials the visual feedback deviated from their actual movements by 25, or 50 degrees (defined as other) while the remaining trials were left unperturbed (defined as self). The results of this experiment revealed an increase in blood flow to the right inferior parietal lobe (rILP) when participants made other judgments and an increase in blood flow to the insula (primarily right hemisphere) when participants made self-judgments. The PET study was a follow-up to a previous functional magnetic resonance imaging (fMRI) study that also highlighted the involvement of the anterior insula and rIPL for self vs. other generated movements respectively (Farrer and Frith 2002).

Further evidence for right hemisphere dominance in the sense of agency comes from neuropsychology. Symptoms following right hemisphere damage frequently involve disorders of self-awareness. Such disorders include: hemispatial neglect, a disorder in which a patient is unaware of the side of space contralateral to the lesion, often including their own body parts (Driver and Mattingley 1998); anosognosia, in which the patient is unaware of their contralesional disabilities (for example their hemiplegia) (Paysant et al. 2004, Jehkonen et al. 2006) and asomatognosia, in which patients can deny ownership of their own limb (Pia, et al. 2004,). Another patient group with a disrupted sense of agency are those presenting with passivity (delusions of control). This is one of the first order positive symptoms in schizophrenia and involves the patient believing that his or her actions are being controlled or influenced by an external agent. This specific symptom has been associated with abnormal activity in the rIPL. For example, Spence et al. (1997) observed hyperactivity in the rIPL using PET in schizophrenic patients experiencing passivity compared to patients without this symptom and a non-schizophrenic control group. This specific patient group has also been found to have reduced cortical volume in the rIPL (Maruff et al., 2005).

There are, however, also some studies providing evidence for a connection between agency attribution and the left hemisphere. Sirigu et al. (1999) found patients with left inferior parietal damage to be impaired on a self/other discrimination task. In this experiment participants were required to make postures with their fingers behind a mirror on to which an image representing their movements was projected so that it appeared to be in the same spatial position as the actual hand. The image was either the participant’s own hand

(self) or the hand of the experimenter (other). It was found that when the image was other (experimenters hand) and the posture was incongruent to the actual posture, all participants answered correctly. However, if the action of the hand presented on the mirror was congruent with the intended action, significant errors were observed in which patients with left parietal damage were more likely to misattribute the action produced by the experimenter to self. This was apparent even when the participant’s own action failed to successfully produce the desired posture, therefore making the feedback incongruent with the actual actions. However, producing finger postures involves very small movements and the postures themselves are often meaningful (e.g. cross fingers for good luck). This, therefore, may have resulted in the emphasis of the task to be weighted towards the final position of the fingers (posture), rather than the actual movement itself. It has been suggested in previous studies that the left hemisphere is involved with representing movement of our own body parts. Tomasino et al. (2003) identified patient M.T., a 49 year old man with a large left hemisphere lesion following a stroke, who had difficulty performing tasks involving mental rotation of images of his own hands, particularly when performing finger postures (e.g. victory sign). Moreover, patients following left hemisphere damage (specifically the left IPL) have been found to have disorders of praxis, involving movement production and execution (e.g. Goldenberg, 2001). This deficit seems to be particularly pronounced with movements involving a high degree of precision and coordination of independent finger movements (Hanna-Pladdy et al., 2002) such as those required to make finger postures. Therefore, the findings of Sirigu et al. (1999)

could be explained by a deficit in movement production or representation rather than a deficit in a sense of agency.

Another study by Macdonald and Paus (2003) looked at delay detection of finger movements following application of repetitive transcranial magnetic stimulation (rTMS) to the left superior parietal lobule (SPL). Participants were subjected to two sessions of 15 minute low frequency (1 Hz) rTMS. In one session the TMS coil was positioned over the experimental site (left SPL) whilst in the other session the coil positioned over a control site (secondary auditory cortex in the left temporal lobe). Participants were then required to make active and passive finger movements whilst wearing a data glove, from which online accurate representations of hand and wrist movements could be relayed on to a virtual hand displayed on a computer monitor. In all trials movement onset of the virtual hand was temporally asynchronous with the actual movement onset, the size of which was variable between trials (60 - 270ms pre or post actual movement onset). The task of the participants was to indicate whether or not they had detected a delay between their actual movement and that of the virtual hand. It was found that compared to the control site, rTMS to the left SPL reduced the participants ability to detect the smaller delay sizes with active movements. This difference was not observed with passive movements, indicating that the effect of TMS was not a general impairment of visual processing of movement, but specifically an impairment of processing self-generated movements. Disrupting the left SPL with rTMS reduced participant’s ability to detect when the virtual hand was not accurately reflecting the temporal aspects of their own movements and as a result implicates this area in the attribution of agency.

However, these results could again be explained by a deficit in movement production. Because reaction times were not recorded it is unclear as to whether the TMS had affected action execution mechanisms associated with this region (Goldenberg, 2001) opposed to mechanisms involved in agency attribution. Disrupting the execution of movements in this way, would of course only have affected active and not passive movements, which were executed by the experimenter (moving the participants finger).

Callosal Agenesis

A method frequently used to investigate the hemispheric asymmetry of function is to observe patients who have a damaged or absent corpus callosum. The corpus callosum is responsible for the transfer of cortical information between the cerebral hemispheres. Cases in which this is disconnected (by surgery) or absent (by agenesis) allow stimuli to be presented both visually and (to large extent) proprioceptively to an individual hemisphere (Gazzaniga, 2000). Each hemisphere processes information from the contralateral visual field (see Figure 3.1), so when an acallosal individual fixates on a central point a visual stimulus presented to the left of centre is processed by the right hemisphere and a stimulus to the right of centre by the left hemisphere. Unlike with primates (Gazzaniga, 1965), this complete absence of visual information to the ipsilateral hemisphere is apparent with humans, even with a fully intact anterior commissure (Seymour et al., 1994).

Figure 3.1: Schematic representation of lateralisation of the visual field. The left hemisphere processes information from the right hemifield, whilst the right hemisphere processes information from the left hemifield.

The processing of information from the muscles in the limbs is also largely lateralised as sensation perception by the ipsilateral hemisphere is found to be significantly reduced under normal conditions. For example, Stein et al. (1989) examined intensity ratings of heat stimuli presented to a patient (J.W.) with complete corpus callosum separation following surgery. When presented ipsilaterally to the responding hemisphere, J.W. rated the stimuli as significantly less intense than when presented to the contralateral hemisphere and to ratings made by a control group. However, these differences disappeared at the higher temperatures when the sensations were highly intense and noxious. The current experiment involved reaching under normal conditions, therefore it is anticipated that sensory information from the reaching limb was largely unavailable to the ipsilateral hemisphere. A disconnected hemisphere can, however, control both arms in reaching movements, although dominance over the contralateral limb is still maintained for precise and complex movements (Gazzaniga, 2000). The current experiment uses full arm reaching movements, therefore, each hemisphere should successfully be able to guide the ipsilateral limb to a contralaeral visual target whilst fixating. This means that any effects observed are unlikely to be a result of deficits in action execution which may have been a factor using more intricate finger movements.

The current experiment tested patient T.C.A., a 65 year-old male born without a corpus collosum. T.C.A. only became aware of his callosal agenesis at the age of 61 years following routine scans to investigate persistent chronic headaches. Prior to this point he had no inclination of his condition, with no obvious symptoms and an IQ score within the normal range (117). The current study tested T.C.A.'s performance on a self/other judgment task when visual information was exposed to either his right or his left hemisphere. T.C.A. was required to make unilateral reaching movements with each hand, either whilst fixating on a central point or with free gaze allowed. Visual feedback about the movement of his index finger was given in the form of a cursor presented using a projector and mirror set-up (see Figure 2.4) so as to appear in the same spatial location as his actual finger (vision of his real limb was occluded). At the end of each movement T.C.A. had to make self/other verbal judgments as to whether visual feedback of his movements was either an accurate representation of the actual movements (self) or had an angular spatial perturbation applied (other). T.C.A.'s callosal agenesis allowed the comparison of task performance of the separate hemispheres. It was predicted the isolated left hemisphere (right hand reaching in the right hemifield while fixating) would perform below that of a control group whilst performance of the isolated right hemisphere (left hand reaching in the left hemifield while fixating) would not. In all other conditions no such pattern was expected.

3.2: Method

Participants

Patient: One male 65 year-old participant with callosal agenesis (T.C.A.) was recruited. He was right handed, with corrected to normal vision and an IQ of 117. Structural MRI and DTI images show that T.C.A.'s callosal agenesis is complete except for a small anterior connection that serves ventral prefrontal cortex and an enlarged anterior commissure. There are no connections that serve parietal areas (see Figure 3.2).

Figure 3.2: a) MRI images of A -T.C.A. and B - age and gender matched control reveal a clear and complete absence of the corpus callosum for T.C.A.. b) The DTI images of the same participants show the probst fibres, which run from occipital -parietal areas to frontal regions. From these images it appears that there are no connections between the probst fibres and the anterior connections of the corpus callosum or the anterior commissure.

Control group: An opportunity sample of eight participants formed the control group. Two of which were male and six female, with an average age of 23

years (range of 21 -27 years). All were students at the University of Nottingham with normal or corrected to normal vision and all except for one 21 year-old female were right handed.

Materials

The experimental set up was similar to that in Chapter 2 (Figure 2.2) except that the movements were tracked using the miniBIRD 800. Participants were seated in front of a horizontal mirror, raised on a wooden board 300mm above a 900 x 900mm table. Attached to the nail of the index finger of the reaching hand was an electromagnetic sensor from which movements were recorded using a miniBIRD electromagnetic motion-tracking device (Ascension Technologies Corporation) sampling at 86.1 Hz. The experiment was run on LabVIEW 5 using a Macintosh, Powerbook, G3 series computer (233MHz). The image was projected onto a screen 300mm above the mirror using a Toshiba TLP560 projector suspended a further 910mm above it. A video camera was also mounted on the wooden board in front of the participant to monitor eye movements.

Procedure

The participants were required to sit at the table and look down onto the raised mirror where they could see a blank (white) screen (a reflection of the image from the projector on the projection screen). Participants placed their index finger on the start position with their hand in a pointing posture (extended index finger) and were required to return to the same start position at the end of each trial. At the beginning of each trial a red target bar appeared for 500ms

(bar: 160x20mm, with the inner edge 40mm from the midline and 300mm from the start point). The participants were required to make a reaching movement toward where the target bar had appeared. Their movements were represented by the movements of a black cursor that was projected along with the rest of the screen to appear in the same plane as their actual hand movements. The visual feedback they received of the movements was either self (ZERO degree perturbation); an exact representation of the participant's own movements which made up 50% of the trials, or other; their movements perturbed by either a FOUR (25% of trials) or SIXTEEN (25% of trials) degree perturbation. In half the trials the perturbations were linear and in the remaining trials they were curvilinear (see Figure 3.3). All perturbations were angled toward the centre of the screen in order to reduce the likelihood of any peripheral effects.

Figure 3.3: Schematic representation of a) linear and b) curvilinear perturbations. Solid lines represent the unperturbed cursor trajectory. Dashed lines represent perturbed cursor trajectories.

With the linear perturbations, the distance between the actual limb and the cursor increased with movement distance so that at the largest distance

between the two occurred at the end of the movement (see Chapter 2). With the curvilinear perturbations, however, the cursor was in the same position as the actual limb at the start point and target location, with maximum deviation occurring half way through of the reach. The maximum deviation between the actual movement and the cursor position was determined by the perturbation size (0, 4 or 16-degrees) and was reached at the mid point between the start and target location. The cursor trajectory curves away from actual limb position from the start to the mid point and back towards the actual limb position between the mid point and the target location (Figure 3.4).

Figure 3.4: Schematic representation of a curvilinear perturbation in which the position of the cursor relative to the limb is dependent on the distance travelled along the Y axis. The maximum deviation between the cursor position and the limb position (max) occurs at the mid point between the start point (S) and target location (T). The solid line depicts the actual movement trajectory and the dashed line depicts the cursor trajectory.

There were four spatial conditions, two crossed and two uncrossed each performed in a separate block (see Figure 3.5). In the uncrossed conditions the target was presented on the same side as the reaching hand; the left hand reaching to the target in the left hemifield (LHLP) and right hand reaching in right hemifield (RHRP). In the crossed conditions the target was presented on the opposite side of the reaching hand; the left hand reaching in the right hemifield (LHRP) and the right hand reaching in the left hemifield (RHLP).

Start points for the reach were on the same side as target presentation. The four spatial conditions were completed with linear and curvilinear perturbations whilst maintaining central fixation. T.C.A. also completed the task with free gaze allowed. In this condition information was available to both hemispheres so that T.C.A. could act as his own control. Therefore control participants took part in a total of eight blocks (four spatial conditions x two perturbation types) whilst T.C.A. took part in sixteen (four spatial conditions x two perturbation types x fixation and free gaze), all counterbalanced within participants (ABCDDCBA). Each block consisted of eight trials, four self and four other (two 4-degree and two 16-degree perturbations) presented in a pseudo-random order. At the end of each trial the participants were asked to make a verbal judgment as to whether the movement of the cursor was that of self (exactly represented their actual movements) or other (had a spatial perturbation applied). All participants were informed that the trials consisted of 50% self and 50% other.

At the beginning of the experiment there was a short practice session to allow the participant to become accustomed to the equipment and making a self/other judgment. The number of practice trials was purely dependent on the requirements of the individual. All participants gave informed consent and were told they could leave at any point. Any trials in which the cursor representing the movements crossed the mid-line, or a participant moved their eyes (fixation conditions) were rejected and replaced with an identical trial at the end of the block.

Figure 3.5: Schematic representation of the four spatial conditions RH and LH refer to the reaching hand (right and left respectively). RP and LP refer to the location of target presentation. These four conditions were performed with both linear and curvilinear perturbations with central fixation for all participants (eight blocks). T.C.A. also performed these conditions with free gaze allowed (total of sixteen blocks) in which the information was available to both hemispheres.

3.3: Results

Each individual’s responses were converted into percent correct scores (correct judgments were self for ZERO degree perturbations and other for FOUR and SIXTEEN degree perturbations). Scores were collapsed across perturbation type and 95% confidence intervals were calculated from the control group for each condition in order to compare T.C.A.’s scores against them. The experiment had three factors, SPATIAL CONDITIONS, with four levels (LHLP, LHRP, RHRP, RHLP), PERTURBATION with three levels (ZERO, FOUR, SIXTEEN) and for T.C.A. only, EYE MOVEMENT, with two levels (FIXATION, FREEGAZE). The control group demonstrated equivalent performance irrespective of the side of target presentation or hand used performing above chance for both the ZERO and SIXTEEN-degree perturbations, only having difficulty with the FOUR-degree perturbation for which their performance was poor (failing to detect the perturbation).

Uncrossed Conditions

In the fixation LHLP condition (right hemisphere) a significant difference was found between T.C.A. and controls at the ZERO degree perturbation, T.C.A.’s score (87.5%) falling outside and above the 95% confidence intervals of the control group (mean=73.21%). No significant differences were found between T.C.A. and controls at either the FOUR or SIXTEEN degree perturbations (Figure 3.6a). When freedom of eye movement was allowed T.C.A.’s percent correct scores were not found to be significantly different from controls (95% confidence intervals) for any of the perturbation sizes.

While fixating in the RHRP condition (left hemisphere) T.C.A.’s percent correct score was significantly different from controls for the ZERO degree perturbation with T.C.A.'s score (62.5%) falling below the control group's 95% confidence interval (mean=79.46%). No significant difference was found at the FOUR-degree perturbation. A significant difference was also found at the SIXTEEN-degree perturbations with T.C.A.'s score (50%) again falling below the control’s confidence interval (mean=78.57%)(see Figure 3.6b). While allowed free gaze, however, T.C.A.’s score did not fall outside the 95% confidence intervals for any of the perturbation sizes.

Figure 3.6: Graphs depicting percent correct judgments for crossed spatial conditions of control group (open circles) in addition to T.C.A. whilst fixating (black crosses) and free gaze (filled squares). Error bars show 95% confidence intervals. a) LHLP left hand reaching in the left hemifield (both visual and proprioceptive feedback received by the right hemisphere). In the free gaze conditions T.C.A. performed within the control group’s 95% confidence intervals at all perturbation sizes. Whilst fixating, T.C.A.’s scores only fell outside the normal range with the ZERO -degree perturbation, performing better than the control group. b) RHRP right hand reaching in the right hemifield (both proprioceptive and visual information received by the left hemisphere). T.C.A.’s free gaze conditions fell within the control group confidence intervals for all perturbation sizes. Whilst fixating T.C.A.’s performance falls below that of controls for both the ZERO and SIXTEEN -degree perturbations.

Crossed conditions

In the Fixation LHRP condition (Figure 3.7a) T.C.A.'s percent correct score (75%) was significantly greater than the control group (mean=23.43%) for the FOUR-degree perturbation. Whilst T.C.A.'s score (50%) is significantly lower than controls (mean=75%) for the SIXTEEN-degree perturbation. No significant difference was found at the ZERO-degree perturbation. Whilst allowed free gaze T.C.A.’s scores fell within the control group’s 95% confidence intervals for all perturbation sizes.

Figure 3.7: Graphs depicting percent correct judgments for crossed spatial conditions of control group (open circles) in addition to T.C.A. whilst fixating (black crosses) and free gaze (filled squares). Error bars show 95% confidence intervals. a) LHRP left hand reaching in the right hemifield (right hemisphere receives proprioceptive feedback and left hemisphere, visual). In the free gaze conditions T.C.A. performed within the control group’s 95% confidence intervals at all perturbation sizes. Whilst fixating T.C.A.’s scores fell outside and below confidence intervals for the SIXTEEN -degree perturbation, outside and above confidence intervals for the FOUR -degree perturbation, whilst performance was as controls at the ZERO -degree perturbation. b) RPLP right hand reaching in the left hemifield (left hemisphere receiving proprioceptive feedback, right hemisphere, visual). T.C.A.’s free gaze conditions fell within the normal range for all perturbation sizes. When fixating T.C.A.’s performance was as controls for the ZERO -degree perturbation and falls below that of controls at FOUR and SIXTEEN -degree perturbations.

In the fixation (Figure 3.7b) RHLP condition a significant difference was found between T.C.A. and the control group at the level of the FOUR-degree perturbation with T.C.A.'s score (12.5%) being lower than that of the controls (mean=23.43%). A significant difference was also found at the SIXTEEN-degree perturbation with T.C.A.'s score (50%) falling outside and below the 95% confidence interval of the control group (mean=68.75%). No significant

difference was found at the ZERO-degree perturbation. When T.C.A. was allowed free gaze no significant differences were found between his score and the control group for any of the perturbation sizes.

3.4: Discussion

Uncrossed Conditions

T.C.A.'s results in the uncrossed fixation conditions demonstrate a clear dissociation in task performance between the hemispheres. Control participants seemed to have difficulty with this task only when the perturbation was small, with their performance dropping close to chance regardless of the side of presentation for 4-degree perturbations. T.C.A.’s performance in the LHLP condition (visual and proprioceptive information presented to the right hemisphere) was very similar to that of control participants for all perturbations (in fact his performance was slightly better than controls for the zero-degree perturbation). In the RHRP condition, however, (visual and proprioceptive information was presented to the left hemisphere) T.C.A. performed significantly worse than controls for both the 0 and 16-degree perturbations, his performance on which, like for the 4-degree perturbations, was close to chance. These findings support those of previous studies using similar paradigms (e.g. Farrer et al., 2003) indicating that the processes involved with attributing agency to action are lateralised to the right hemisphere.

Crossed Conditions

Due to T.C.A.’s callosal agenesis the RHLP fixation condition allows visual information but not the majority of the proprioceptive information to be available to the right hemisphere. Ipsilateral connections to the proximal muscles of the limbs also allow the right hemisphere to successfully guide the right arm toward the target presented in the left hemifield. Therefore, in this condition, the right hemisphere, proposed to be responsible for attribution of agency, can do so based on visual and efferent (motor command) signals only. The absence of the proprioceptive information appears to have a detrimental effect on performance. Although T.C.A.’s responses are in line with controls for the 0-degree perturbation they fall below the normal range for the 4 and 16degree perturbations.

Previous studies have implicated proprioceptive information to have an important role in attribution of agency. For example, Farrer et al. (2002) conducted a similar study on patient G.L., who suffered deafferentation (loss of proprioceptive feedback) from the nose down. G.L. made self/other judgments of joystick movements, the visual feedback of which was either an exact representation of her movements (self) or had an angular perturbation applied (other). They found that G.L.’s ability to detect the perturbations was significantly reduced compared to controls, suggesting that proprioception is important for the task. In the current experiment there are two key differences between the fixation LHLP and RHLP conditions, that is the hand used (left and right respectively) and that the latter has reduced proprioceptive information available to the guiding (right) hemisphere. The results are not likely to be a consequence of the reaching hand per se, as although there is evidence of a general handedness effect for self-generated movement recognition (Daprati and Sirigu, 2002), it suggests that performance would be higher for the dominant (in this case right) hand. Therefore, if the difference in T.C.A.'s performance between the LHLP and RHLP was simply a function of hand, it would be expected that performance on the LHLP condition would be lower than RHLP, for which the opposite is true. Consequently, the current results not only support the lateralisation of agency processes to the right hemisphere, but also the significance of proprioceptive information in these processes.

T.C.A.'s results for the fixation LHRP condition are more ambiguous. In this condition it is the left hemisphere that receives the visual information

whilst the right hemisphere only receives proprioceptive feedback. If indeed the right hemisphere is solely responsible for attribution of agency, it has no information on which to do this, as all perturbations are applied to the visual feedback, not accessible to the right hemisphere. Therefore, the results would be expected at chance level (akin to the RHRP fixation condition). However, although T.C.A.'s performance is indeed at chance for the 16-degree perturbation (significantly lower than controls) he performs normally for the 0degree perturbation and significantly better than the control group for the 4degree perturbation. These results seem counter-intuitive as in this condition

T.C.A. finds it easier to detect the small 4-degree perturbation than the comparatively large 16-degree perturbation. Therefore, the isolated left hemisphere performs at chance (RHRP fixation) except in the conditions in which proprioceptive information is absent (LHRP fixation) when he is able to accurately discriminate (greater than using both hemispheres and controls)

between the 0 and 4-degree perturbations whilst continuing to perform at chance at 16-degrees.

These results indicate a role for the left hemisphere in the specialisation for detecting small discrepancies between the planned and actual movement. There is a large body of evidence indicating the left hemisphere to be specialised in executing precise movements (Gazzaniga, 2000) and it has been found to have a functional advantage over the right hemisphere for controlling the ipsilateral hand (De Stefano and Salvadori, 1998). Other findings with neurologically intact participants using ERP (Yoshida et al., 2007) and fMRI (Martinez et al. 1997) and also with brain-damaged patients (Robertson and Lamb, 1991) suggest that the left hemisphere has an advantage for the processing of high frequency spatial information. This means that the left hemisphere is more refined in detecting the fine details of a scene rather than the low frequency global features, which could explain the higher performance at detecting the smaller 4-degree perturbation (high spatial frequency) compared to the larger 16-degree perturbation (low spatial frequency).

A further explanation is that these results could be reflecting an advantage of the left hemisphere for detecting temporal discrepancies. Macdonald and Paus (2003) associated the left inferior parietal lobe with the detection of temporal perturbations applied to self-generated movements. In the current study there were two types of perturbation used, linear and curvilinear. Linear perturbations (see Figure 3.3a) involve the cursor (visual feedback representing the movement) trajectory to be rotated by a given angle away from the actual limb trajectory. Thus, resulting in a spatial dissociation between the two, which becomes larger with increasing reach distance, but

importantly, the cursor moves at the same speed and for the same distance as the actual movement. With curvilinear perturbations the distance that the cursor is perturbed away from the actual limb trajectory is also based on reach distance. However, with these perturbations the size of the dissociation between the cursor and actual limb position only increases in the first half of the movement, decreasing back towards the limb in the latter half (total reach distance assumed to be the target location). Therefore, in addition to the curvilinear perturbation producing a spatial discrepancy, the cursor also has to travel a greater overall distance than the actual reach (taking a longer route to the same destination). As a result the cursor moves at a faster velocity than the limb (see Figure 3.8 for example velocity profiles) Consequently, if the left hemisphere has an advantage over the right for the detection the temporal differences, this could have been manifested in the curvilinear trials of the current experiment (results collapsed across perturbation types).

Figure 3.8: Typical velocity profiles from curvilinear perturbations. Grey line represents velocity of the actual movement whilst the black line represents the velocity of the cursor movement. The cursor has a greater peak velocity than the actual movement.

However, why any of the explanations would not be apparent with full proprioceptive feedback (RHRP fixation) is unclear, perhaps the left hemisphere specialises for comparing visual and efferent information, with other afferent signals causing interference. Whatever processes are taking place in this condition they clearly differ from when performing the task with both

hemispheres (free gaze and controls) and when performing with his isolated right hemisphere (LHLP fixation). As such, from the current results it appears that the mechanisms involved in normal agency attribution are based in the right hemisphere. Crucially, when T.C.A. was allowed freedom of eye movements, so that visual information is available to both hemispheres, he performed within the normal range for all perturbation sizes and spatial conditions.

Free gaze conditions

When allowed freedom of eye movements T.C.A. performed as controls, not falling outside of the normal range for any of the perturbation sizes for crossed or uncrossed spatial conditions. Free gaze allowed visual information to be available to both of T.C.A.'s hemispheres regardless of the side of target presentation. Therefore, if right hemisphere is solely responsible for attributing agency, it would have had full access to the visual feedback of the reach even with a right sided target. However, although visual information is available to both hemispheres with free gaze, the same cannot be said for proprioceptive feedback, the majority of which only being available to the contralateral hemisphere. In the fixation RHLP condition the visual information is, like with free gaze, available to the right hemisphere but due to reaching with the right hand, proprioceptive information is not. In the equivalent free gaze condition visual information is also available to the right hemisphere and similarly, due to reaching with the right hand, proprioceptive information is not. However, despite these similarities, T.C.A.'s performance is different in these two

conditions, performance being impaired in comparison to controls when fixating, whilst with free gaze T.C.A. performs within the normal range.

The reduced performance evident in fixation RHLP was interpreted as the result of limited proprioceptive feedback being available to the right hemisphere. However, if this was the case it would be expected that T.C.A.'s performance would also be impaired in the free gaze conditions that involved reaching with the right hand, but these were not the findings of the current experiment. One possible explanation for this is that the drop in performance for condition fixation RHLP is not due to a reduction in proprioceptive signals available to the right hemisphere, but due to the reduced ability of the right hemisphere to control the left hand. Each hemisphere is less able to control movements of the ipsilateral limb compared to control over the contralateral limb. As the visual information required for accurate guidance of the movement (target and cursor) was only availably to the right hemisphere, it is likely that the right hemisphere was controlling the right limb. When allowed free gaze this information was also available to the left hemisphere, which in these conditions, could have helped guide the limb. Therefore, the reduction in performance evident in condition RHLP when fixating, could be the result of

T.C.A. producing a less accurate movement than in the same condition with free gaze, due to the former condition only being able to guide the movement with the ipsilateral (right) hemisphere.
However, disconnected hemispheres have been found to maintain control over movements involving the proximal muscles (such as those in the current experiment), only showing a real deficit with intricate movements using the distal muscles Gazzaniga (2000). Therefore, each hemisphere should

be able to successfully guide the ipsilateral limb in a full arm reaching movement. Moreover, an additional explanation for the results is that in free gaze conditions T.C.A. is allowed to foveate the target, thus making vision more dominant in that task. When maintaining central fixation, the target appears in the visual periphery, so the emphasis of the task is shifted away from vision and proprioception becomes more important. Previous studies have found that the relative contributions of visual and proprioceptive signals in the
guidance of human movement can vary dependant on the emphasis of the task (Warren and Schmitt, 1978). In the current study when T.C.A. is fixating, the visual feedback that appears in the periphery is less useful compared to with free gaze and therefore increases the importance of proprioceptive signals.

General Discussion

The lateralisation effect observed in T.C.A. supports the functional imaging evidence by Farrer and colleagues (Farrer et al., 2002 and Farrer et al., 2003) as well as the majority of the neuropsychological data implicating a right hemispheric dominance for self-awareness and agency attribution. However, such findings do seem to contradict those studies implicating the left hemisphere in a sense of agency due to T.C.A.'s isolated left hemisphere only performing at chance level. For example, MacDonald and Paus (2003) found interference in the detection of temporal perturbations applied to self-generated
movements apparent following left parietal rTMS. This could be explained by the latter experiment disrupting movement production mechanisms as already discussed, or there is an additional explanation for the results for which the different laterality effects are dependent on the type of perturbations used. In

the experiment by MacDonald and Paus (2003) the movements were perturbed temporally with the movements of the visual feedback (virtual hand) commencing prior to or post actual movement onset. The studies demonstrating right hemisphere involvement, however, including the current experiment used spatial perturbations to create the other movements.

Processing of spatial information has long been associated with right hemisphere regions (e.g. Perenin and Vighetto, 1988), whilst temporal aspects of movement, such as movement sequencing and temporal binding of spatial information, have been associated with the left parietal cortex (Weiss et al., 2006). Therefore, it is possible to explain these findings, not in terms of the feeling of agency, but in terms of the detection of visual-kinematic discordance between the seen and felt position of the hand, for which the right hemisphere specialises in detecting spatial discordance and the left, temporal. Lateralised deficits in spatial processing have been found previously in patients with callosal agenesis. Martin et al. (1985) found an acallosal patient to have difficulty in localising a dot presented visually right of fixation (left hemisphere). Presentation to the left of fixation (to right hemisphere), however remained unimpaired. Similarly Meerwaldt (1983) found an 8 year-old girl with callosal agenesis to have impaired spatial processing of tactile information with the right but not left hand (rod orientation test). Therefore, T.C.A. may have a general spatial impairment when using his isolated left hemisphere, which reduced his ability to detect the spatial perturbations in the RHRP fixation condition.

The majority of neuropsychological evidence, however, finds disruption of self and body awareness to occur following damage to the right

hemisphere. Such disorders have been specifically related to damage of the rIPL (Driver and Vuilleumier, 2001), the same area at which activation has been observed when completing a spatial agency task (Farrer et al. 2003a). Therefore, it seems more likely that this area is involved in feelings of agency and agency attribution than its left hemisphere counterpart. Following on from this, there is a further explanation that can account for both left and right hemisphere involvement in agency, for temporal and spatial aspects respectively. There are two components of a movement from which feelings of agency can derive. Firstly, movement initiation, which can be related to temporal perturbations, whether the time at which you feel that you have initiated a given movement, matches the movement onset of the visual feedback and which may be associated with left hemisphere structures. Secondly, there is the feeling of agency during the movement, whether the visual feedback accurately represents your actual movement trajectory. This is more likely to depend on spatial aspects of the movement and it consequently it is likely to be this aspect of agency that is associated with the right hemisphere.

3.5: Conclusions

The findings from the current study show a clear dissociation between left and right hemisphere performance in detection of the spatial perturbations applied to self-generated movement. T.C.A.’s right hemisphere performed as controls, whilst his left hemisphere performed at chance level. This therefore, suggests that mechanisms involved with self/other attribution of movement to be lateralised to the right hemisphere. Previous studies investigating self/other attribution of movement have identified the right inferior parietal lobe to be

activated during detection of other movements (e.g. Farrer et al., 2003a) and neuropsychological evidence has also associated this area with self-awareness and experience of agency (e.g. Pia et al., 2004, Spence et al, 1999). However, there have also been left hemisphere associations with agency tasks using a different (temporal perturbations) paradigm. This can be explained by, the left and right hemispheres specialising in to different aspects of agency, action initiation and action during a movement respectively, or it may reflect each hemisphere’s ability to detect different types of visual-kinematic discordance (temporal and spatial respectively). In Chapter 4 the nature of the self/other response in a cursor rotation paradigm is addressed explicitly by introducing a physical dissociation between the visual feedback and the actual movement.

This has the effect of reducing the spatial relationship between the visual and proprioceptive feedback. Therefore, if the participants' responses are based on detection of visual-kinemetic discrepancies only, such a dissociation should reduce detection of the spatial perturbations. In addition, participant's ability to detect perturbations applied to externally generated movements (movements produced by the computer) is examined, so as to assess the likelihood of agency mechanisms being specialised only for self-generated movements.

Chapter 4
Detecting Perturbations

4.1: Introduction

In Chapter 3 the percentage of correct self/other judgments of acallosal participant, T.C.A., whilst fixating on a central point and with free gaze, were compared against a fixating control group. Because of T.C.A.'s callosal agenesis, fixation on a central point allowed for experimental testing of the individual hemispheres. Visual feedback presented left of centre was processed by the right hemisphere whilst that presented to the right of centre was processed by the left hemisphere, with a similar dissociation being present for proprioception (Gazzaniga, 2000). It was found that when fixating and reaching with his right limb to a right-sided target (left hemisphere), T.C.A.'s performance at detecting the perturbations applied to the visual feedback of his movement dropped to chance level. In the analogous right hemisphere condition (left limb reaching to a left-sided target), however, his performance was found to be in line with the fixating control group and his own free gaze conditions (visual feedback available to both hemispheres). This was interpreted to represent a right hemisphere advantage in distinguishing between self and other actions and, as such, was compatible with previous experiments on agency attribution that also associate the right hemisphere with self/other judgments (e.g. Farrer et al. 2003, Farrer and Frith 2002).

However, a criticism of this type of task, making self/other judgment over actual and perturbed visual feedback of self-generated movement (see Chapter 2), is whether or not it is a true reflection of agency. It could be argued

that the detection of the visual perturbations, such as the ones used in the Chapter 2 and Chapter 3, may not be associated with feelings of agency over the action but instead may represent the detection of visual-kinematic discordances. As discussed in Chapter 3, this can also explain the right hemisphere advantage found for detecting spatial perturbations, as the right hemisphere has been found to be specialised for spatial processing (e.g. Perenin and Vighetto, 1988). Therefore, the right hemisphere is likely to have a general advantage for detecting spatial discrepancies. Furthermore, a study by Balslev et al. (2006) examining the brain activation of participants making self/other judgments of actual and perturbed visual feedback of finger movements, found no difference between neural networks activated when the participants actively produced their own movements, compared to when the movements of their finger were passively produced by the experimenter. This could be argued to be the result of the participants basing their judgments, not on agency, but on the difference perceived between the proprioceptive and visual feedback.

In the experiment by Balslev et al. (2006) the spatial relationship between the action and visual feedback was removed, meaning that proprioception would be less useful for the detection of spatial differences. This was achieved by the visual feedback being in a different spatial plane to the actual movements and also the movements of the visual feedback were to the left or the right, whilst the actual movements were either back or forth. However, because the perturbations applied were temporal and not spatial, a direct spatial relationship was not needed to detect the perturbations. The participants only needed to match when they felt their finger moving with

when they saw the cursor moving on the screen, regardless of what direction that movement was in. However, despite no differences being detected in neural activation, Balslev et al. (2006) did find a behavioural difference, in that correct judgments were greater with the active movements. This behavioural difference suggests that the two tasks are not identical, the difference most likely being due to the presence of the efferent signals in the active conditions.

For detection of spatial perturbations a close physical relationship between the action and the visual feedback is likely to be of key importance. Clower and Baussaoud (2000) conducted a study investigating the effects of actual and representational visual feedback on prism adaptation. Prism adaptation occurs when a participant's visual field is optically shifted (normally from wearing prism goggles) so that visual objects or targets appear to one side of their actual location. Therefore, as the participant reaches toward a target, they misreach in the direction of the visual deviation. The error, however, gradually reduces over consecutive trials (reaches toward the target/object) and participants are soon able to reach directly to the target (become adapted). On removal of the visual shift (removing the goggles) the participants again initially misreach on the first few trials, this time in the opposite direction. This is known as the negative aftereffect and demonstrates that the participant had successfully adapted to their optically shifted environment. Clower and Baussaoud (2000) found the aftereffect to be reduced using representational feedback from a computer, compared to when the visual feedback received derived directly from the actual limb (LED attached to the index finger of the pointing hand). The authors interpreted this to be as a result

of the perceived physical relationship between the visual feedback and the actual movements (this being reduced with representational feedback).

The ability to spatially relate the visual feedback to the actual limb position enables more proficient mapping between the limb movements and the consequences of those movements. Therefore, more efficient correction mechanisms can be implemented to the movements, which can explain the greater degree of adaptation observed with such feedback. In this case, if there

is a physical dissociation between the action and the visual feedback it would be more difficult to accurately determine the size of spatial differences, so that correction mechanisms implemented by the motor system would be less precise and spatial perturbations would be more difficult to detect. Therefore, if participants base their self/other judgments over actual and perturbed visual feedback on visual-proprioceptive discordance alone, reducing the physical coincidence of the visual feedback would reduce detection of the perturbations, thus leading to an increase in self-judgments.

However, removing the close physical relationship between the action and the visual feedback also has the effect of moving the visual feedback outside of peripersonal space. Peripersonal space is the multisensory space that immediately surrounds the body (Makin et al., 2007) and previous research has identified differences in processing information from near and far space relative to the body, in both brain-damaged patients (e.g. Cowey et al. 1994) and in neurologically normal participants (e.g. Kaas and van Mier, 2006 and Bjoertomt et al., 2002). An example of the importance of near/peripersonal space in regards to self-processing comes from the rubber hand illusion. The rubber hand illusion is induced by simultaneous stroking of an actual (hidden

from view) and a rubber hand (in view) with the effect of the participants feeling self-embodiment of the rubber hand. For example, the rubber hand illusion has been found to alter perception of the actual limb position so that it is perceived closer to the location of the rubber hand (e.g. Tsakiris and Haggard, 2005).

Lloyd (2007) found that the magnitude of the illusion can be drastically affected by proximity of the rubber hand (visual feedback) to the actual limb (proprioceptive feedback). Participants were subject to the rubber hand illusion (simultaneous stroking of the rubber and actual hand) with the rubber hand positioned in six separate locations relative to the limb (ranging from 175mm - 675mm). The participants were instructed to stop the trial when they felt as though the touch felt to their actual hand was the result of the experimenter touching the rubber hand, and were then asked to rate the intensity of this feeling. It was found that the strength of the illusion declined significantly at a distance further than 275mm away from the actual limb. This was interpreted as when the rubber hand was further than this distance from the limb, it fell outside of peripersonal space and so was less likely to be incorporated as part of self. This suggests that by removing visual feedback of reaching movements outside of peripersonal space, it is likely to dissociate that feedback from self.
Consequently, if the participants are making their judgments on agency opposed to detecting visual-kinematic discordance, this would be likely to reduce the sense of agency, thus leading to an increase in other judgments.

A further possibility for the nature of the task is that the perturbations are detected by comparing the visual feedback to that predicted, regardless of whether the movements were self-generated or not. Parietal areas have been

associated with processing information of occluded moving objects (Olson et al. 2004), which was suggested to reflect processes that are predicting the location of unseen stimuli. Participants lay in the MRI scanner and observed the movements of a virtual ball across a screen in the middle of which was an occluding bar. In one condition the virtual ball was seen to pass behind the occluding bar and re-emerge on the adjacent side. In a second condition the ball travelled up to the bar, then abruptly disappeared to equally abruptly reappear on the other side. Increased activity was observed in the intaparietal sulcus in the occluding compared to disappearing condition. Interestingly, similar to that observed in the agency experiments, this activity was more pronounced in the right hemisphere. However, the right parietal areas similar to that identified in self/other attribution tasks using a spatial perturbation paradigm (Farrer et al., 2003a), have also been associated with disorders specifically involving self-awareness. For example, Spence et al. (1997) observed similar activity in the rIPL of schizophrenic patients experiencing delusions of alien control over their actions, to that observed when detecting spatially perturbed visual feedback applied to self-generated actions (Farrer et al., 2003a), thus suggesting that the same processes are involved.

With self-generated movements, not only does the individual have access to information concerning initial reach trajectory and velocity from observing the action, but also specific knowledge about the intended action from having access to the efference copy of the motor commands that produced the movement. Therefore, it is unlikely that, even if similar prediction processes are used for predicting self-generated, as well as externally generated movement, that the two processes are identical. Access to

the efference copy of the motor commands is likely to result in more efficient predictions in order to attribute that action, or not, to the self. Consequently,
the extra information available to the participants in self-generated movement should result in a higher detection rate of the spatial perturbations, thus demonstrating a general increase in correct judgments.

The current experiment explicitly examined the nature of the spatial perturbation paradigm for judgments of agency. Self/other judgments were made over perturbed and unperturbed visual feedback of reaching movements. In one condition the movements were self-generated and spatially coincident with the participants' actual movements such as that described in Chapter 3. In a second condition the movements were self-generated but did not share spatial coincidence with the actual movements in order to reduce the likelihood of the participants basing their judgments on detection of visual and kinematic discrepancies. Visual feedback was provided in the form of a virtual hand that part way through the reach disappeared behind an occluding bar. In all trials the movements of the virtual hand were veridical with the actual movements up to occlusion and for half of the trials this was also true following occlusion.
In the remaining trials, however, when occluded by the virtual bar, a spatial perturbation was applied to the trajectory of the virtual hand so that when it reemerged
from behind the bar it was to one side of the actual location of the limb. Participants had to make self/other judgments as to whether the visual feedback was an exact representation of their actual movements (self) or had a spatial perturbation (4 or 16-degrees) applied (other). In a third condition, the
task was identical, except that the reaching movements were produced by the computer (participants made no movements). At the end of each trial, the

participants were required to make a perturbed/unperturbed judgment as to whether the movements of the virtual hand had been perturbed from their initial trajectory (perturbed) or not (unperturbed) when they re-emerged from behind the occluding bar. It was predicted that removing the direct spatial relationship between the action and the visual feedback would not reduce the participants' ability to detect the perturbations, but would reduce the sense of

agency over the action so that percentage correct judgments would be lower for the 0-degree perturbation compared to with physically coincident visual feedback. Therefore, planned comparisons were conducted between percent correct judgments for coincident and non-coincident feedback of self-generated actions for each perturbation size. It was also predicted that detection of perturbations would be reduced with computer-generated movements compared to self-generated movements so that percent correct judgments would be lower for the 4 and 16-degree perturbations. Therefore, planned comparisons were conducted between the coincident self-generated movements and the computer-generated movements for each perturbation size.

4.2: Method

Participants

An opportunity sample of 12 healthy participants was collected, consisting of 10 females and 2 males (mean age 24 years, range 19 – 29 years). All participants gave informed consent and were right-handed with normal or corrected to normal vision.

Materials

For the physically coincident feedback the experimental set up was similar to that described in Chapter 2 (see Figure 4.1a). Participants were seated in front of a horizontal mirror (450x300mm) raised on a wooden board 300mm above a 900x900mm table. A projection screen (800x540mm) was suspended horizontally 300mm above the mirror. A Toshiba TLP560 projector was also suspended a further 910mm above the projection screen. Thus, the image projected onto the screen appeared to the participant to be in the same plane as the table surface (see Figure 5.1). Hand movements were recorded at 240Hz by an electromagnetic sensor (Polhemus Liberty) attached to the index finger of the reaching (right) hand. A circular plastic disc (10mm diameter) attached to the leading edge of the table was used to mark the start point and a life-sized projected colour image of the experimenter's (female) hand positioned in a pointing posture (extended index finger) was used as a representation of the participant's own hand. For the perpendicular feedback a second mirror was used to replace the horizontal mirror (45x45cm) and placed at a 45-degree angle from the participants gaze between the wooden board and the projection screen so that the image, when viewed in this mirror, appeared perpendicular (90-degrees) to the participants actual movements (Figure 4.1b). For the externally generated movements the set up was the same as for the coincident condition except that participants were not required to wear a movement sensor as no movements were made (Figure 4.1c).

Figure 4.1: Schematic representation of experimental setup. a) The COINCIDENT conditions, in which visual feedback of the participant's actual movements was projected onto a horizontal mirror so that it appeared in the same spatial plane as the participant's own movements. b) The PERPENDICULAR conditions in which visual feedback of the participant's own movements was projected onto a mirror resting at a 45-degree angle from the participant's gaze so that it appeared in the mirror to be perpendicular (90-degrees) from the participant's actual movements. c) The COMPUTER condition in which the participant made no movements but the movements of the virtual hand were projected to appear in the same plane as the tabletop and were completely controlled by the computer.

Procedure

Self-generated Movements

Participants sat at the table and looked down into the mirror in which they could see a black screen (a reflection of the image from the projector on the

projection screen). Participants placed their index finger on the start position with their hand in the same posture as the image that represented their movements (a pointing posture) and were required to return to the same start position at the end of each trial. At the beginning of each trial a red target bar appeared for 500ms (bar: 160x20mm, with the inner edge 40mm from the midline and 300mm from the start point). Immediately following removal of the target bar image a tone indicated to the participant that they should make a unimanual reaching movement towards where the target bar had been. During the reach, participants saw the virtual hand image pass beneath a virtual occluding bar (440x160mm) before re-emerging on the other side.

Figure 4.2: At the beginning of each trial a red target bar appeared for 500ms and then disappeared again before movement onset. During the reach, participants saw the virtual hand pass beneath a virtual occluding bar before re-emerging on the other side. On 50% of trials the hand was perturbed from its veridical position while occluded by either 4 (25% of trials) or 16 (25% of trials) degrees. At the end of the trial participants made a verbal self /other judgment.

For the first 100mm of the movement the trajectory and velocity of the virtual hand was calculated online using position data from the motion tracker on the index finger and was thus the same as the actual movement (delay <10ms) before becoming occluded by the virtual bar. In half of the trials, following occlusion, the virtual hand continued to accurately represent the actual reach trajectory (‘self’). In the other half, whilst occluded, the image undertook a lateral shift (‘other’) equivalent to a cursor rotation of 4-degrees (25%v of the trials) or 16-degree beginning at the initial start location so that when the hand reappeared its spatial position was to one side of the actual hand position (Figure 4.3). Perturbations were equally divided between leftward and rightward directions. This task was completed with visual feedback that was presented at a 90-degree angle to actual movements (PERPENDICULAR) and feedback that was physically coincident (COINCIDENT).

Figure 4.3: Schematic representation of perturbed hand path. Horizontal solid lines represent edges of occluding bar. The dashed white line represents actual limb trajectory, solid red lines represent perturbed trajectory of visual feedback equivalent to a 4-degree perturbation commencing at the beginning of the movement (demonstrated by the dotted white line). 16degree perturbations were applied in the same way

Externally-Generated Movements

The third condition (COMPUTER) was identical in set up to the COINCIDENT condition in which visual feedback was presented on a horizontal mirror in front of the participant so that it appeared to be in the same spatial plane as the table top. In this condition, however, participants were required keep their hands stationary as the movement trajectories of the virtual hand were completely controlled by the computer. Participants had to decide whether the virtual hand’s trajectory had been perturbed or not during occlusion based on it’s initial trajectory prior to occlusion, for which the participants made a verbal perturbed (4 or 16-degree perturbation)/ unperturbed (0-degree perturbation) judgment.

Trajectory of the Virtual Hand

The computer-generated movements of the hand were pre-programmed into the computer. The Y data points of the reach were calculated using an integrated Gaussian distribution, whilst the X data points were generated by fitting a third order polymodal interpolation on a start, end and central point. Moving the central point towards the periphery (to the right of a right handed reach and to the left of a left handed reach) allowed curvature to be applied to the hand path in an attempt to simulate noise similar to that found in normal, biological reaches (Figure 4.4).

Figure 4.4: Schematic representation of the hand path curvature applied (0, 3 and 9cm) to externally-generated (computer controlled) trajectories of the virtual hand.

In one third of the trials there was no curvature on the hand path, therefore, the central point was in a straight-line position with respect to the start and end points. In another third of the trials the central point was moved 3cm from the straight-line position causing a small curvature to the handpath, whilst in the remaining the central point was moved 9cm from the straight-line position (see Figure 4.4). The 4 and 16-degree perturbations were then applied (or not) to these pre-programmed trajectories.

The tasks were completed in six separate blocks (two of each condition, one reaching with the left hand/ viewing movements of a virtual left hand and one reaching with the right hand/ viewing movements of a virtual right hand) counterbalanced within participants using an ABCCBA design and also counterbalanced between participants. Each of the blocks for both the COINCIDENT and PERPENDICULAR conditions consisted of 48 trials (total of 96 trials per condition), 24 self and 24 other (12 four degree perturbations and 12 sixteen). In the COMPUTER condition, however, each block consisted of 72 trials (total of 144 trials), 36 unperturbed and 36 perturbed (18 four and 18 sixteen degrees). The additional trials present in the COMPUTER condition were to control for the different hand-path curvatures (24 straight, 24, 3cm curvature and 24, 9cm curvature) described above.

4.3: Results

Judgments were converted into percent correct scores with self being the correct judgment for the 0-degree perturbation and other being correct judgment for the 4 and 16-degree perturbation for the COINCIDENT and PERPENDICULAR conditions, whilst perturbed was the correct judgment for the 4 and 16-degree perturbations and unperturbed the correct judgment for the 0-degree perturbation in the COMPUTER condition. The data were then analysed using a 3x3 repeated measures ANOVA with the factors FEEDBACK (three levels, PERPENDICULAR, COINCIDENT and COMPUTER) and PERTURBATION (three levels, ZERO, FOUR and SIXTEEN-degrees).

There was a significant main effect of PERTURBATION (F(1,18)=101.1, p<0.001) with SIXTEEN-degrees (99.58%) having the highest percent correct score, followed by ZERO-degrees (89.17%) and FOUR-degrees (36.%) having the lowest score. There was a significant main effect of FEEDBACK (F(2,22)=9.14, P<0.01) with PERPENDICULAR producing a lowest percent correct score (72.57%) followed by COINCIDENT (75.17%) and then COMPUTER (78.55%). There was also a significant PERTURBATION * FEEDBACK interaction (F(4,44)= 3.17,p<0.05).

Planned comparisons were conducted between PERPENDICULAR and COINCIDENT feedback for each of the perturbations. A significant difference was found at the ZERO-degree perturbation ($F(1)=4.72$, $p<0.05$) with COINCIDENT (90.8%) having a higher percent correct score than PERPENDICULAR (84.03%). No significant differences were found at either FOUR ($F(1)= 0.61$, $p=NS$) or SIXTEEN ($F(1)=0.2$, $p=NS$) degrees.

Planned comparisons were also completed between COINCIDENT and COMPUTER for each perturbation size. A significant difference was found at the FOUR-degree perturbation ($F(1)=10.19$, $p<0.01$) with COMPUTER (46.76%) having greater percent correct judgments than COINCIDENT (36.81%). No significant differences were found at either ZERO ($F(1)=0.03$, $p=NS$) or SIXTEEN ($F(1)=0.05$, $p=NS$) degrees (Figure 4.5).

Figure 4.5: FEEDBACK*PERTURBATION interaction. Participants have higher percent correct judgments at the ZERO-degree perturbation with physically coincident visual feedback compared to visual feedback presented perpendicular to the actual movements. Higher percent correct judgments are also produced by visual feedback entirely controlled by the computer compared to coincident self-generated feedback. The single asterisk (*) denotes significant differences at $p<0.05$, whilst the double asterisks (**) denote a significant difference of $p<0.01$.

4.4: Discussion

Performance on the coincident condition demonstrates a similar pattern to that observed by the control group in the previous chapter, participants performing close to chance with the small 4-degree perturbation whilst performing above chance with the 0 and 16-degree perturbations. When physical coincidence of the visual feedback was removed in the perpendicular condition, however, participants performed normally for the 4 and 16-degree perturbations whilst producing significantly fewer correct (self) judgments for the 0-degree perturbation. Performance on the computer conditions, in which participants had to detect perturbations applied to movement trajectories controlled entirely by the computer, also differed from the coincident condition. For this condition, performance was similar to with self-generated movements for the 0 and 16-degree perturbations, but a higher percentage of correct judgments (perturbed/other) was recorded for the 4-degree perturbation.

Removing the spatial relationship between the actual movements and the visual feedback reduced the amount of self-judgments given to unperturbed (self) visual feedback. These results are in line with the participants basing their judgments on agency as opposed to detecting visual-kinematic discordance. If the participants were basing their judgments on the visual-kinematic discrepancies, removing physical coincidence would make the discrepancies more difficult to detect, thus predicting more self-judgments to perturbed (other) visual feedback. The current experiment, however, found an increase of other judgments given in response to unperturbed (self) visual feedback. In addition to this, some of the participants spontaneously reported to feel less in control of the movements in this condition, which again would not be expected if the judgments were not based on agency.

Detection of visual-proprioceptive discordance is likely to have an effect on the sense of agency. Previous studies testing the performance of deafferented patients on a self/other judgment task over actual and perturbed

visual feedback, found patient performance to be impaired in comparison to control performance (Farrer et al., 2003b and Balslev et al., 2007). However, this had the effect of increasing self-judgments to perturbed visual feedback, suggesting that in the absence of proprioception, the patients were less able to detect the perturbations. Non-physically coincident visual feedback reduces the usefulness of proprioception in the current task, as the actual limb position no longer corresponds directly to the virtual hand. However, in the current experiment an increase in other and not self-judgements was found, which suggests that the change in performance is likely to be the result something other than reduced usefulness of proprioception, such as visual feedback being outside of peripersonal space. In addition, although performance was reduced with the deafferented patients (Farrer et al., 2003b and Balslev et al., 2007), they did not perform at chance level, again suggesting that the task involves more than detection of visual-proprioceptive discordance.

For computer-generated vs. self-generated movement it was expected that more correct judgments would be observed with self-generated movement. This was because more accurate predictions would be made due to the extra information available on which to make such predictions, namely the efference copy of the motor commands. This, however, was not what was found. Judgments for the computer-generated movement show an increase in correct detection of the 4-degree perturbation compared to when the movements were self-generated. This indicates that the predictions made over the computer-generated movements were more accurate, so that when the visual feedback deviated from the predicted path, it was easier to detect. However, a possible

explanation for the current results is that the computer-generated movements had less noise.

In the current experiment an attempt was made to simulate noise of actual reaches for the computer-generated reaches, by applying curvature to the movement trajectory. However, there were only three different sizes of curvature throughout the experiment, all with peak curvature occurring at the same point in the movement. This was not representative of actual reaches, which do not show this systematic, consistent pattern of curvature. It has been found that when reaching between two targets, similar to that in the current study (start point and target), participants normally produce relatively straight hand trajectories. Moreover, when asked to apply curvature to their reaches, the curvature observed is not uniform (Abend et al., 1982) like that applied to the computer-generated movements of the current study. In addition to this, the velocity of the virtual reaches also differed from that of actual reaches, as the virtual hand in the computer-generated condition moved at a constant velocity. Actual human limb movements do not move at a constant velocity, but demonstrate a bell shaped velocity profile (Abend et al., 1982). Therefore, the computer generated reaches in the current study are not equivalent to the self-generated reaches, and it is this lack of noise of the computer-generated movement that is likely to account for the difference in results (perturbations were easier to detect with computer-generated movement). However, the fact that a difference was found in the perpendicular condition suggests that participants were basing their judgments on more than just predictions based on initial reach trajectory, as if this were the case, no difference would be expected as a result of changing the orientation of the visual feedback.

4.5: Conclusions

The current results suggest that self/other judgments over actual and spatially perturbed visual feedback of reaching movements is a useful method for the investigation of agency attribution. The participants in the current study were unlikely to be basing their judgments on visual-kinematic discordance alone, due to the detection of perturbations being unaffected by perpendicular visual feedback (reducing the usefulness of proprioception). Whether or not the task involves prediction mechanisms equivalent to those used for externally generated movements remains unclear due to experimental confounds with the computer-generated movements. However, the reduction in self-judgments with perpendicular feedback suggests that, even if these processes are similar, there is something special about self-generated movement that differs from other forms of motion prediction and allows for the experience of agency. The following experiment investigates this further by examining performance of neurologically intact controls on a similar task with and without TMS over the right inferior parietal lobe (area identified by previous neuroimaging studies – Farrer et al., 2003). Transient disruption in this manner should help, not only to specify brain region more specifically in neurologically normal participants (opposed to the abnormal brain of T.C.A. in Chapter 3), but also to determine the nature of the mechanisms involved.

Chapter 5

Misattribution of Actions Following Right Parietal TMS

5.1: Introduction

Results from previous experiments (including those from Chapter 3) place the neural processes involved in agency attribution within the right hemisphere, specifically implicating the rIPL. For example, Farrer et al. (2003a) and Farrer and Frith (2002) identified activation localised in this area when participants detected a spatial incongruence between their own actions and visual feedback (making an other judgment). Due to disorders involving agency and other forms of self-awareness being associated with the right parietal lobe (e.g. asomatognosia, Paysant et al., 2004 and Schizophrenic delusions of control, Spence et al., 1997) the activation was interpreted as representing a feeling of agency over the movement, although the exact nature of the processes underlying this activation remains unclear.

Previous studies have also found the rIPL to be involved with different forms of self-processing. For example, in an fMRI study by Uddin et al. (2005) participants made self/other judgments over images of faces that were morphed between their own face and that of a gender matched familiar other. Increases in rIPL activations were found to correspond with participants making self-judgments. A later follow up study (Uddin et al., 2006) found that following application of repetitive TMS (rTMS) to the rIPL a significant increase in self-judgments was observed. However, the activity recorded by Farrer et al. (2003) and Farrer and Frith (2002) is likely to reflect a different underlying process than that found by Uddin et al. (2006) due to the increases in rIPL activity being associated with other and not self-judgments. In addition to this, cases of abnormal experience of agency such as schizophrenic delusions of control do not appear to be a result of a general deficit in self-recognition as although some schizophrenic patients have been found to have problems with recognising their own voice (Allen et al., 2004) a similar deficit has not been identified for self-face recognition (Lee et al., 2007), suggesting that self/other judgments over actions involve separate underlying mechanisms to that of self/other judgments of faces.

A further possibility for the mechanisms underlying the rIPL activity observed by Farrer et al. (2003a) and Farrer and Frith (2002) could be that opposed to being responsible for feelings of agency or control over an action, the rIPL detects general incongruence between visual and proprioceptive inputs. There is a large body of evidence implicating the parietal lobes with sensory integration. Single cell recordings in monkey parietal neurons have found an increased firing rate on receipt of simultaneous visual and tactile information (Avillac et al., 2007). This has also been found in humans, not only with visual and proprioceptive/tactile information (Riccardi et al., 2006) as from self-generated movements, but also with sensory integration of different modalities. For example, detecting spatially congruent audio and visual information (picture and bark of a dog) (Dhamala et al., 2007). However, these instances of sensory integration found greater activation in the rIPL when the relevant senses were coincident or congruent, whilst Farrer et al.

(2003a) and Farrer and Frith (2002) observed increased activation when the

visual and proprioceptive signals were conflicting. Moreover, the results of Chapter 4 suggest that participants are not making their judgments solely on visual-kinematic discordance, as reducing the spatial relationship between visual and proprioceptive feedback (proprioceptive feedback is less useful) reduced feelings of agency (self-judgments) opposed to reducing the ability to detect the perturbations (other judgments).

Outlined in Chapter 1 are two main theories of agency, firstly there is the narrative approach in which it was suggested that high-level conscious processes retrospectively infer agency over our actions based on prior knowledge and beliefs (Stephens and Graham, 2000). Secondly there is the comparator model of agency in which low-level mechanisms detect mismatches between the predicted and actual, and the desired and actual state of the motor system (Frith et al. 2000). Recent theorists have suggested that opposed to agency being caused by either high or low-level processes that it is informed by both (Syofzik et al., 2007, Gallagher, 2007). Therefore the activity

of the rIPL observed in the aforementioned imaging studies may reflect either of these processes.

Increased activity of the rIPL has been observed in schizophrenic patients whilst experiencing delusions of control (Spence et al. 2007). Whilst lying in a PET scanner the patients made random movements with joystick, over which they reported to have feelings of external control. Whilst having this experience hyperactivity of the rIPL was recorded in comparison to schizophrenic patients not experiencing delusions of control, and a non-schizophrenic control group. There is evidence in the literature that schizophrenics may have difficulty with both high and low-level agency. For

example, Bulot et al. (2007) conducted an experiment in which the participants were required to stop a swinging pendulum by applying sufficient grip force to a force cell. All participants were instructed to use the minimum grip force possible to stop the pendulum, whilst not letting the force cell slip through their
fingers (not applying enough force). It was found that healthy participants demonstrated an advantage for releasing the pendulum themselves opposed to the experimenter releasing it (less grip force used). The same was not true of the schizophrenic group, who applied a similar degree of grip force regardless of who was releasing the pendulum. This was interpreted as a low-level deficit in using predictions based on self generated actions.

The prediction element of the comparator model is the predicted state representation, which is a prediction of the next state of the motor system based on the efference copy of the issued motor commands, and is compared to the estimated actual next state of the motor system that is based primarily on afferent feedback. The predicted state representation has been connected with imagined movements (Frith et al., 2000) as they not only involve similar networks in the brain (Decety et al., 1994) but also conform to the same constraints imposed on actual movement (Decety and Michel 1989). Schizophrenic patients suffering from passivity on the other hand do not demonstrate these constraints over their imagined movements, suggesting that they have a deficit in motor imagery (Maruff et al. 2003). In addition they have also been found to be impaired in answering questions that require imagining movement (Maruff et al. 2003) and mental rotation of body parts (de Vignemont et al. 2006). Therefore, the activity in the rIPL could be associated with the low-level predictive mechanisms involved in the comparator model.

However, schizophrenic patients also demonstrate abnormal beliefs. The narrative (high-level) approach to agency emphasises a great importance on internal dialogue. This particular process is likely to be disturbed in many schizophrenic patients, because patients suffering from symptoms of passivity often also suffer from, or have suffered from, auditory hallucinations (Jones and Fernhough, 2007). Harvey et al. (1985) suggested that these auditory hallucinations represent a failure to recognise inner speech as being produced by the self. Therefore, disrupted inner speech and abnormal beliefs that are characteristic of schizophrenia suggest that it could be a high and not low-level deficit that is responsible for delusions of control, and is represented by the hyperactivity seen in the rIPL of these patients (Spence et al., 1997). However, the activity observed by Farrer et al. (2003) was found to increase with increasing size of perturbation, which is more in line with a low-level comparator system (detecting larger and larger comparator mismatches) opposed to high-level deficits of internal dialogue (associated more with the left hemisphere, McGuire et al., 1996).

With most previous experiments that attempt to identify the functional properties underlying pre-determined brain activity, it is difficult to differentiate between high and low-level mechanisms. For example, in the rTMS experiment by Uddin et al. (2006), because rTMS involves prolonged exposure to low frequency stimulation (in this case 20 minutes of 1Hz TMS) the neurons underneath the coil are disrupted for several minutes. Therefore these neurons are impaired for the entire task and so it cannot be determined which part of the task is being disrupted. In order to tackle this, the aim of the current experiment was to functionally determine a causal role of the rIPL in

agency attribution, using single pulse TMS. A benefit of single pulse TMS is that it only disrupts the underlying neurons for a limited time period, so as to specifically attempt to disrupt low-level opposed to high-level processes. In a paradigm similar to that used by Farrer et al. (2003a), participants made judgments about full limb movements while receiving TMS (or no TMS) to either rIPL or the vertex. The visual feedback received was either an exact representation of the participant’s actual movement (self) or had a 4-degree spatial perturbation applied (other). Crucially, the TMS was delivered when movement of the hand was occluded from view (i.e. at a time when there was no discordance between the seen and felt positions of the hand), which was also the time when the perturbation was applied (before which the visual feedback was veridical). Therefore an extra burden was placed on the predictive mechanisms at just the time when the TMS pulse was applied, so that if the predicted state representation is located within rIPL, this should be affected by the TMS pulse.

Although the finger was obscured from view for an average of 155ms, total hand occlusion was only achieved for approximately 25ms, restricting TMS delivery to a single pulse. The vertex was chosen as the control site for this experiment as it is a frequently used control site to test for non-specific effects of TMS (e.g. Nyffeler et al. 2006, Muggleton et al. 2006, Bestman et al. 2002). The analogous left hemisphere location, the left IPL, was not used as a control site due to the associations between this location and other (temporal) aspects of agency attribution (MacDonald and Paus, 2003) in addition to its association with movement production (Goldenberg, 2001). Planned comparisons were conducted to test directly whether TMS stimulation

disrupted self/other judgments when applied to the rIPL (and not when applied to the vertex) at a time when spatial discordance could not be detected. Therefore, planned comparisons were conducted at the rIPL and the vertex between TMS and no-TMS trials for both the 0 and 4-degree perturbations.

5.2: Method

Participants

A sample of 10 healthy right-handed volunteers consisting of 8 females, and 2 males with a mean age of 22 years, gave fully informed written consent to participate in the study. All were screened for contraindications to TMS using a self-report questionnaire based on the TMS Adult safety Screen (Keel et al., 1999). The study was approved by the University of Nottingham School of Psychology ethics committee and conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Materials

The experimental set was similar to that in Chapter 4. Participants were seated in front of a horizontal mirror (raised on a wooden board 300mm above a 900x900mm table. A projection screen was suspended horizontally 300mm above the mirror. A projector was also suspended a further 910mm above the projection screen. Thus, the image projected onto the screen appeared to the participant to be in the same plane as the table surface (see Figure 5.1). Hand movements were recorded using a Polhemus Liberty electromagnetic sensor attached to the index finger of the reaching (right) hand. A circular plastic disc attached to the leading edge of the table was used to mark the start point and a

life-sized projected colour image of the experimenter’s (female) hand positioned in a pointing posture (extended index finger) was used as a representation of the participant’s own hand.

A Magstim Rapid TMS machine (the Magstim Company LTD) with double 70mm coil was used to deliver the magnetic pulse to the appropriate areas on the scalp marked out using disposable surgical caps. The coil was placed tangentially to the skull and was set to stimulate at 110% of motor threshold (defined as the minimal TMS intensity required to cause involuntary twitching of the contralateral hand in at least 5 out of 10 trials). For the rIPL condition the TMS wand was positioned 50mm posterior to the motor hand area (Nager et al., 2004) and the vertex was found at the intersection between the naison-inion line and the line between the pre-auricular points.

Figure 5.1: Schematic representation of experimental set up. When looking into the mirror,

images projected into the upper screen appear to be in the same plane as the table surface.
Thus, an unperturbed image of a virtual hand appears to be in the same location as the participant's actual hand.

Procedure

The experimental procedure was identical to that described in Chapter 4 except that movements were only made with the right limb and perturbations of only 4-degrees were used. Participants made unimanual reaching movements towards the previous position of a target bar that had disappeared prior to movement onset. During the reach, participants saw the virtual hand image pass beneath a virtual occluding bar (440x160mm) before re-emerging on the other side (Figure 5.2).

Figure 5.2: At the beginning of each trial a red target bar appeared for 500ms and then disappeared again before movement onset. During the reach, participants saw the virtual hand pass beneath a virtual occluding bar before re-emerging on the other side. TMS was applied on 50% of trials at random while the hand was occluded. On 50% of trials the hand was also perturbed from its veridical position while occluded. At the end of the trial participants made a verbal self vs. other judgment.

For the first 100mm of the reach the movement of the virtual hand was veridical with the actual movement before becoming occluded by the virtual bar. In half of the trials, following occlusion, the virtual hand continued to accurately represent the actual reach trajectory ('self'). In the other half, whilst occluded, the image undertook a lateral shift ('other') equivalent to a cursor

rotation of 4-degrees beginning at the initial start location so that when the hand reappeared its spatial position was to one side of the actual hand position (see Figure 4.3).

In half of the 'other' trials (25% of total trials) this shift was to the left and in the remaining trials it was to the right. Each participant took part in two sequential experimental blocks, one for each stimulation site, the order of which was counterbalanced between participants. Within each block there were 96 trials (192 in total), which were conducted in a pseudo-randomised order (perturbed and unperturbed trials with and without TMS). In half of the trials TMS was applied as a single pulse delivered at the moment the virtual hand became fully obscured behind the occluding bar. In the remaining trials no TMS pulse was delivered.

Participants were informed that visual feedback up to the occluding bar would accurately represent their own movements and that this would also be true in half of the trials following occlusion. It was explained that in the remaining trials, when the virtual hand emerged from behind the occluding bar, visual feedback would be controlled by the computer and would deviate the path of the virtual hand laterally either left or right of their actual hand path.
Participants made their responses verbally: being instructed to respond "self" if they felt that the virtual hand accurately represented their movement throughout the entire reach (i.e. that they were in control of the movement) and

“other” if they felt that the hand path, after re-emerging, had been controlled by the computer. Participants were instructed to move at a comfortable and natural speed. It was also explained that the target bar, which extended across most of the display, was intended only as an indicator of the distance that they

should travel and that there were no directional accuracy requirements. The width of the target bar was such that it prevented participants from using its remembered location as a target to use as an indicator of the relative difference between their intended and actual reach direction. Note, also, that perturbations were in the lateral direction only so that it was not possible to use memory of the distance of the bar to detect perturbations. Participants were aware that the representational image of their hand position was not their own real hand (although one participant did make this mistake).

5.3: Results

Self/other judgments were converted into percent correct scores for each participant (correct judgments were self for ZERO-degree perturbations and other for FOUR-degree perturbations). The data were entered in a 2x2x2 repeated measures ANOVA with the factors STIMULATION (TMS and NOTMS), BRAIN AREA, (RIPL and VERTEX) and PERTURBATION, (ZERO and FOUR-degrees).

There were no significant main effects of STIMULATION (F(1,9)=0.031, p=NS) or BRAIN AREA (F(1,9)=0.909, p=NS). There was, however, a significant main effect of PERTURBATION (F(1,9)=17.183, p<0.01) with mean percent correct judgments being greater for ZERO (mean=76.3) than FOUR degrees (mean=60.4%).

There was also a significant two-way STIMULATION * PERTURBATION

interaction (F(1,9)=12.27, p<0.01), but this interaction was not informative as it used data collapsed across brain areas and can be completely explained by the results of the planned comparisons (see below). There were no significant interactions for STIMULATION * BRAIN AREA (F(1,9)=1.56, P=NS), BRAIN AREA * PERTURBATION (F(1,9)=0.43, p=NS) or STIMULATION

* BRAIN AREA * PERTURBATION F(1,9)=2.794, p=NS.)
Planned comparisons were conducted between the predicted variables of interest (see Figure 5.3) revealing significant differences in percent correct judgments between TMS and NO-TMS over the RIPL for the ZERO-degree perturbation (F(1)=11.96, p<0.01) with percent correct judgments being greater for NO-TMS (mean=81.25%) than TMS (mean=68.75%) trials. A significant difference was also found at the RIPL for the FOUR-degree perturbation (F(1)=6.432, p<0.05) with percent correct judgments being greater for TMS (mean=62.92%) than NO-TMS (mean=53.75%). No difference was found at the VERTEX between TMS and NO-TMS trials for either ZERO (F(1)= .332, p=NS) or FOUR (F(1)=4.3, p=0.07) degree perturbations.

Figure 5.3: Percent correct judgments for ZERO -degree (self) and FOUR -degree (other)

perturbations when TMS was delivered (open circles) or not delivered (filled squares) over rIPL (left figure) or vertex (right figure). Asterisks denote significant differences revealed by planned comparisons.

5.4: Discussion

When TMS was applied over the rIPL, participants were more likely to give a judgment of other (for both present and absent perturbations) compared to when no TMS was applied (that is: percent correct judgments were reduced for the 0-degree perturbation, but increased for the 4-degree perturbation). By contrast, this TMS effect was not observed when stimulation was over the vertex. At first glance these results may seem counter-intuitive given the results of previous imaging experiments using similar paradigms. For example, Farrer and colleagues (Farrer et al., 2003a and Farrer and Frith 2002) reported increased activation in the rIPL when participants made other judgments compared to self-judgments in tasks involving perturbed vs. real feedback of cursor or joystick movements. In accordance with these findings one might expect that disrupting the area thought to be heavily involved in other attribution (rIPL) would lead to a disruption in the ability to make other judgments -and hence an increase in self-judgments. However, if, as suggested in the introduction, the rIPL activity reflects prediction processes within the comparator model, it would follow that disruption to these processes could result in an inaccurate prediction of the next state of the motor system, thus producing more other judgments for both perturbed and unperturbed visual feedback.

Comparator models have been proposed as one of the mechanisms responsible for successful agency attribution and it has been suggested that lesions to the system can result in the abnormal agency attribution seen in, for example, anosognosia and schizophrenia (e.g. Frith et al., 2000). The transient nature of the TMS pulse meant that it is more likely to be these low-level systems, opposed to higher-level conscious processes that were directly affected by the TMS in the current experiment. The comparator model that was proposed by Frith et al. (2000) (see Figure 5.5), explains the activity observed in the rIPL, not as a process for detecting an other movement per se, but detection of a comparator mismatch between the expected position of the limb, and the actual (perceived) position of the limb. Whenever the CNS (central nervous system) plans a movement, a copy of the motor command is generated (efference copy) and this can be used by the CNS to predict the consequences of that movement. Such a prediction mechanism can be used in many ways, but importantly it allows the CNS to anticipate and correct for movement errors, filter expected sensory input and help maintain the estimate of the current state of the motor system. An accurate representation of one’s own current limb position depends on accurate sensory feedback as well as accurate current state predictions. The study by Farrer et al. (2003a) found that the rIPL activity increases with perturbations size, which could reflect the comparator detecting larger and larger discrepancies. Therefore, in terms of the current findings, the TMS may have disrupted the predicted state representation (predicted next state of the motor system); as a result the comparator may no longer have access to what self is, so that even with accurate visual feedback the comparator would produce an other judgment (Figure 5.4).

A unique and important factor in the current study relates to the timing of the TMS pulse: crucially it occurred when vision of the virtual hand was not available to the participant. Correct self/other judgments in a task such as this, requires that the participant accurately predicts where their hand will re-emerge from behind the occluding bar. Occluding the hand for a portion of the reach places an extra burden on predictive mechanisms at precisely the time at which the TMS pulse is delivered. Therefore, it is most likely that it is this predictive process that is disrupted. The comparator model of agency attribution explains schizophrenic delusions of control in a similar way. This suggests that these patients have impaired predicted state representations and as a consequence they perceive a false discordance between the predicted and actual states of their own movement. It is for that reason they feel as though an external agent is controlling their actions even though the intended goal is still achieved (the rest of the system remains intact so that the patient can still successfully construct and execute the desired movement and their intended goals match their perceived outcome).

Figure 5.4: Schematic representation of the comparator model. Frith et al. (2000) explained the passivity symptom in schizophrenia (delusions of control), in which patients perceive self-movements to be produced by other agents, to be a result of impaired predicted state representations. Disruption to the predicted state representation causes the CNS to loose track of what self is so that even when actions are carried out as intended the comparator detects a false discrepancy between the predicted and estimated state representations (comparisons represented by the crossed circles). The current results also demonstrate an increase of inaccurate other judgments as a result of the rIPL TMS, suggesting that TMS over the rIPL is also disrupting the predicted state representation. Figure adapted from Frith et al. (2000).

The misattribution of agency observed in the current experiment mirrors that seen in schizophrenic delusions of control, with participants making more other judgments. As outlined above, the comparator model predicts that disrupting predicted state representations would lead to such an increase in other judgments and as such suggests that it is this element of the comparator process that is disrupted with rIPL TMS.

In relation to previous studies it has been argued that the rIPL activation observed in the Farrer et al. (2003a) study might simply reflect the detection of spatial discordance rather than the sense of agency itself. In the current experiment, however, TMS is delivered at a time at which there is no sensory discordance. The felt position of the limb remains unperturbed and the seen position of the limb is occluded. While the rIPL may indeed be heavily implicated in the detection of sensory discordance, that is not the process that is being disrupted by TMS in the current experiment. Similarly, whilst other, non-action forms of self/other discrimination have been associated with the rIPL, such as self-face recognition (Uddin et al., 2005) they are unlikely to reflect the same processes. Uddin et al. (2005) found increased activity in the

rIPL when making self-judgments, and found rIPL rTMS to produce an increase in self-judgements (Uddin et al., 2006). Farrer et al. (2003a) and Farrer and Frith (2002), on the other hand, found increased rIPL activity when making other judgments with rIPL TMS in the current study increasing other judgments.

It is interesting to note that the planned comparison between TMS and NO-TMS at the vertex stimulation site also approached significance (p=0.07) with perturbations of 4-degrees. The direction of the difference here was in the same direction as the equivalent TMS vs. NO-TMS comparison at the rIPL stimulation site. This probably reflects a general effect of TMS on the frequency of other judgments (that is, participants might generally report 'other' more frequently when receiving TMS regardless of stimulation location). However, unlike rIPL TMS, the difference for 0-degree perturbations at the vertex did not approach significance. Thus, the effect of TMS over the rIPL, which significantly affects responses at both the 0 and 4-degree perturbations, suggests that parietal TMS has an effect that is over and above any general effects of TMS. As a further point of interest, there appears to be a substantial self-judgment bias which can be accounted for as a consequence of the inherent difficulty of the task: previous research (e.g. Farrer et al., 2003b) has demonstrated that whereas participants can easily detect perturbations of around 10 – 15-degrees, they find perturbations as small as 5-degrees particularly difficult and tend to give many more self than other judgments. The high proportion of self-judgments evident in the current experiment could, therefore, be a reflection uncertainty, giving ‘self’ as a default response. Consequently, more self-judgments would be expected if the TMS pulse was simply increasing this uncertainty, the opposite of which was true of the current results with more other, rather than self-judgments being observed.

Relating the comparator model back to the callosal agenic patient (T.C.A.) in Chapter 3, the results are quite straightforward. The bulk of the evidence previously discussed, suggests that agency mechanisms are primarily rooted within the right hemisphere. In which case, in the fixation RHRP conditions (isolated left hemisphere) none of the relevant information is available to the comparator (right hemisphere) so that T.C.A. performs at chance level. However, in LHLP conditions (isolated left hemisphere) all the information is available to the comparator so that T.C.A. performs as controls.

5.5: Conclusions

The result of the current study supports the involvement of a neural comparator in agency attribution and adds further support to the idea that the inability to accurately predict the consequences of self-generated actions underlies delusions of control in schizophrenia. In addition, the data presented here suggest that the comparator’s involvement directly affects low-level sensational aspects rather than higher-level judgments.

The comparator model at present (described above) suggests that self/other judgments are made by comparing the estimated actual state with efferent signals (predicted state representation). However, a recent study by Balslev et al. (2006) identified the detection of perturbations of active (efferent signals) and passive (no efferent signals) movements to involve the same neural networks, which include the rIPL. It would be expected that detecting perturbations applied to passive movements would involve matching visual and proprioceptive feedback, as there are no efferent signals available. However, in the current account of the comparator model, the role of proprioception is limited to the formation of the estimated actual state, with no reference to visual-proprioceptive comparisons that could help explain the Balslev et al.

(2006) findings. The following section attempts to investigate role of proprioception in relation to agency attribution, by examining self/other judgments of perturbed and actual visual feedback with both active and passive movements and relating these findings back to the comparator model.

Section 2

PROPRIOCEPTIVE CONTRIBUTIONS TO AGENCY

Chapter 6
Active vs. Passive Movements

6.1: Introduction

One criticism of the comparator explanation of agency claims that the model overstates the role of efferent signals to the neglect of afferent feedback, particularly proprioception (Synofzik et al., 2007). This type of afferent feedback is especially pertinent in agency attribution as it originates directly from the moving limb. Unlike visual information, which could derive from another agent's actions and be mistaken for being self-produced, any proprioceptive information received could only have self pertained origins. Therefore proprioceptive signals are reliably and unmistakably feedback from the actual (self-produced) movement. One method with which previous studies have attempted to investigate proprioception in agency is through self/other judgments of active (participants move their own limb) compared to passive (the participant's limb is moved by the experimenter) movements. The theory underlying this type of paradigm is that active movements involve full efferent as well as afferent signals whilst the passive movements only involve afferent signals (the same task in the absence of the motor command). According to the comparator model, agency judgments are based on information from the motor command, which is only present in the active conditions, and the absence of which would result in an inability to successfully complete the task. An alternative view (Balslev et al., 2006) suggests that the observed action is compared to proprioceptive information, which is present in both active and

passive conditions, in which case there will be no difference in task performance.

Balslev et al. (2006) used the active vs. passive paradigm in a neuroimaging study in which fMRI analysis revealed no significant difference in recorded activations between active and passive movements. Participants made finger movements on a mouse both actively (controlled by themselves) and passively (mouse was moved, with participants finger on it, by the experimenter). Visual feedback of the participant's movements was provided that was either temporally synchronous (delay< 50ms) or asynchronous (between approximately 260ms pre and 460ms post actual movement onset) with the actual movements. Participants were required to make judgments as to whether the feedback for each trial was synchronous or not with their own movements. They found a behavioural difference in the error rate between the active and passive movements, in that there were more errors recorded for the asynchronous passive trials (participants were less able to detect the delays when the movements were passive). Importantly, the activations evident in the task were similar to those identified in previous agency experiments (e.g. Farrer et al., 2003a and Farrer et al., 2002) predominantly in the right temporoparietal cortex (including right inferior parietal lobe). However, the additional finding of this study is that both passive and active movements produced equivalent brain activity with no significant differences. This means that activity recorded in the brain was of a similar magnitude and location regardless of whether the task involved active or passive movements, thus suggesting that both tasks were completed using the same process regardless of the presence or absence of the motor command. Therefore, Balslev's results do

not support the comparator explanation of movement recognition in which visual feedback is compared to the motor command in order to identify a movement as being produced by the self. The lack of difference in brain activity suggests that both tasks are completed using the same strategy. As no efferent signals are present in the passive conditions this strategy cannot include the motor command.

The passive movements in the Balslev experiment, however, were highly predictable. The movements were tightly controlled to eliminate any confounding variables so that each passive movement was always performed with a straight trajectory at the same distance and speed. A consequence of these controls, however, leaves open the possibility of participants forming anticipatory motor commands and actively assisting the passive movements. Moreover, a spatial dissociation was introduced between the participant's own movements, which were always performed moving away from and back towards the participant, and the visual feedback, which was presented so that the cursor representing their movements traveled either to the left or the right.
The purpose of this translation was to prevent anticipatory saccades (participants did not know whether the movement would be towards the left or right as it varied randomly between trials). However, it may have changed the nature of the task, as there is evidence that movements with similar translations
are processed differently in the brain compared to regular movements. For example, Clower and Boussaoud (2000) found that when visual feedback was not presented so that it shared close physical coincidence to the actual movements, the aftereffect normally following prism adaptation was significantly reduced. The visual feedback presented in the Balslev et al.

(2006) study was also not physically coincident in addition to the aforementioned directional translations applied.

MacDonald and Paus (2003) conducted a similar experiment using rTMS that also looked at ability to detect temporal discrepancies as a function of agency. Participants wore a cyber-glove, which could represent movements of the actual hand on a computer screen. In the active conditions participants were required to extend either their index or middle finger and in the passive conditions the participant's finger was extended by the experimenter. Judgments were given at the end of each movement as to whether the visual feedback was perceived to be synchronous or not with their actual movement (varying delays were applied to the movement onset of the virtual hand). The experiment was performed under normal conditions (no TMS), following rTMS over the left parietal cortex (experimental site) and following rTMS to left temporal cortex (control site). No significant behavioural difference was found in delay detection of active and passive movements. However, rTMS over the left parietal lobe reduced the accuracy of active and not passive movements. These findings implied that there was a difference between the neural networks involved in each task and it was interpreted that this difference
was the efferent signals present in the active conditions. However, MacDonald and Paus stimulated the left parietal cortex, which has been predominantly associated with action execution (e.g. apraxia, Goldenberg et al., 2001) opposed to action awareness (for reviews of see Decety and Chaminade, 2003 and Barresi and Moore, 1996). Therefore, it is possible that the TMS was affecting a different part of the process concerned with producing the active movement rather than feelings of control. The participants may have failed to

successfully produce the planned movement, although, this explanation would also implicate the motor command as being the significant component separating the two tasks.

Farrer et al. (2003b) used the active vs. passive paradigm in a behavioural study using a sample of neurologically intact participants. The participants were required to make joystick movements, the visual feedback of which was either an accurate representation of their actual movement or had a spatial angular perturbation applied. In their experiment they used an array of eight different perturbation sizes (0, 5, 10, 15, 20, 30, 40, 50) all presented in equal proportion of the total trials. For each trial the participants had to identify if the feedback they received was spatially concordant or not with their actual movements (yes or no verbal response). This task was performed both when the participants actively made the movements themselves and when the movements were made passively by the experimenter pulling the joystick forward with a metal rod (whist the participant was holding on to the joystick.)

On average participants became aware of the perturbation (over 50% correct) at the same degree for both active and passive movements. However, they were also more accurate in the active conditions with the larger perturbation sizes. These results suggest that whilst people are more accurate at determining self from other movements when allowed to produce a motor command (active conditions), they can still successfully complete the task when relying predominantly on proprioceptive signals. It could be argued, however, that even in the passive conditions a motor command was not completely absent due to the predictability of the passive movements. The metal rod used to create these movements always pulled the joystick in a straight trajectory towards the top of the screen. This could allow participants to make an anticipatory motor command and even actively assist the passive movement. An attempt was made to control for this by monitoring muscle signals with EMG to ensure that the participants were not assisting the movement. However, this control was only conducted on two participants not included in the actual results and who may have been aware of the purpose of the study and altered their behaviour accordingly.

Other studies, however, have found proprioceptive information to have less of a role in agency attribution. Tsakiris et al. (2005) conducted a study in which participants also had to make self/other judgments over active and passive movements for which they found performance in the passive conditions to drop close to chance level. In their experiment, however, they used small finger movements in which the participant’s right index finger was lifted on a lever that was controlled by either the participant’s own left hand (active) or the experimenter (passive). A key difference between this study and that of Farrer et al. (2003b) is that the actual observed action was always passive. In the active conditions the active element was indirect to the observed action (left hand controlling the lever out of view). Although one benefit of this method is that it reduces the possibility of assisting or producing an anticipatory motor command for the passive movements, which are meant to be completely absent of efferent signals (even in the active conditions a motor command is not made for the right index finger). It immediately presents a problem as the active conditions not only have the extra motor command of the movement, but also extra proprioceptive information from the active left hand as well as the passively moved right index finger. This could mean that the difference in accuracy observed between the conditions may not be completely explained by the additional efferent signals in the active conditions, but could also be explained by the extra afferent information that was available. Moreover, as the participants had extra information in the active condition of exactly when the movement was to commence they could have actively raised their right index finger to assist with the movement. Therefore, in this particular paradigm it is likely that there is substantially more information absent in the passive compared to active conditions than just the motor command.

The nature of other in the Tsakiris experiment also differs from the other aforementioned studies as instead of a perturbed self-produced movement, they used a separate image of the experimenter’s finger undergoing the same action. Therefore, participants would have made a judgment of whether the image presented was that of their own finger moving or the experimenter’s. The task required judgments to be made exclusively on movement onset (temporal discrepancies) because the possibility of spatial discrepancies was eliminated given that the path of the observed index finger would always follow the same rise and fall of the lever. Any trials with grossly deviating other movements were removed thus making the task very difficult. In the other aforementioned studies some of the feedback was also very ambiguous when the perturbations were small, however, this was combined with trials in which the distortions were much more obvious so that the participants could be more confident of their response, opposed to being uncertain throughout the entire experiment, for which case it is arguable whether the participants would ever actually feel a sense of agency. Another consequence of this paradigm is that it does not provide any indication as to what degree of perturbation (spatial or temporal) is still considered self, because the exact amount of deviation between self and other movements was not controlled or recorded.

All these previous studies used relatively small movements, movements of a single finger (MacDonald and Paus, 2003, Balslev et al., 2006 and Tsakiris et al, 2005) or the wrist (Farrer et al., 2003b). Despite the presence of a greater number of muscle spindles in the finger than along the arm, reaches that involve extension the entire arm are more complex with greater degrees of freedom. Such movements involve rotation at the shoulder, elbow as well the wrist (see Figure 6.1). These extra rotations provide further, detailed information about that spatial location of the reaching limb. Therefore, in such instances proprioception may have a greater role in self-identification of action simply because the information obtained is more useful. The current experiment uses full limb reaching movements in order to reduce the likelihood of overestimating the role of efferent signals due to underestimation of the role of proprioception in this way.

Interestingly most of the previous studies, found that the difference between active and passive movements was specifically due to a reduction in accuracy on the passive other trials only. In other words participants were less able to detect perturbed (other) visual feedback when their limb was moved

Figure 6.1: Schematic representation demonstrating the rotations evident in a reaching movement involving the entire limb. Rotation takes place at the shoulder, elbow and wrist.

passively. One exception to this observation is the study by Tsakiris et al. (2005) as they found a reduction in accuracy for both the self and other passive trials. One explanation that can account for this is due to a function of difficulty. All other aforementioned tasks, aside from Tsakiris et al. (2005) used an array of perturbation sizes from very small (difficult to detect) to very large (easier to detect). In the study by Tsakiris et al. (2005), however, any larger discrepancies between self and other were screened for and removed, therefore making the task more difficult, which could have resulted in a difference on the self as well as other trials. However, uncertainty seems to be reflected by a greater number of self-judgments due to the smaller (more difficult) perturbations yielding a large percent self-performance opposed to performance of chance (e.g. Farrer et al., 2003b). The passive conditions in the Tsakiris study do show greater percent correct judgment for self than other, however, this is secondary to a more global reduction in accuracy. Therefore, perhaps this difference in pattern of results reflects a difference in the nature of the task and not just difficulty per se. In all aforementioned studies in which a reduction in accuracy was evident on the other trials only, the passive movements had a degree of predictability (possible anticipatory motor command). This was not the case in the Tsakiris et al. (2005) study, however, in which the active movements had additional information available (aside from the motor command) in comparison to the passive movements. The current study intends to eliminate these limitations, reducing the predictability of the passive movements and controlling for differences between active and

passive conditions in order to gain more insight into the exact role of proprioception.

The current study is the first of a series of experiments attempting to examine how proprioceptive signals contribute to the experience of agency. Participants were required to make self/other judgments over perturbed (other) and unperturbed (self) visual feedback of both active and passive full arm reaching movements. A robot arm motion-tracking device was used in order to track the active movements and produce the passive movements. An attempt was made to control for the predictive nature of the movements in the passive conditions by withholding exact knowledge of reach endpoint prior to completion of the trial (arm could be passively moved to any one of four target locations). Similarly the robot would be inaccurate to a given target by X and Y distances selected from a Gaussian distribution. This not only aided with eliminating predictability but also reduced the possibility of completing the task using visual information only (based on accuracy). For this reason a delay was also introduced between the disappearance of the targets and the movement onset to allow for decay of any target after-image. It was predicted that responses would be far greater than chance for both the active and passive conditions. However, there would be a significant reduction in percent correct judgments of the passive movements but this would be specifically at the larger 16-degree perturbation due to previous studies generally finding any differences on the other (perturbed) conditions, particularly Farrer et al. (2003b) who also used spatial perturbations. To investigate this, therefore, planned comparisons were conducted between the active and passive movements at each perturbation size.

6.2: Method

Participants

An opportunity sample of 12 participants was used (3 male 9 female) with a mean age of 23 years (range of 20 -29 years). All were right handed with normal or corrected to normal vision and gave informed consent to take part in the study.

Materials

Movement trajectories were recorded at 1000Hz using a vBOT 2D robot arm motion tracking device of which the participants had to grasp the handle with their right hand so to fully depress the activation button at all times. Participants were seated in front the robot with a horizontal mirror (1220x580mm) positioned 450mm above the base of the robot handle. A projection screen (1220x840mm) was suspended horizontally 450mm above the mirror and a Toshiba EZ pro 610H projector was also suspended a further 420mm above the projection screen so that the image projected onto the screen was reflected on to the mirror so that it appeared to the participant to be in the same spatial plane as the robot handle (Figure 6.2). The movements were tracked so that visual feedback could be presented to the participant online in the form of a white circular cursor (10mm in diameter) that represented the robot handle (the same location as the participant's actual hand).

Figure 6.2: Schematic representation of experimental set up. Images projected onto the projection screen are reflected in the mirror to appear in the same spatial plane as the actual movements. The robot recorded active movements and produced the passive movements.

Procedure

Active Movements

Before the commencement of each trial the robot arm moved the participant's arm to the predefined start location directly in front of the their midline. Following a delay of 500ms four circular targets appeared, each 30mm in diameter. Two of the targets were 200mm forward from the robot's start position, one to the left and one to the right (both 40mm from the centre of the screen). The remaining two targets were 300mm from the start location (one to the left and one to the right). Three of the targets were red and one was green. The position of the green target varied randomly within the four target locations between trials. After a further 500ms the targets disappeared and were subsequently followed (after 1000ms) by a tone, which indicated for the participant to begin their reach. The participants had 1000ms in which they

were required to reach toward the previous location of the green target with their right hand which was holding on to the robot (Figure 6.3b). In half of the trials the movements of the cursor were unperturbed from the coordinates of the robot's actual trajectory (accurate representation of participant's reach). In the remaining trials, an angular, linear perturbation was applied which rotated the trajectory of the white cursor by either four or sixteen degrees (each making up 25% of total trials) from the actual reach trajectory (half to the left and half to the right).

Passive Movements

The passive conditions were almost identical to the active conditions except that all four targets were red so that the participants were unaware of exactly where the final reach location would be (Figure 6.3a). A further difference was that instead of the participant moving the robot with their reach, the robot arm passively moved the participant's limb. The passive movements were created based on the minimum jerk model of human movement (Flash and Hogan, 1985). This model imitates biological movement by maximising smoothness of the reach (minimises jerk), producing similar velocity profiles to that found in normal reaches. Minimum jerk algorithm:

Timeterm = (15t4 -6t5 -10t3)

t
= t/tf , in which t = time and tf = time at the end of the movement. Timeterm is then substituted for time in to the standard equation for velocity.

Speed = distance / time

tf was programmed to vary between trials and was selected from a normal distribution of movement times with a mean of 700ms and a standard deviation of 50ms. A degree of error for both X and Y coordinates was applied to the end point of each passive reach the distance of which was independently selected from a Gaussian distribution with a mean of 0mm and a standard deviation of 10mm.

At the end of each trial participants had to make a verbal judgment as to whether the movement of the cursor was perturbed (other) or not (self) from their actual movements. The experiment took place in four experimental blocks two active and two passive in an ABBA design that was counterbalanced (ABBA, BAAB) between participants.

Figure 6.3: a) Passive conditions in which all targets were red and movements were created by the robot, using minimum jerk algorithm. b) Active conditions in which participants reached toward the prior location of the green target.

Verbal responses

Participants were informed that in half of the trials the movement of the cursor would accurately represent their actual movements (corresponding to the centre of the robot’s handle they were holding) and in the remaining trials the feedback would be controlled by the computer to deviate laterally either left or right from the actual hand path. Participants gave their self/other judgments verbally responding self if they felt like the cursor accurately represented their movements and other if they felt its trajectory had been deviated from the actual path of their moving limb. These instructions were the same for both the active and passive conditions, participants stating whether or not the cursor accurately represented the actual movements of their limb.

6.3: Results

Responses were converted to percent correct scores for each participant for each perturbation size (self being the correct judgment for a ZERO-degree perturbation and other being the correct judgment for the FOUR and SIXTEEN-degree perturbations). The data were then analysed using a repeated measures 2x3 ANOVA with the factors; MOVEMENT (ACTIVE and PASSIVE) and PERTURBATION (ZERO, FOUR and SIXTEEN-degrees).

There was a significant main effect of MOVEMENT, ($F(1,11)=6.101$, $p<0.05$) with ACTIVE (68.14%) having greater percent correct judgments than PASSIVE (63.29%) (see Figure 6.4). A significant main effect was also found of PERTURBATION ($F(2,22)=212.184$, $p<0.001$) with FOUR-degrees having the lowest percent correct judgments (29.2%) followed by ZERO (78.67%) and

SIXTEEN-degrees having the highest percent correct judgments (87.33%). There was also no significant MOVEMENT * PERTURBATION interaction (F(2,22)=2.71, p=NS).

Figure 6.4: Percent correct judgments for main effect MOVEMENT. Passive movements (open bar) revealing a lower percent correct score than the active movements (filled bar). The asterisk denotes a significant difference and error bars represent standard error.

Planned comparisons were conducted at each perturbation size (Figure 6.5) between ACTIVE and PASSIVE MOVEMENT revealing a significant difference at the SIXTEEN-degree perturbation (F(1)=5.661, p<0.05) with the ACTIVE movements having higher percent correct judgments (92.87%) than PASSIVE (81.53%). There were no significant differences, however, at the FOUR (F(1)= 0.66, p=NS) or ZERO (F(1)= 2.203, p=NS) degree perturbations.

Figure 6.5: Percent correct judgments for 0 (self) 4 (other) and 16 (other) degree perturbations with movements actively produced by the participant (filled squares) or passively produced by the robot (open circles). The asterisk denotes a significant difference. Error bars show standard error.

6.4: Discussion

When the movements were passively created by the robot the error rate for distinguishing between self and other was found to be higher (lower percent correct judgments) compared to when the movements were actively produced by the participant. However, this is predominantly explained by the difference at the 16-degree perturbation, as planned comparisons revealed a significant difference at this perturbation size only. Such results mirror those found in the previous studies. For example, in the Farrer et al. (2003b) experiment in which they also found accuracy of judgments to be significantly reduced in the passive conditions only at the larger perturbation sizes. The current experiment reveals this difference despite using full arm reaching movements with more degrees of freedom from which limb position can be determined.

Another important finding from the current as well as the Farrer et al. (2003b) study, is the accuracy at which participants performed in the passive conditions. Percent correct judgments at the 16-degree passive condition were still well above chance level (>80%) which, similar to the findings of the Farrer study (performance of participants surpassed 50% correct at the same size perturbation for active and passive movements), indicated that the participants can still successfully complete the task in the absence of making a complete motor command and despite the controls for predictability. Accuracy of perceived limb position for an unseen stationary limb decreases over a short time period, only to be attenuated following active or passive movement (Brown et al., 2003). However, when a limb is moved passively there is still a reduction in signal output from proprioceptive receptors compared to when the movement is active (Jones et al., 2001). This marginal difference in receptor output could explain the small behavioural difference found in the current and other previous studies. This would mean that despite a small behavioural difference, the current findings are compatible with the idea of a single neural network for self/other identification of active and passive movement as suggested by Balslev et al., (2006) who also found a similar difference in accuracy. This explanation implies that recognition of our own bodily movement is achieved using the same processes regardless of whether or not we actively planned the movement.

Within the current version of the comparator model the only space for proprioceptive signals is in the formation of the estimated actual state, for which these signals are incorporated along with visual information. In order to make a self/other judgment, the estimated actual state is then compared to the predicted state, created from an efference copy of the motor command (Figure 6.6a). The extra controls incorporated into the design of the current study to prevent the formation of an anticipatory motor command and assistance of the passive movement, (holding back information of the exact end point of the reach through target ambiguity and the addition of error to the reach) help to confidently suggest that proprioceptive information has a role over and above what has been currently proposed in the comparator model. Therefore, in addition to aiding with the formation of the estimated actual state (which is in turn compared to predictions based on the motor command), proprioception is likely to have a further independent role in which signals are compared directly to the visual feedback (Figure 6.6b).

Figure 6.6: a) Comparison between predicted state and estimated actual state found in comparator model (Frith et al. 2000). b) Proposed comparison between proprioceptive and visual signals.

An alternative explanation for the current results, however, is that the participant’s knowledge of limb position is being disrupted by their gaze direction (cursor position). Vision of the workspace adjacent to an unseen limb has been found to enhance knowledge of limb position (Newport et al., 2001). However, when the participant’s gaze is 11-degrees away from the unseen limb, it serves as a distracter, thus leading to greater uncertainty of limb position (Blangero et al., 2005). This effect is found to desist again after a distance of around 20-degrees (Henriques and Crawford, 2000). The difference between the active and passive conditions in the current experiment, is most apparent at the 16-degree perturbation. In this condition the participants are fixating on a cursor 16-degrees adjacent to their unseen limb, which is a prime distance for creating uncertainty of limb position. The active movements could be less affected by the gaze direction due to the additional information available, such as efferent signals and heightened proprioceptive signals, which occur with active movements (Jones et al., 2001). If this explanation were true, a gaze distance of 4-degrees would be expected to aid knowledge of limb position as it is below the critical distance of 11-degrees. However, the percent correct judgments for the 4-degree perturbation were substantially lower than the other perturbation sizes on both active and passive trials, suggesting there is no such benefit. The current results also mirror findings for which no spatial properties were shared between the actual action and visual feedback (Balslev et al., 2006) for which gaze direction would have no such detrimental effect.

6.5: Conclusions

The current findings support the importance of proprioception in self/other attribution of actual and perturbed movements. Participants were successfully able to complete the task in the absence of efference signals (passive movements). However, a noteworthy problem with using an active vs. passive movement paradigm to investigate a sense of agency is that agency is defined as a feeling of being the cause of an action or event (Gallager, 2000). Passive movement by its very nature requires an absence of control and therefore lacks a feeling of agency. It is also questionable whether a difference in behavioural performance on such a task can give a true indication of shared or distinct processes. Balslev et al. (2006) found a significant difference in performance between active and passive movements but no difference in brain activity, whilst MacDonald and Paus (2003) found no difference in behavioural performance but a difference in effect of rTMS. The following chapter, therefore, expands from these results by examining performance on an identical task, comparing correct self/other judgments with normal and disrupted proprioceptive feedback. This will be achieved using a patient with somatosensory loss following stroke and by reducing proprioception in controls using tendon vibration.

Chapter 7

Contributions of Proprioception to the Experience of Agency

7a: Evidence from a Patient with Somatosensory Impairment

7a.1: Introduction

Fourneret et al. (2002) conducted an experiment examining action recognition performance in deafferented patient G.L. Patient G.L. is a middle aged woman who suffered two episodes of sensory polyneuropathy (simultaneous malfunction of a large number of peripheral nerves). This involved the permanent loss of large sensory myelinated fibres in all four limbs, resulting in her almost complete deafferentation from the nose down. In the experiment G.L. and a group of healthy control participants were required to draw a continuous straight line on a graphics pad whilst receiving only virtual feedback of their movements. The visual feedback of their movements had angular perturbations applied, which increased in size (1-degree for each trial) incrementally throughout the trials in a clockwise direction.

The visual perturbation meant that the participants had to deviate their own movement trajectory at an equivalent degree anti-clockwise in order to maintain a straight line with the visual feedback. After each trial they were given a reference sheet with lines drawn at different angles from a start location and were asked to verbally state which line corresponded most accurately with their own actual hand trajectory. Like controls G.L. performed the task accurately, with her performance actually more stable than the control group at the larger perturbation sizes. However, her verbal report indicated that she was unaware of her actual reach trajectory and so unaware of the perturbation. Control participants, on the other hand, realised the deviation at an average perturbation size of 6-degrees.

These findings are interesting as G.L. was still unaware of the deviation in a post hoc version of the experiment with deviations as large as 40-degrees for which she successfully compensated for. Therefore, G.L. was making significant changes to her motor commands yet remained unaware of this, whilst controls with normal proprioception became aware of the mismatch early on in the study. One possible explanation is that although the perturbations became large, each angle was only slightly bigger than the last; therefore, no mismatch of the comparator was significant enough to result in an other judgment. Controls were also unaware of the changes made to their motor command for the same reason. However, as they have normal proprioceptive input they could detect a mismatch between the seen and felt position of their hand and thus became aware of the perturbation. This detection of a proprioceptive mismatch might explain the variability apparent in the control's performance not observed with G.L. An other output from this additional comparison could be preventing the participants from feeling a full sense of agency over the feedback, leading to a reduction of control and accuracy.

Farrer et al. (2003b) examined the feeling of agency more explicitly with patient G.L., recording her judgments as to whether visual feedback of unimanual reaching movements accurately represented her actual movements

or not. G.L. was asked to make movements with a joystick (attached to her right hand) in a predefined direction (either the top, left or right of the screen).
Visual feedback of her movements was presented in the same spatial plane as her actual movements and was either; an exact representation of her movement, or was her movement but with a spatial perturbation applied. Seven perturbation sizes were used including 0-degrees (0, 40, 50, 60, 70, 80 and 90).

At the end of each reach she was then required to make a yes or no verbal response as to whether the movement on the screen corresponded exactly with the actual movement or not. It was found that G.L.'s performance was significantly reduced compared to an aged matched control group lending support to the suggestion that proprioception plays an important role in the task. However, due to limitations of her condition, G.L. had to make the movements with her eyes closed and thus made the self/other judgments based on the final position of the limb rather than the movement itself. This minor alteration could be argued to change the very nature of the task as the judgment

is made only when the limb is stationary and so that self/other judgments are not made in response to the action but the stationary position of the limb.

A further problem with the Farrer et al. (2003b) experiment is that they do not control for effects of movement accuracy. Previous studies have found that in the absence of vision and proprioception, movement accuracy is impaired. Ghez et al. (1995) found that vision of the hand or even a cursor representing the hand on a computer screen, significantly improved accuracy of reaching movements made by deafferentated patients (including G.L.), compared to movements made in the absence of vision. Vision of the limb moving prior to occlusion was also found to aid reach accuracy. This fits in

with the Fourneret et al. (2002) study on G.L. in which she was able to accurately complete the task (drawing a straight line) by adapting her actual movements based on the previous visual feedback, despite not noticing the perturbation. Fourneret at al. (2002) also conducted a second task almost identical to the first except that visual feedback of the beginning of the movement was occluded. Control participants adjusted their movement trajectory after occlusion (feedback was visible) whilst G.L. made these adjustments before receiving visual feedback (during occlusion). This demonstrates that G.L. is more proficient at using prior visual information in order to produce accurate movements (movement planning), likely to be compensatory strategy learnt due to her absence of proprioception. In the Farrer et al. (2003b) study, G.L. had vision of her stationary limb prior to movement onset, but not vision during the movement or of any previous movements. As the accuracy of G.L.'s movements was not recorded it cannot be discounted that she was unable to accurately perform a planned movement. Leaving the possibility that her poor performance on the task was due to execution of the movement and not agency per se.

Farrer's (2003b) result could also be explained by general attentional factors as deafferented patients have been found to have a deficit in dividing their attention between making a movement and an additional cognitive task (in this case making a self/other judgment). Ingram et al. (2000) conducted an experiment on deafferented patient I.W., a 43-year-old male with a complete loss of proprioception below the neck that was a result of an acute large fibre sensory neuropathy at the age of 19. In the experiment I.W. had to make a reaching movement toward a target, attempting to be as accurate as possible.

Trials were completed under normal conditions and with a cognitive load (counting backwards). I.W.'s performance was significantly impaired in comparison to controls in all conditions. Moreover, the effect of the cognitive load was far more pronounced with I.W. than with controls, in that his reach errors, relative to the target, increased by over 60% whilst controls less than 10%. Therefore, it was concluded that in the absence of proprioception, more attention is needed for accurate control of movement. As such, in situations that involve attention to be divided between an action and an additional task, deafferented patients are likely to perform poorly. This again was not controlled for in the Farrer et al. (2003b) study leaving the possibility that the result can be explained by a general attentional deficit.

Baslev et al. (2007) conducted an experiment similar to that of the Farrer et al. (2003) study using deafferented patient I.W., for this study I.W. was now 53, having suffered his deafferentation 34 years prior to the experiment. Balslev and colleagues (2006) used temporal rather than spatial perturbations in an attempt to eliminate errors in movement accuracy as an explanation for the results. An additional control experiment was also included in order to rule out any differences being explained by general attentional factors. In their experiment, finger movements were made on a mouse that was adapted with a constraint so that movements could only be made along the Y axis (eliminate spatial discrepancies). Visual feedback, in the form of a filled white square, was presented on a computer screen in front of the participant, the movement onset of which occurred either synchronously or asynchronously (pre or post) with the actual movement. At the end of each trial the participants had to make a me (synchronous) or not me (asynchronous) verbal response. To

increase the difficulty of the task the movement of the cursor was always in the horizontal plane, randomly to either the left or the right, whilst finger movements were made forwards and backwards on a mouse pad. The purpose of this translation was so that the task could only be completed using the temporal onset of the movement as no spatial properties were shared. A second task was conducted to control for attentional factors and involved the same finger movements but with the cursor jumping to either the left or the right. In this case the participants had to state in which direction the cursor had moved.

The results of the study revealed that I.W. made significantly more errors in the agency task than controls despite no significant difference in movement onset.

In addition, I.W.'s performance was actually better than of controls in the attentional task.

Balslev et al. (2006) claimed that their experiment gave support for the role of proprioception in agency attribution whilst avoiding many of the criticisms of the Farrer et al. (2003b) study. Whilst this may be the case for some criticisms (I.W. performed the task with eyes open and there was no difference found in measured error (reaction time and duration) of the movements), it does not eliminate all alternative explanations. For example, the attentional task may not have truly controlled for all attentional factors. In the experiment by Ingram et al. (2000), in which greater movement errors were recorded in deafferented patients when also completing a cognitive task, I.W. had to attend to the motor component of the task in order to produce an accurate movement, so that although the tasks were separate, each required a significant amount of attention. In the Balslev et al. (2006) experiment, however, the constraint imposed in order to eliminate spatial attributes to the movement also had the effect of reducing movement complexity, meaning that less attention was needed to control the movements, as there were less degrees of freedom over which to control. However, in the agency task, attention had to be paid to the movement in order to make an accurate self/other judgment because the movement made had a direct relationship on the cognitive element of the task. The movements produced in the attentional task, on the other hand, did not require this level of attention, as the movement made had no direct bearing on the task goal (verbal judgment based on direction of the visual feedback, not directly related to the actual movement). Therefore, in the agency task the participants were likely to be consciously attending to their movement in order to inform their verbal judgment, whilst in the attentional task the movements may have been under automatic control allowing full conscious attention to be paid to the cognitive component of the task.

The aim of the current experiment was to compliment the aforementioned studies using patient A.B. a 55-year-old male who suffered proprioceptive impairment due to a thalamic lesion. A.B.'s proprioceptive impairment is central rather than peripheral and as a result affects only the right side (evident from clinical pre-tests), which allowed him to so act as his own control. At the time of testing A.B.'s symptoms had greatly improved, although he still had problems identifying objects placed in his right hand and imitating left limb postures with his right limb. This improvement helps to expand from previous studies as it reduces the aforementioned complications normally associated with complete deafferentation, and in addition, it allows for further insight into the scale of importance of afferent signals, as his proprioceptive input is unreliable opposed to absent. Moreover, a complete absence of proprioception has been found to be particularly detrimental for performing accurate multi-joint actions (Sainburg et al., 1993), therefore, due to A.B.'s deficit being not complete, the current experiment avoids this problem, allowing full arm reaching movements to be used. A.B. and a group of 12 healthy controls made reaching movements with both hands using the vBot 2D manipulandum. Participants had to make self/other verbal judgements over visual feedback of their movements that was either an accurate representation of the actual movements (self) or had an angular spatial perturbation applied (other). It was predicted that A.B.'s performance with his impaired right limb would fall below performance of his unimpaired left limb and that of controls.

7a.2: Method

Participants

Patient: A.B. is a right-handed 55-year-old male who suffered unilateral somatosensory loss of the right upper limb, following a heamatoma within the left thalamus and internal capsule four months prior to testing (see Figure 7.1).

At the time of testing A.B.'s symptoms had greatly improved, although he still complained of numbness and reduced sensation on the right side. On a battery of proprioceptive tests A.B. still had problems with matching the position of his iplilesional (left) limb with his contralesional (right) limb although no problems were observed in the reverse condition. In addition to this he was also found to be impaired on his right compared to left side with two point discrimination and identifying objects that were placed in his right hand (a spoon and a key) although other object were identified successfully (pen, coin and brush).

Figure 7.1: MRI scans of A.B. reveals a small lesion in his left thalamus and internal capsule.

Controls: The control group consisted of 10 healthy participants, 8 female and 2 male, with a mean age of 20 years (range of 19 - 26 years). All participants had normal or corrected to normal vision and were right handed.

Materials

The materials were identical to those in Chapter 6. A vBot 2D motion tracking device enabling online visual feedback of movement to be presented on a mirrored surface so that they appeared in the same spatial plane as the actual movements. (see Figure 6.2).

Procedure

The procedure was identical to Chapter 6 except that all participants completed both active and passive conditions with their left and right limbs in separate blocks (4 conditions in total, completed using an ABCDDCBA design).

Therefore, in summary, participants made reaching movements with the vBOT (robot arm) towards a green target. Their movements were represented by a white cursor, which either exactly represented their movements (50% of total trials) or had a linear perturbation applied, that was either 4 (25% of total trials) or 16 (25% of total trials) degrees. Participants had to make a verbal response at the end of each trial as to whether the cursors movements exactly represented their actual movement (self) or not (other). The experiment was completed in 8 blocks, 4 of which the participant's reach moved the robot (active), whilst in the remaining blocks the robot movements passively moved the participant's arm (passive).

7a.3: Results

Responses were converted to percent correct scores for each participant at each perturbation size (self = correct judgment for a ZERO-degree perturbation and other = correct judgment for the FOUR and SIXTEEN-degree perturbations).

95% confidence intervals were calculated from the control group for each condition in order to compare A.B.'s scores against them. The experiment had three factors; MOVEMENT; with two levels (ACTIVE and PASSIVE), LIMB; also with two levels (LEFT (unimpaired) and RIGHT (impaired)) and PERTURBATION; with three levels (ZERO, FOUR and SIXTEEN).

Active Conditions

In the ACTIVE conditions when A.B. was reaching with his RIGHT (impaired) LIMB (Figure 7.2a) no significant difference was found at the ZERO-degree PERTURBATION. A significant difference was found, at FOUR with A.B.'s percent correct score (0%) falling outside and below the control group's 95%

confidence intervals (23.13%). A significant difference was also found at SIXTEEN, A.B.’s score (68.75%) falling below confidence intervals (89.63%).

Figure 7.2: Percent correct judgments for patient A.B. (open circles) and controls (filled squares) for the ACTIVE conditions. a) RIGHT (impaired) LIMB: A.B.’s scores are significantly lower than that of the control group for both the FOUR and SIXTEEN-degree perturbations. There is no significant difference at ZERO-degrees b) LEFT (unimpaired) LIMB. A.B.’s score is greater for the ZERO-degree perturbation and reduced for FOUR-degree perturbation when compared to the control group. There is no significant difference at SIXTEEN-degrees. Error bars show 95% confidence intervals. Asterisks denote significant differences.

When reaching with his LEFT (unimpaired) LIMB (see Figure 7.2b) A.B.’s percent correct score at the ZERO degree PERTURBATION (100%) was significantly greater than controls (84.29%). At the FOUR-degree PERTURBATION A.B.’s score (12.5%) falls below that of controls (25.65%). No significant difference was found at SIXTEEN.

Passive Conditions

In the PASSIVE conditions when A.B. was reaching with his RIGHT (impaired) LIMB (see Figure 7.3a) his percent correct score at the ZERO-degree PERTURBATION (100%) was significantly greater than controls

(80.87%) At the FOUR degree PERTURBATION A.B.’s score (0%) fell below the controls confidence intervals (29.38%) and also at SIXTEEN with A.B.’s score (62.5%) also falling outside and below 95% confidence intervals (75.63%).

Figure 7.3: Percent correct judgments for patient A.B. (open circles) against the controls group (filled squares) for the PASSIVE conditions. a) RIGHT (impaired) LIMB: A.B.’s score on the ZERO-degree perturbation is significantly greater than controls whilst performance for both the FOUR and SIXTEEN-degree perturbations falls below that of the control group. b) LEFT (unimpaired) LIMB: A.B.’s score is significantly greater than controls for the ZERO-degree perturbation, but reduced for the FOUR-degree perturbation. There is no significant difference at SIXTEEN-degrees. Error bars show 95% confidence intervals. Asterisks denote significant differences.

When reaching with his LEFT (unimpaired) LIMB (see Figure 7.3b) A.B.’s percent correct score at the ZERO-degree PERTURBATION (96.88%) was significantly greater than controls (80.78%) above the 95% confidence intervals. At the FOUR-degree PERTURBATION A.B.’s, score (0%) falls below that of controls (22.86%). There was no significant difference at

SIXTEEN.

Reach Error

Reach error was calculated for A.B. in degrees from the target location with two separate measures endpoint error; defined as the furthest position along the Y axis and error at 25% of the reach defined as 25% of total reach distance. Paired samples t tests revealed no significant difference (see Figure 7.4a and b) between LEFT (unimpaired) and RIGHT (impaired) LIMB for Endpoint error (T(1)= 0.528, p = NS) or error at 25% of the reach (T(1)= -0.823, p =NS).

Figure 7.4: Absolute reaching error for A.B. LEFT and RIGHT LIMB. a) Endpoint error: there is no significant difference between conditions in which A.B. reached with the LEFT (unimpaired) compared to RIGHT (impaired) LIMB. b) Error at 25% of the reach: there is no significant difference between conditions in which A.B. reached with the LEFT (unimpaired) compared to RIGHT (impaired) LIMB.

7a.4: Discussion

All control participants had difficulty detecting the smaller 4-degree perturbation, as their self/other judgments were consistently less than 50% correct. Judgments for the 0 and 16-degree perturbations, on the other hand, reliably produced percent correct scores in excess of 70% for both active and passive conditions. The pattern apparent for A.B., however, is slightly different. When reaching with his right (impaired/contralesional) limb, he performs as expected, his performance dropping significantly below that of controls for both the 4 and 16-degree perturbations with the active and passive trials. In addition to this, however, his performance also drops below that of controls when reaching with his left (unimpaired /ipsilesional) limb at the 4degree perturbation of the active and passive conditions and, in the same conditions, his percent correct scores for the 0-degree perturbation are greater than that seen with controls.

These significant differences observed when reaching with his ipsilesional (left) limb are likely to reflect a deficit in the detection of the smaller 4-degree perturbation, as although in these conditions he appears to have little difficulty in detecting the 16-degree perturbation, he is responding self to almost every this else (high percent correct score for the 0-degree perturbation and low percent correct score for the 4-degree perturbation). With his contralesional hand A.B. also shows this pattern except his deficit in performance also extends to the detection of the 16-degree perturbations as well. Therefore A.B. demonstrates reduced performance compared to controls with both limbs. When reaching with his ipsilesional limb an impairment is only evident in the difficult trials (4-degree perturbations), whilst reaching with his contralesional limb, A.B.’s impairment is evident for both the difficult (4degree perturbations) and easy (16-degree perturbations) trials.

One possible explanation for A.B.’s ipsilesional impairment is due to the age difference, as A.B. is 35 years older than the mean age of the control group. However, A.B. may also have additional impairments as a result of the stroke he suffered four months prior to testing that were not detected by the clinical tests. Afferent neurons that provide feedback from the proximal muscles have ipsilateral as well as contralateral connections (Gazzaniga, 2000).

Previous studies have found evidence for ipsilesional impairment following brain damage particularly in tasks that require monitoring of proprioceptive feedback (e.g. Haaland and Delaney, 1981), similar to those required for the current experiment. Therefore, A.B.'s brain damage may have disconnected ipsilesional connections, as well as those on the contralesional side, the resultant effect being a mild/sub-clinical deficit in his ipsilesional limb, in addition to the observable clinical deficit in his contralesional limb.

In order to clarify the results further, an additional analysis was conducted in which, as opposed to A.B.'s performance being compared directly against the control group, the difference in intra-limb performance was calculated for each participant. This analysis allowed for examination of performance of A.B.'s contralesional/more affected limb relative to his ipsilesional/less affected limb, avoiding any problems of possible sub-clinical deficits. The original data were converted a new intra-limb difference score by subtracting the percent correct score obtained when reaching with the left limb from the percent correct score reaching with the right limb for each perturbation size. This was completed for both A.B. and each member of the control group from which 95% confidence intervals were calculated to help determine if A.B.'s intra-limb differences were significantly different from that expected with controls (see Figure 7.5).

It was found that the control participants did not differ greatly between hands for either the passive or the active conditions and any difference that was apparent was mainly demonstrated by a relative impairment of the left (non dominant) hand (represented by a positive score on the graph). A.B., on the other hand, does not follow this pattern.

Figure 7.5: The intra-limb differences calculated for A.B. (filled bar) and control group (open bar) a) the ACTIVE conditions, A.B. demonstrates a greater difference between his hands than controls, with his right hand performing significantly worse than his left (negative scores) in comparison to controls for all perturbation sizes. b) PASSIVE conditions A.B. demonstrates a greater difference between his hands than controls with his right hand performing significantly worse than his left in comparison to controls for the 16-degree perturbation only. Asterisks denote significant differences, error bars show 95% confidence intervals.

In the active conditions, A.B.'s intra-limb difference in performance was greater than that observed with controls for all perturbation sizes (falling outside control group confidence intervals) demonstrating consistent impairment with his right (contralesional) limb (negative score on the graph). In the passive conditions A.B. also falls outside the control groups confidence intervals but only for the 16-degree perturbation. With 0 and 4-degree perturbations A.B.'s intra-limb differences are no different from that seen with controls.

The control group demonstrated a sizable difference in intra-limb performance for the 16-degree perturbation in the active condition. This difference, however, was in the opposite direction to that observed with A.B., as performance was reduced when reaching with the left limb (positive score on the graph). This difference can be explained in terms of motor dominance as Daprati and Sirigu, (2002) found that participants demonstrated greater accuracy in self-recognition of movement produced with their dominant hand compared to those performed with their non-dominant hand. As the control group and A.B. are all right handed any difference in level of performance would be expected to favour reaching with their right hand. The intra-limb deficits observed with A.B., however, were favouring his left, non-dominant, limb so cannot be explained in the same way.

An additional explanation for A.B.’s intra-limb differences, could be due to deficits in motor production. Ingram et al. (2000) found that deafferented patients had difficulty in distributing attention between making a movement and an additional simultaneous cognitive task (self/other judgment) which was found to result in increased reaching error. This, however, was unlikely to account for the results found with A.B., as he was not fully deafferented and so was unlikely to have this deficit in dividing his attention.

In addition, the results were also unlikely to be caused by a motor deficit of the contralesional limb brought on by his stroke, as no significant differences were found in reach error between reaches of his left and right limbs for either of the measures analysed (25 and 100% of the reach). Therefore, the reduced accuracy of self/other judgments observed when reaching with his right (contralesional) limb is most likely to be a direct result of the reduced proprioceptive feedback received from his right compared to left limb, as evident from the results of the clinical tests. The results, therefore, compliment findings from previous studies (Farrer et al., 2003b, Balslev et al., 2007) in which the absence of proprioceptive feedback was found to also reduce accuracy of self/other judgments. Additionally, however, the current results demonstrate that this effect can occur with reduced as well as absent proprioceptive signals.

Interestingly, the deficits observed in A.B.’s performance were only evident on the perturbed trials, in that he responded self more to perturbed visual feedback. Performance in the unperturbed trials, however, was unaffected, in fact, in three out of four conditions he exhibited a greater percent correct score than seen with controls i.e. responding self more to unperturbed visual feedback. Similar results were also found in the previous studies with deafferented patients giving more self-judgments in response to other visual feedback (Farrer et al, 2003b, Balslev et al. 2007). Therefore, these results suggest that, for high-level self/other judgments at least, proprioception is useful in the detection discrepancies opposed to directly informing the experience of agency.

However, a problem with single subject patient data, which is highlighted by the ipsilesional deficits seen with A.B., is that brain damage can result in numerous additional symptoms that could complicate the results. Therefore, in order to strengthen the current findings the following experiment uses tendon vibration to recreate A.B.’s impairment in neurologically intact participants. This method helps to investigate the affects of reduced proprioceptive signals in the absence any additional complications that are a result of deafferentation or brain injury.

7b: Evidence from Healthy Controls using Tendon Vibration

7b.1: Introduction

A further method to investigate the contribution of proprioception in a given task is to temporarily disrupt proprioceptive signals in neurologically normal participants. One approach commonly used for this, is to induce ischemia to the limb. Obstructing blood flow from afferent receptors decreases their ability to fire a signal, therefore reducing sensory (proprioceptive) signals coming from the limb. For example, Mazzaro et al. (2005) introduced ischemia to the leg by inflating a pneumatic cuff positioned just above the knee. With this technique they were able to successfully degrade proprioceptive feedback in order to investigate the role of afferent signals in human walking. However, this method can be painful for participants, therefore, an additional approach has been considered of tendon vibration.

Roll and Vedel (1982) investigated the effect of vibration on afferent signals of the arm. They used vibration of the tendons in the biceps or triceps of healthy controls and were able to distort proprioceptive feedback. It was found that such vibration induced a constant illusion of joint rotation at the elbow. It was reported that the illusion gave the sensation as if the vibrated muscle was stretching. Therefore, vibration of the triceps felt as if the arm was drifting towards the body (rotating at the elbow) and vibration of the biceps produced an illusion of the arm rotating away from the body. Roll and Vedel (1982) experimented with several vibration frequencies ranging from 10 to 120Hz. The perceived velocity of the illusion was found to steadily increase from 10 to 80Hz and then decrease again from 80 to 120Hz. Goodwin et al. (1972) had completed similar studies in which they also found the same illusion. Instead of measuring velocity of the illusion they looked at magnitude. The participants demonstrated the perceived position of the vibrated limb by moving their non-vibrated limb so that they felt aligned. This method revealed mismatches of up to approximately 40-degrees with vibration of 100Hz.

However, although this method of distorting proprioceptive feedback is less uncomfortable than ischemia it does not simply reduce the sensation but induces incorrect sensations from the vibrated limb. Cordo et al. (1995) also found similar illusions evident in moving limbs as vibration of the biceps lead participants to over estimate the rotation of their elbow during passive movement. The participants arms were moved about the elbow during which they were required to open their hand at a predefined target angle. This task was completed both with and with out bicep vibration of the moving limb, for which accuracy was exceptionally high in the absence of vibration. With vibration, however, participants constantly undershot the target, corresponding to overestimating the stretch of the vibrated muscle.

To try to eliminate this problem Bock et al. (2007) conducted an experiment in which they applied simultaneous vibration to both the agonist and antagonist muscles of the forearm. Healthy participants took part in a series of tasks investigating the strength of proprioceptive sensation whilst vibration was applied to both the flexor and extensor muscles of the forearm and also with no vibration. It was found that whilst vibration to either one of the flexor and extensor muscles of the forearm produced converse illusions (extension and flexion respectively), simultaneous vibration to both sides induced a general derogation of the proprioception. Moreover, verbal reports from the participants stated that simultaneous vibration of both sides of the forearm produced a feeling of numbness in the arm opposed to illusionary movements.

In the current experiment participants were required to make self/other judgments over perturbed (other) and unperturbed (self) visual feedback of both active and passive full arm reaching movements. A robot arm motion tracking device was used in order to track the active movements and produce the passive movements. Participants completed the study with tendon vibration to the agonist and antagonist muscles of the forearm so to degrade proprioceptive sensation coming from the reaching limb. Participants underwent the experiment with vibration at two different frequencies one at approximately 100Hz, which should reduce the afferent signals, and one at 40Hz, which should not have this effect (Roll and Vedel 1982).

The lower vibration speed was used opposed to no vibration to ensure that any difference could not be due to attensional factors of a vibrating sensation on the limb. It was predicted that when the forearm is vibrated at 100Hz performance would be impaired in comparison to when the arm is vibrated at 40Hz, similar to the differences found in A.B. between his contralesional and ipsilesional limbs. Therefore, planned comparisons were conducted between the two vibration frequencies (100 and 40Hz) for each perturbation size of the active and passive movements.

7b.2: Method

Participants

An opportunity sample of 12 neurologically normal participants was selected, 10 female and 2 male with a mean age of 26 years (range 19 - 30 years). All participants had normal or corrected to normal vision and were right handed.

Materials

The materials were identical to those in Chapters 6 and 7a except with the addition of two physiotherapy vibrators. The vibrators were both three speed Omax rechargeable massagers (Figure 7.6) which have a counter-weight mechanism in the head. The Omax is a rechargeable handset with a 5800rmp motor and a running time of 25 minutes at top speed from full charge. The two vibrators were attached to the participants arm using a stretch bandage and secured with tape. Short breaks were introduced between each block in order to top up the Omax charge.

Figure 7.6: The Omax physiotherapy vibrator. Three-speed (40Hz, 75Hz and 100Hz) rechargeable handset with revolving counter-weight system in the head. Figure adapted form
omax website.

Procedure

Before the experimental trials commenced, the appropriate muscle tendons were located. Participants closed their eyes and outstretched their right arm. A vibrator was then placed at different locations along the muscle whilst vibrating at the maximum (100Hz) frequency. The participants were asked to report any perceived movement of the limb so that the location at which the illusion was induced could be marked on the arm with a washable marker. This was completed for both the extensor and flexor muscle tendons of the forearm following which both vibrators were attached to the arm, with the head of each vibrator secured over the marked area.

Participants then performed 4 experimental blocks of active and passive movements (2 active and 2 passive) identical to those described in Chapters 6 and 7a. Unimanual reaching movements were made with the right limb (whilst holding the robot arm) towards a green target. Their movements were represented by a white cursor, which either exactly represented their movements (self) or had a linear perturbation applied of 4 or 16-degrees (other). At the end of each trial participants had to make a verbal response as to whether the cursor movements were that of self or other. Two of the experimental blocks (one active and one passive) used 100Hz tendon vibration of the flexor and extensor muscles, with the remaining blocks using 40Hz tendon vibration. The active and passive blocks for the same frequency were always completed sequentially. The order of movement type (active and passive) and frequency (100Hz and 40Hz) was counterbalanced between participants.

7b.3: Results

Self/Other Judgments

Self/other judgments were converted to percent correct scores for each participant for each perturbation size (self being the correct judgment for a ZERO-degree perturbation and other being the correct judgment for the FOUR and SIXTEEN-degree perturbations). The data were then analysed using 2x2x3 repeated measures ANOVA. With the factors MOVEMENT, with two levels (ACTIVE and PASSIVE), VIBRATION, also with two levels (HIGH and LOW frequencies) and PERTURBATION, with three levels (ZERO, FOUR and SIXTEEN-degrees).

There was a main effect of MOVEMENT (F(1,11)=17.318, p<0.01 with ACTIVE (72.21%) having a greater percent correct score than PASSIVE (62.15%). There was also a significant main effect of PERTURBATION (F(2,22)=89.58,p<0.001) with FOUR (27.17%) having the lowest percent correct score followed by ZERO (86.92%) and then SIXTEEN (87.44%). There was no main effect of VIBRATION (F1,11)=0.68, p =NS, however, there was a significant interaction (Figure 7.7) of VIBRATION * MOVEMENT (F(1,11)= 14.02,p<0.01) with LOW ACTIVE having the highest percent correct score (74.23%) followed by HIGH ACTIVE (70.2%), HIGH PASSIVE (62.9%) and LOW PASSIVE (61.39) having the lowest. All other interactions were non significant (minimum, F(2,22)= 0.741, p<NS).

Figure 7.7: Interaction VIBRATION * MOVEMENT: Vibration frequency has more effect on
percent correct scores for the ACTIVE conditions than compared to the passive conditions.
Percent correct scores for LOW ACTIVE are greater than those recorded for HIGH ACTIVE.

Planned comparisons were conducted between the predicted variables of interest (see Figure 7.8) revealing a significant difference in percent correct judgments between HIGH and LOW VIBRATION for the ACTIVE movements at the FOUR degree PERTUBATION (F(1)=5.14,p<0.05) with LOW (38.5%) having a greater percent correct score than HIGH (29.17%). There was no significant difference between ACTIVE HIGH and LOW at the ZERO (F(1)=0.019, p=NS) or SIXTEEN (F(1)=0.708, p=NS) PERTURBATION. There were no significant differences between HIGH and LOW VIBRATION with PASSIVE MOVEMENT for ZERO (F(1)=0.689, p=NS), FOUR (F(1).074, p=NS) or SIXTEEN (F(1)=0.001, p=NS).

Figure 7.8: Planned comparisons between HIGH (100Hz) and LOW (40Hz) FREQUENCY for

each PERTURBATION size. a) ACTIVE: LOW (filled squares) FREQUENCY percent correct scores were significantly greater at the FOUR-degree PERTURBATION than with HIGH (open circles) FREQUENCY vibration. There were no significant differences at ZERO or SIXTEEN. b) PASSIVE: There were no significant differences between HIGH (open circles) and LOW (filled squares) FREQUENCY at any PERTRUBATION sizes. The asterisk denotes the significant difference.

Reach Error

Reach error was calculated in degrees from the target location with two separate measures (Figure 7.9a and b) endpoint error; defined as the furthest position along the Y axis and error at 25% of the reach; defined as 25% of total reach distance. Paired samples t tests revealed no significant difference between HIGH and LOW VIBRATION for endpoint error (T(1)= 0.62, p = NS) or error at 25% of the reach (T(1)= 0.26, p =NS).

Figure 7.9: Absolute reaching error for HIGH (100Hz) and LOW (40Hz) vibration frequencies.
a) Endpoint error; there is no significant difference in reach accuracy when the vibrators were oscillating at the HIGH FRQUENCY compared to when oscillating at the LOW FREQUENCY. b) Error at 25% of the reach; there is no significant difference in reach accuracy when the vibrators were oscillating at the HIGH FRQUENCY (filled) compared to when oscillating at the LOW FREQUENCY (open).

7b.4: Discussion

In the active conditions, when the vibrators were oscillating at 100Hz, percent correct scores were, in general, lower than when the vibrators were oscillating at 40Hz. This was particularly evident at the 4-degree perturbation, the only perturbation size to reveal significant difference with the planned comparisons.

This effect, however, did not extend to the passive conditions, at which there were no significant differences due to vibration. This initially seems counter intuitive as the passive conditions rely more heavily on proprioceptive signals so it would be expected that performance in these conditions would be more greatly affected than when movements are performed actively. There are two possible explanations to this; firstly participants could be using a different strategy for the active and passive trials, with proprioception being more important for the active task. For example, in the passive conditions

participants could be making their judgments based on vision only, on how accurate the cursor is to the target. However, this is unlikely due to the controls implemented in the experiment in order to prevent such a strategy form being used. A delay was introduced between the target's disappearance and the onset of the reach to reduce the presence of a target after image on the retina. End point error was also added to the robot’s reach so that even in the self conditions the robot was still not completely accurate. Consequently, you would expect that if the participants used vision only their performance would be lower. The second possible explanation for the results is that the vibration may only be affecting the active element of proprioception. Jones et al. (2001) found that when a movement is actively produced the afferent receptors in the limb elicit a greater signal than when movement is passive. This difference, albeit marginal, could account for the results, eliminating the proprioceptive advantage of the active movement.

As with A.B, there was no significant difference in reaching error between the high and low frequencies at either the 100% or at 25% of the reach. This means that the results cannot be explained by the stronger vibration frequency disrupting reach accuracy, so that the reach did not match the original motor command. Therefore, it is most likely a specific reduction in signal strength from the afferent receptors of the limb that produced the change in performance. This is important as it also helps to support the suggestion that the results in experiment 7a are due to a proprioceptive deficit and not any additional factors attributable to the brain lesion.

Interestingly, similar to A.B.'s performance, described in 7a, the deficit present with high frequency tendon vibration was only at the 4-degree perturbation (the difficult part of the task). The fact that the difference in percent correct judgments is only evident in the active movements, demonstrates that tendon vibration of this nature only degrades part of the afferent output from the muscles. This, therefore, may explain why the performance deficit did not extend to the 16-degree perturbations, as the signals getting through from the muscles, not affected by the tendon vibration, were enough to inform the high-level conscious processes (responsible for making self/other judgments) of large but not small mismatches.

It is important to note the current experiment shows a general reduction in performance on the passive compared to active trials, an effect also observable (although not analysed) in the preceding experiment (7a) for both controls and A.B. This is in line with the results of the experiment in Chapter 6, in that participants are more accurate at the task when forming a motor command. The replication of this finding suggests that it is robust, and furthermore, that all participants across the three experiments were using the same strategy for the task.

7b.5: Conclusions

The current findings along with those from the preceding chapters suggest that proprioceptive signals play a greater role in agency attribution than is described by the comparator model. In addition to this, the current results suggest proprioception to have only a negative effect on agency, in that, it informs on the presence of other movements opposed to directly contributing to a sense of

agency. In fact, reducing proprioceptive signals was found to increase the sense of agency (more self-judgments). However, it remains unclear as to the relative importance of proprioceptive and efferent signals in regards to both high and low-level agency mechanisms. This is addressed in the following section of the thesis, specifically, Chapter 8 utilises both visual and physical perturbations in order to manipulate the accuracy of the visual feedback and its relationship to the actual limb position (proprioceptive feedback). Therefore, the effects of accurate and perturbed visual feedback can be directly compared against the effects of accurate and perturbed proprioceptive feedback, for low-level mechanisms, measured by the motor response to the perturbation, as well as high-level mechanisms measured by the self/other judgments.

Section 3

Chapter 8
Weighting of Afferent and Efferent Signals

8.1 Introduction

Visual and proprioceptive signals have been found to contribute to the accurate guidance of human movement. For example, Lateiner and Sainburg (2003) found that visual information was of particular importance in planning movement direction and distance. In their experiment, participants had to reach towards targets using a virtual reality set up in which visual feedback was only presented prior to movement onset (cursor representing their limb disappeared immediately after the movement was initiated). In some of the trials the cursor (visual feedback) exactly represented the actual position of the limb (proprioceptive feedback) whilst in other trials the cursor location was shifted in comparison to the actual limb position. The participants were found to adjust the direction and distance of their reaches in accordance with the visual and not proprioceptive feedback. A similar study conducted by Bagesteiro et al. (2006) agreed with these findings, that vision was responsible for planning movement distance and direction, as the initial movement direction, peak velocity and time to peak velocity of a given movement were dependent on the location of the visual feedback. However, Bagestiero et al. (2006) also found that other elements of the reach, such as time at peak velocity, were more strongly influenced by the actual limb position (proprioceptive feedback), suggesting that these signals are more useful for the on-line correction of movements.

In terms of localisation of limb position, visual feedback has been found to help strengthen proprioceptive signals (Blangero et al., 2005) even if the feedback itself is non-informative (Newport et al. 2002). However, if the visual feedback contradicts the actual limb position, it can dominate over proprioception changing the perceived position of the limb in accordance with the visual input. This is known as a visual dominance or visual capture effect. For example, Holmes and Spence (2005) conducted an experiment in which asymmetrical visual feedback of right arm movements was provided by a mirror reflection of the left arm, located just in front of the right limb. However, the left limb was positioned so that it appeared in the mirror to be either nearer or farther from the body than the actual position of the right limb.
Initially participants performed in phase tapping movements with both hands whilst looking at the reflected image of the left hand. This was done in order to strengthen the illusion that the reflected left hand movements corresponded to right hand movements. Following this, participants made a unimanual right arm reaching movement towards one of two targets. Accuracy of the reaches was found to have strong directional effects according to the position of the left hand. Participants moved their right hand as if it was nearer to the location of the left limb as it appeared in the mirror. Another example of the strong influence of visual signals on perception comes from phantom limb patients. These are patients who, following limb amputation, still feel, and can sometimes perceive voluntary movement of, the amputated limb. Phantom limb pain, akin to involuntary clenching of the phantom fist, can become alleviated by viewing the mirror image of the existing fist unclenching when the reflection appears spatially concordant with the phantom (Ramachandran

and Rogers-Ramachandran, 1996b). This occurs despite full knowledge that the image seen is just a mirror reflection.

However, the integration of visual and proprioceptive signals is not always that straightforward. The degree to which visual information presides over proprioception has been found to be task dependent and there are even some instances in which proprioception becomes the dominant modality. Warren and Schmitt, (1978) found that the context in which the reach was made had a strong influence on the relative visual and proprioceptive contributions to reach accuracy. If participants were required to reach towards propriocetively defined targets they used predominantly proprioceptive feedback on which to guide their movement, even in the presence of conflicting visual feedback (no visual capture). Similarly when reaching to a visually defined target, participants relied more on visual feedback. The previous two chapters have helped to highlight the importance of proprioceptive information in agency attribution using patients and controls. In Chapter 6, neurologically intact participants made self/other judgments over active and passive movements for which only a small behavioural difference was found between the two tasks. This demonstrated that successful completion of the task can still be achieved despite the absence of efferent signals. Chapter 7 took this further by examining performance on the same task of participants with proprioceptive feedback reduced by pathology (following stroke) and tendon vibration (neurologically intact participants). In these experiments the target was purely visual and yet in the passive condition participants did not appear to be basing their judgments on visual accuracy alone, likewise performance was reduced with impaired proprioceptive

feedback. The current experiment attempts to expand on this by investigating the exact nature and magnitude of proprioceptive influence in relation to visual and efferent signals.

The visual dominance/visual capture effect can explain results in which visual perturbations are applied incrementally so that relatively large disparities go unnoticed, which when presented in a non-incremental fashion are easily detected. For example, Michel et al., (2007) found neurologically normal participants to remain unaware of a 10-degree prismatic shift, following gradual adaptation to increasingly larger perturbations presented incrementally (2 - 10-degrees). The effect of the incremental perturbations meant that the overall visual-proprioceptive disparity became gradually larger over a series of trials. When directly exposed to the 10-degree perturbation, however, the participants became immediately aware of the shift. Slachevsky et al. (2001) used an incremental paradigm when applying perturbations to visual feedback of participants attempting to draw a straight line. At the end of each trial participants were asked whether the line presented via the visual feedback matched the line they actually drew. The mean angular deviation at which the participants noticed the perturbation was relatively large, approximately 14degrees. The reason for this being that motor system adapted to the small changes in perturbation size from trial to trial, so that visual feedback did not deviate sufficiently from that predicted to become noticeable. The accurate visual feedback dominated over any conflicting proprioceptive signals until approximately 14-degrees angular deviation from the actual limb position (although one neurologically intact participant remained unaware of the perturbations throughout the experiment, up to 42-degrees). Such experiments directly relate visual dominance to action awareness and suggest that proprioception only becomes important at larger visual-proprioceptive deviations.

Interestingly, previous studies investigating agency with impaired or absent proprioception (including the two experiments in the previous chapter) have found the resultant effect to be an increase in self-judgments rather than performance dropping towards chance. This too suggests that proprioception contributes to detection of comparator mismatches rather than directly informing the experience of agency (feeling in control of an action). In this explanation, the roles of vision and proprioception in action awareness extend logically from their roles found in the accurate guidance of movement. Vision influences initial planning of direction and distance, so that the small visual mismatches influence the adaptation of the motor command, whilst proprioception is utilised for on-line corrections and the detection of discrepancies during the movement.

Relating this further to the comparator model, there are two main possibilities for the role of proprioception. Firstly, that proprioceptive information is important only in the formation of the estimated actual state, which is in turn compared to the predicted state (based predominantly on the efference copy). The estimated actual state is constructed mainly from visual and proprioceptive feedback originating from the actual movement. When disparities between these two modalities are small, the actual limb position is perceived in a location between the two. Due to the visual dominance effect, the new location is mainly perceived nearer to the position of the visual feedback (van Beers et al., 1999). Therefore, small perturbations remain

unnoticed as long as the visual feedback matches that predicted (Slachevsky et al., 2001). However, when the disparity becomes larger, the perceived limb position moves further away from the visual feedback. This means that the estimated actual state is more ambiguous and no longer matches the predicted state, even if the visual feedback remains accurate. Consequently, participants no longer feel a sense of agency over the action (noticing the perturbation and/

or producing an other judgment). Furthermore, when proprioceptive signals are weakened by pathology or tendon vibration (Chapter 7), less information is available to contradict the visual feedback when forming the estimated actual state. Therefore, visual dominance presides for larger perturbation sizes. Under

such circumstances a self/other judgment is based predominantly on matching the visual feedback to the predicted state representation, which in the experiments in Chapter 7 were likely to be ambiguous due to the targets size relative to the cursor and disappearance of the target prior to movement onset. In short, this explanation suggests a self/other judgment to be predominantly determined on the accuracy of the visual feedback unless the visualproprioceptive
deviation is large.

The problem with this explanation is that it only recognises a proprioceptive contribution in the formation of the estimated actual state, which is in turn compared to the efferent signals in order to attain successful self/other attribution. It cannot therefore, account for passive movement recognition, for which there is no efferent information (motor command) available. Balslev et al. (2006) found no significant differences in brain activation between active and passive movements when participants had to distinguish between synchronous and asynchronous visual feedback, despite

there being significantly more errors in the passive condition. This finding suggests that both tasks implement similar neural processes and therefore, could represent activation of the same comparator system. The reason for the increased response accuracy for the active movements being that actively producing a movement allows for the recruitment of an additional component of the comparator, comparing the estimated actual state (comprised predominantly of visual feedback due to visual capture) to the predicted state representation (efferent signals). Therefore, the second possibility for the role of proprioception in the comparator model, is that in addition to forming the estimated actual state, proprioceptive signals make a second, independent contribution in which they are compared directly to the available visual information. In this case visual-proprioceptive congruence or incongruence would have a significant affect on self/other judgments. Thus, independent of reach accuracy, a self-judgment would be more likely when the visual and proprioceptive feedback were congruent than in the presence of even a small disparity.

One of the main problems with previous experiments investigating agency attribution is that they do not differentiate between high and low-level mechanisms. Self/other verbal responses, which are the measurement of choice in most of these experiments, represent the high-level processes only. Therefore it is possible that whilst proprioception only informs high-level verbal judgments to large discrepancies, it may have a more direct, positive contribution to low-level agency mechanisms. Therefore in the current experiment, not only are the high-level self/other judgments recorded for actual and perturbed visual feedback, but also the low-level motor response.

Previous experiments using rotated visual feedback generally consist of trials that have both visual-proprioceptive and visual-efference discrepancies (inaccurate visual feedback), as the cursor is perturbed away from the target and away from the actual limb position (Farrer et al., 2003b). Whilst other studies consist of trials in which the discrepancies present between the visual and proprioceptive information are obtained using incremental perturbations (Founeret et al., 2002 and Slachevsky et al., 2001). In such trials the visual feedback remains accurate whilst the visual and proprioceptive signals are in conflict. The current study extends on these previous experiments by including trials akin to both those described above (in addition to unperturbed trials) with the exception that instead of using incremental perturbations to produce a visual-proprioceptive discrepancy with accurate visual feedback, a similar affect was achieved in a single trial by simultaneously applying equivalent and opposing visual and physical perturbations. This allowed the actual limb (proprioceptive feedback) to be perturbed away from the target whilst maintaining accurate visual feedback, due to the cursor being perturbed back in the opposite direction so that in continued along the original trajectory. A further condition was also implemented in the current experiment in which a physical perturbation deviated the actual hand from the original trajectory whilst the visual feedback remained unperturbed. The desired affect of this condition was that both the visual and proprioceptive feedback were perturbed away from the target, maintaining visual-proprioceptive congruence, yet the visual feedback was inaccurate relative to the target.

Participants made unimanual reaching movement towards visually presented targets and were required to make self/other judgments as to whether visual feedback exactly represented their movement (self) or was manipulated by the computer (other). In order to attempt to differentiate between the possible roles of proprioception, a small perturbation size was required. Previous studies have found varying results for the size of a detectable discrepancy with accurate visual feedback. For example, Slachevsky et al. (2001) found participants to only become aware of the deviation at an average of 14-degrees, whilst Fourneret et al. (2002) found awareness to be achieved at an average of just 6-degrees. The current study used 4-degree perturbations to ensure that it falls below that found to be noticeable in the previous studies

in
order to avoid ceiling effects.

It was predicted that both visual-proprioceptive and visual-efferent (predicted compared to estimate actual state) comparisons would affect the percentage of self-judgments. Therefore, planned comparisons were conducted for percent self-judgments between the unperturbed trials and all other conditions, and also between the trials in which visual feedback was accurate but there was a visual-proprioceptive incongruence and the trials in which the visual feedback perturbed away from the target but visual-proprioceptive congruence was maintained (one having visual-proprioceptive congruence only and one having visual-efferent congruence only). In addition to self/other judgments, accuracy of the visual feedback was also recorded using two measures, degrees of error at 25% of the reach and degrees of error at 100% of the reach. This measure was included not only to examine the effects of reach accuracy on a self/other judgment but also to measure the low-level motor response to the perturbations. It was predicted that the trials in which both physical and visual perturbations were applied (opposing directions), would

demonstrate error equivalent to the unperturbed conditions for both measures (accurate visual feedback). Whereas, it was predicted that error would be increased in comparison to the unperturbed trials, for both physical only and visual only perturbation conditions (inaccurate visual feedback). Consequently planned comparisons were also conducted between the unperturbed and all other conditions for both, error at 25% and, error at 100% of the reach.

8.2: Method

Participants

An opportunity sample of 12 healthy participants was used consisting of 6 males and 6 females with a mean age of 25 years (range 21 -31 years). All participants had normal or corrected to normal vision, and were right handed.

Materials

The materials were identical to those in Chapter 6. A vBot 2D motion-tracking device was used to enable online visual feedback of movement to be presented on a mirrored surface so that it appeared in the same spatial plane as the actual
movements (see Figure 6.1).

Procedure

The procedure was identical to that of the active conditions in Chapters 6 and 7; participants made reaching movements with the vBOT (robot arm) towards a green circular target that disappeared prior to movement onset. However, one key difference was the nature of the perturbations. Only the smaller 4-degree

perturbation was used and in addition to the visual perturbations, physical perturbations were also applied to the movements (see Figure 8.1).

Figure 8.1: Schematic representation of the four different conditions V1 and V0 referring to the
presence and absence of a visual perturbation respectively (white arrow) that pushed the cursor
(white circle) away from the robot arm (open circle). P1 and P0 referring to the presence and
absence of a physical perturbation (yellow arrow) that pushed the robot arm away from the
target (T). Solid lines represent limb position at the beginning of the movement. Dashed lines
represent the relative limb position at the end of the movement.

In 25% of the trials the movements of the white cursor exactly represented the participants actual movements, in a further 25% of the trials the cursor's movements had a 4-degree angular perturbation applied. Another 25% of the trials involved the cursor trajectory being unperturbed, however, the participants actual movements were physically perturbed by 4-degrees (cursor

and arm deviated from original trajectory). In the remaining trials the movements had both physical and visual perturbations applied in opposite directions. This allowed the participant's actual reach trajectory to be perturbed away from the target, whilst the cursor would continue along the approximate initial trajectory (towards the target). Therefore, although the actual limb trajectory was perturbed the visual feedback was accurate in relation to the target.

All perturbations were equally distributed between leftward and rightward directions (For all outcomes see Figure 8.2). The experiment took part in two identical successive blocks each composed of 40 trials (ten of each condition). The physical perturbations were created in a similar way to the visual perturbations (see Chapter 2) physically pushing the participant's limb away from the target.

At the end of each movement participants had to give a verbal judgment as to whether the feedback received accurately represented their movements (self) (i.e. they were in full control of the cursor movements), or whether is had been manipulated by the computer (other).

Figure 8.2: Table depicting the key features of each of the four different trial types. V1 and V0 referring to the presence and absence of a visual perturbation respectively whilst P1 and P0 refer to the presence and absence of a physical (proprioceptive) perturbation respectively.

8.3: Results

Self-Judgments

The data were converted into percentage self-judgments and analysed using a repeated measures 2x2 ANOVA. There were two factors: VISUAL PERTURBATION with two levels; present (V1) and absent (V0) and PHYSICAL PERTURBATION also with two levels; present (P1) and absent (P0). There was a significant main effect of VISIUAL PERTURBATION (F(1,11)= 22.132, p<0.001) in that V0 mean percentage of self-judgments (78.86%) was greater than V1 (50.08%). There was also a significant main effect of PHYSICAL PERTURBATION (F(1,11)= 5.350, p< 0.05) with P1 having greater percentage of self-judgments (68.5%) than P0 (60.43%). There was also a significant VISUAL PERTURBATION * PHYSICAL PERTURBATION interaction (F(1,11)= 18.228, p<0.01) (see Figure 8.3).

Planned comparisons revealed no significant difference between V1-P1 and V0-P1 (F(1)=2.147, p=N.S). A significant difference was found between V1P1 and V0-P0 (F(1)=10.402, p<0.01) with V0-P0 (84.5%) having the greater percent self-judgments compared to V1-P1 (63.81%). A significant difference was also found between V1-P0 and V0-P0 (F(1)=56.3, p<0.001), with V1-P0 (36.35%) having fewer percent self-judgments than V0-P0 (84.5%). No significant difference was found between V1-P0 and V0-P0 (F(1)=3.97, p=NS).

Error at 25% of the Reach

Error at 25% of the reach was measured in degrees from the target at 25% of the total reach distance. The data were then analyzed using a 2x2 repeated measures ANOVA for which there were two factors: VISUAL PERTURBATION with two levels; present (V1) and absent (V0) and PHYSICAL PERTURBATION also with two levels; present (P1) and absent (P0). There was a significant main effect of VISUAL PERTURBATION (F(1,11)=21.49, p<0.001) with V1 (9.98°) having greater degrees of error than

V0 (6.58°). There was a significant main effect of PHYSICAL PERTURBATION (F(1,11)=11.56, p<0.01) with P0 (9.22°) having greater degrees of error than P1 (7.35°). There was also a significant VISUAL PERTURBATION * PHYSICAL PERTURBATION interaction (F(1,11)= 90.37, p<0.001).

Planned comparisons revealed a significant difference between V0-P0 and V0P1 (F(1)=20.92, p< 0.001) with V0-P0 (4.59°) having less degrees of error than V0-P1 (8.57°). A significant difference was also found between V0-P0 and V1-P0 (F(1)=112.95, p<0.001) with the error for V1-P0 (13.85°) being greater than for V0-P0 (4.59°) There was no significant difference between V0P0 and V1-P1 (F(1)=3.09, p=NS.

Endpoint Error
Endpoint error was measured in degrees from the target at the furthest point on the Y axis. The data were then analyzed using a 2x2 repeated measures ANOVA for which there were two factors: VISUAL PERTURBATION with two levels; present (V1) and absent (V0) and PHYSICAL PERTURBATION also with two levels; present (P1) and absent (P0). There was a significant main effect of VISUAL PERTURBATION (F(1,11)=24.62, p<0.001) with V1

(6.92°) having greater degrees of error than V0 (4.83°). There was a significant

main effect of PHYSICAL PERTURBATION (F(1,11)=14.3, p<0.01) with P0 (6.47°) having greater degrees of error than P1 (5.28°). There was also a significant VISUAL PERTURBATION * PHYSICAL PERTURBATION interaction (F(1,11)= 39.22, p<0.001) (see Figure 8.4).

Planned comparisons revealed a significant difference between V1-P0 and V0P0 (F(1)=73.34, p<0.001) with V1-P0 (8.63°) having greater degrees of error than V0-P0 (4.31°). No significant difference was found between V0-P0 and V1-P1 (F(1)=3.13, p=NS) or between V0-P0 and V0-P1 (F(1)=4.247, p=NS).

Figure 8.3: Self-judgments all four conditions. V1 and V0 refer to the presence and absence of a visual perturbation respectively. P1 and P0 refer to the presence and absence of a physical perturbation respectively. Error bars show standard error. Graph depicts the percent self-scores for all four conditions. Condition V0-P0 (unperturbed) produces significantly more self-judgments than both V1-P1 and V1-P0. No significant difference was found between V0-P0 and V0-P1.

Figure 8.4: Error results for all four conditions. V1 and V0 refer to the presence and absence of a visual perturbation, respectively. P1 and P0 refer to the presence and absence of a physical perturbation respectively. Error bars show standard error. Graph depicts degrees of error for the cursor relative to the target for all four conditions at both 25% and 100% of the reach. No

difference was found between V0-P0 and V1-P1 at either 25% or 100% (accurate visual feedback). Condition V0-P0 demonstrates significantly less error than both V1-P0 and V0-P1 at 25% of the movement and less than V1-P0 at 100% of the reach. No difference was found between V0-P0 and V0-P1 at 100% of the reach.

8.4: Discussion

Condition V0-P0 was an exact representation of the actual movement, with no visual or physical perturbations applied and therefore had visual-proprioceptive congruence and accurate visual feedback at both 25% and 100% of the movement. This condition also produced the highest percentage of self-judgments, which, for this condition only, was the correct judgment. Condition V0-P1 had a physical but not a visual perturbation applied that resulted in visual-proprioceptive congruence, as the cursor was not perturbed away from the limb, but greater reach error relative to the target when compared to condition V0-P0. Interestingly, the increase of error was not apparent throughout the entire reach, becoming statistically equivalent to condition V0P0 at 100% (endpoint) of the movement. Percent self-judgments were also not significantly different from condition V0-P0.

Condition V1-P0 had only a visual perturbation applied, which deviates the cursor (visual feedback) from the actual limb position and away from the target, therefore producing visual-proprioceptive incongruence and inaccurate visual feedback. This condition also resulted in by far the fewest percent self-judgments and remained inaccurate even at 100% of the reach. Condition V1P1 had both visual and physical perturbations applied. The physical perturbation deviated the limb away from the target, whilst the visual perturbation was applied in the opposing direction, deviating the cursor back towards the target (along initial trajectory). As such, condition V1-P1 had visual-proprioceptive incongruence whilst maintaining accurate visual feedback (cursor) relative to the target, error not differing significantly from V0-P0 for either 25% or 100% of the reach. Percent self-judgments for this condition were not significantly lower than the percent self-score for V0-P1, but were lower when compared to V0-P0. The aim of the current experiment was to investigate the relative contributions of visual-proprioceptive congruence and accuracy of the visual feedback (attaining the goal) in forming a self-judgment.

Visual-proprioceptive Congruence

One possible factor on which to base a self/other judgment is visualproprioceptive congruence. Participants are more likely to give a self-judgment if the cursor position (visual feedback) matches the actual limb position (proprioceptive feedback). In the current experiment the absence of a visual perturbation reflected the presence of visual-proprioceptive congruence (visual perturbations perturb the cursor away from the limb). Even in condition V0-P1, in which the cursor is initially perturbed away from the target, the cursor deviation only occurred as a consequence of the robot perturbing the actual limb trajectory. Therefore, the significant main affect of vision represents a significant main affect of visual-proprioceptive congruence, for which more self-judgments were given in response to trials in which congruence was maintained (absent visual perturbation, V0). The planned comparisons further demonstrate this, as no difference was found in percent self-judgments between the conditions V0-P0 and V0-P1 (cursor position matches actual limb position).

However, it is unlikely that self/other judgments are based on this one factor alone. If participants only made self-judgments when there was perceived visual-proprioceptive congruence, fewer self-judgments would be expected when visual and proprioceptive signals were incongruent, regardless of cursor accuracy. Whilst fewer self-judgments were recorded for condition V1-P0 in which there was visual-proprioceptive discordance and inaccurate visual feedback (cursor perturbed away from the unperturbed limb position). Condition V1-P1, in which visual-proprioceptive discordance was present but visual feedback remained accurate, produced statistically equivalent self-judgments to condition V0-P1 (visual-proprioceptive congruence). The key difference between V1-P0 and V1-P1 is that the latter has accurate visual feedback relative to the target. Degrees of error between the cursor and target position were not found to differ significantly between V1-P1 and V0-P0 (unperturbed condition) for either 25% or 100% of the reach, whilst V1-P0 demonstrated significantly more reach error than V0-P0 for both these measures.

Accuracy of the Reach

The second factor that could inform a self/other judgment is reach accuracy. The aim of the task in the current experiment was to reach towards a visually presented target, i.e. an accurate movement results in the cursor (visual feedback) reaching the (visual) target. Condition V0-P0, (unperturbed) had the lowest degrees of error between the cursor and target positions for both 25% and 100% of reach and also produced the highest percentage of self-judgements. However, the amount of self-judgments recorded for V0-P0 did not differ significantly from those produced in condition V0-P1, despite the latter condition demonstrating significantly greater error at 25% of the reach. Likewise, when compared to V0-P0, the error recorded for condition V1-P1 did not differ significantly at either 25% or 100% of the reach, yet V1-P1 produced significantly less self-judgments. Therefore, accuracy throughout the reach cannot solely account for the current results.

Endpoint Error (Attaining the Goal)

The third main factor that could underlie a self-judgment is error at 100% (endpoint) of the reach, whether or not the cursor reached the desired location (is accurate with respect to the target). The percentage of self-judgments for condition V0-P1 did not differ significantly from V0-P0, despite demonstrating greater error at 25% of the reach. However, at 100% of the reach, cursor error did not differ significantly between these two conditions. Condition V1-P1 also demonstrated equivalent endpoint error to both V0-P0 and V0-P1, whilst also producing a high percentage of self-judgments (not differing significantly from V0-P1). Condition V1-P0 on the other hand, had the greatest error recorded at 100% of the reach, whilst also producing the fewest self-judgments. Therefore, at first glance, accuracy at 100% of the reach seems to correspond with amount of times participants made a self-judgment. However, despite self-judgments for V1-P1 not being significantly different from V0-P1, they were significantly lower than for V0-P0. If a self-judgment was based on endpoint error alone (100% of the reach) it would be expected that amount of self-judgments for these two conditions would be equivalent. Crucially, however, the number of self-judgments to accurate visual feedback was reduced with visualproprioceptive incongruence.

A Self-Judgment

The current results demonstrate that neither, visual-proprioceptive congruence or reach accuracy (at 25% and/or 100% of the movement) can solely account for a self-judgment. Reach accuracy, particularly at 100% of the reach, does appear to play an important role in self/other judgments. However, self-judgments to accurate visual feedback are reduced if there is also a visualproprioceptive disparity. Likewise, visual-proprioceptive congruence is shown to be important for a self-judgment, however, even with an incongruence of this nature, self-judgments are increased if the visual feedback is accurate relative to the target (V1-P1). One explanation for the processes underlying these findings is that when the proprioceptive feedback conflicts with the visual feedback (such as in condition V1-P1) the actual limb position is

perceived to be between the two.

According to the comparator model, in order to form a self/other judgment, the predicted state representation is compared to the estimated actual state. The predicted state representation is constructed from the efference copy of the motor command whilst the estimated actual state is constructed predominantly from afferent signals received from the movement (vision and proprioception). Van Beers et al. (1999) found that with small visualproprioceptive conflicts, instead of participants noticing that the two types of feedback were at different locations, they perceived their limb (estimated actual state) to be at a single location between the two and that due to the dominance of vision (visual capture), the new location was nearer to the visual feedback. If this is what was happening in the current experiment the recorded reach accuracy, which was measured as the cursor relative to the target, may not reflect the participants perceived accuracy of the reach (relative to their estimated actual state). Thus, the perceived trajectory of the limb would be less accurate than the cursor, but more accurate than the actual limb position (see Figure 8.5a).

Furthermore, for the V1-P0 trials, which also have visual-proprioceptive discordance as the cursor was perturbed away from the unperturbed limb and away from the target, the perceived limb location would again be in between the two and nearer to the cursor position. However, in these conditions the cursor is inaccurate, therefore, the perceived location of the limb will be further away from the target than for V1-P1 when the cursor was accurate (see Figure 8.5b). As such, this explanation can account for the self-judgments in V1-P1 being lower than the condition with equivalent cursor accuracy (V0-P0), yet

higher than the condition with an equivalent visual-proprioceptive incongruence (V1-P0). With this explanation, endpoint accuracy would be of key importance for forming a self/other judgment. The effect of conflicting proprioceptive feedback (of only 4-degrees), being to distort the participants perceived accuracy of their movement and hence indirectly affecting a self/other judgment. However, considering this along side condition V0-P1 and V1-P0 in which the participants appear to increase accuracy of their movement throughout the reach (compensating for the perturbation), if the actual limb position is perceived to be less accurate than the measurements recorded from the cursor, similar corrections to the limb trajectory would be expected, but relating the perceived limb position (not the cursor) to the target.

Figure 8.5: Schematic representation of actual limb trajectory (solid line), cursor trajectory (dashed line) and perceived limb trajectory (dotted line) relative to the target (T) for a) condition V1-P1 and b) V1-P0.

Adapting Motor Commands

When examining the low-level motor response to the perturbations, the role of proprioceptive feedback becomes clearer. For both V0-P1 and V1-P0 endpoint error (100% of the reach) is reduced in comparison to the error recorded at 25% of the reach. This indicates that in both conditions the participants attempted to compensate for the perturbation that had perturbed the cursor away from target. In an attempt to clarify this observation, the original error data were converted into a single measure by subtracting error at 100% of the reach from error at 25% of the reach (25%-100%). These data were then entered in a 2x2 repeated measures ANOVA with two factors: VISUAL PERTURBETION, present (V1) and absent (V0) and PHYSICAL PERTURBATION: present (P1) and absent (P0). The results revealed no significant main effects (minimum F(1,11)= 3.41, p=0.09) but a significant VISUAL PERTURBETION * PHYSICAL PERTURBATION interaction (F(1,11)=58.34, p<0.001)(see Figure 8.6)

Figure 8.6: Graph depicting the significant VISUAL PERTURBATION * PHYSICAL PERTURBATION interaction for error at 25% of the reach - error at 100% of the reach (25%100%).
This measure represents the amount of correction participants made during the movement. Conditions V0-P0 and V1-P1 demonstrate little online movement correction whilst conditions V0-P1 and V1-P0 demonstrate relatively large connections. Error bars show standard error.

These additional results confirm that in conditions V1-P1 and V0-P0 participants did not deviate their trajectory significantly throughout the reach (low 25%-100% scores). When considering this in conjunction with the original error data, both these conditions demonstrated low and equivalent degrees of error at both 25% and 100% of the movement. It is therefore likely that because the cursor was accurate relative to the target participants did not need to change their limb (and hence the cursor) trajectory in order to reach their intended goal, regardless of the presence of conflicting proprioceptive feedback. Thus, these results indicate the participants were using predominantly visual feedback opposed to proprioceptive feedback to guide their reaches (most likely due to the visual nature of the target). V0-P1 and V1P0, on the other hand, both demonstrated far higher 25%-100% scores, which reflect changes in limb trajectory throughout the reach. Both these conditions also demonstrate significant error at 25% of the reach (compared to V0-P0) indicating that at this stage of the movement the cursor was relatively inaccurate in relation to the target (a consequence of the perturbations).

Therefore, in order for the participant to reach their goal (the target) alterations to their limb trajectory (motor commands) were required. Such alterations are reflected in the 25%-100% scores for which condition V0-P1 demonstrates a lower score than V1-P0 (less online correction). Conversely, it is condition V0-P1 (lower 25%-100% score) that demonstrates greater endpoint accuracy (equivalent to the unperturbed reaches), despite the inaccuracy of the cursor in both the conditions being the result of an equivalent 4-degree perturbation. This can be explained by the large difference in error between the two conditions at 25% of the reach, V0-P1 demonstrating greater accuracy.

Thus, suggesting that in condition V0-P1 compensation strategies are implemented earlier in the reach (prior to 25% of reach distance) compared to V1-P0.

If the alterations to reach trajectory observed in V0-P1 were only in response to inaccurate visual feedback, a similar degree of compensation would be expected for V1-P0, due to both these conditions having visual feedback that was perturbed by an equivalent amount (4-degrees) away from the target. This, however, was not the finding of the current results, V0-P1 demonstrating lower degrees of error than V1-P0 at both 25% and 100% of the reach. The key difference between these two conditions is that V0-P1 also had perturbed actual limb trajectory (visual-proprioceptive congruence) this being the same condition with earlier implementation of the compensation strategy and higher endpoint accuracy. However, it is also unlikely that the earlier compensation strategy is only in response to the perturbed actual limb trajectory (proprioceptive feedback inaccurate relative to the target). Previous studies have shown that proprioceptive feedback is more instrumental than vision for online corrections of reaches (Bagesteiro et al., 2006), however, if the motor system was only making corrections based on proprioceptive feedback alone, similar changes of limb trajectory would be expected in all trials with physical perturbations, regardless of nature of the visual feedback.

Condition V1-P1 has a similar perturbation applied to the actual limb (physical perturbation), however, an additional perturbation was applied to the cursor trajectory so that it remained accurate in relation to the target. As previously discussed this condition demonstrates very little difference between the error recorded at 25% and 100% of the reach, both scores being in line with error observed in the unperturbed trials (V0-P0). Therefore, even if the final self/other decision was based predominantly on endpoint accuracy, the greater accuracy observed in condition V0-P1 is most likely to be a result of congruency between the visual and proprioceptive signals, which enhance low-level motor responses that lead to the more accurate movement.

However, an additional explanation for the successful corrections evident in V0-P1 is that the participants may have consciously felt their limb being pushed by the proprioceptive perturbation and so pushed back against it. The physical nature of the perturbations may have altered high-level processes that implemented the correction mechanisms. In condition V1-P0, on the other hand, participants had to wait until there was a sufficient visual deviation before they noticed and could begin to correct their movement. Although this explanation can account for the early compensation strategy implemented in V0-P1, it does not account for the high proportion of self-judgements. The very nature of the task required participants to look out for such deviations to their actual movement. Although the properties of the perturbations were not fully described prior to the experiment, such a deliberate manipulation of their reach, if consciously perceived, would surely produce more high-level other judgments and post-hoc anecdotal reports also suggested that most of the participants were unaware of the perturbations. Moreover, this would again be unable to explain the lack of compensation for the physical perturbation apparent in condition V1-P1.

Two Aspects of Agency

An additional point of interest here, is that compensation strategies, albeit less successful, were still implemented in condition V1-P0. In fact this condition demonstrated the largest difference between 25% and 100% of the reach (highest 25%-100% score). These findings suggest that online alterations were made to the motor command in order to attempt to produce a more accurate movement. Thus, these results could imply that, on some level at least, the visual feedback was treated as self despite being incongruent with proprioceptive feedback and inaccurate relative to the target. Synofzik et al., (2007) and Gallager (2007) have criticised the comparator model for not differentiating between lower-level sensational aspects of agency and the higher-level judgments. The lower-level feelings of agency are described as bottom-up processes derived from the motor system, whilst higher-level judgments are top-down conceptual processes, which are based on phenomenological knowledge (prior knowledge and beliefs etc).

The results for conditions V0-P1 and V1-P0 help to highlight the dissociation of these two aspects, the compensation strategy reflecting lower-level feelings of agency, whilst the verbal responses at the end of the trial reflect the high-level judgments of agency. For example, in condition V1-P0 adjustments are made to the motor commands of the reach in an attempt to overcome the perturbation and guide the cursor to the target. Because the motor system makes these changes to the motor commands it must be treating the cursor movements as self (under the control of the participant). However, despite this the self/other judgments made for this condition were predominantly other. Although in this particular condition the alterations to the motor command in order to compensate for the perturbations were not entirely successful (greatest endpoint error), participants did manage to reduce the error in respect to the target throughout the reach (i.e. participants were controlling the cursors trajectory). However, due to the nature of the task, in which participants were required to detect such deviations from their own movements their high-level verbal judgment, based on this prior knowledge of the task, was more likely to be other.

In regards to the role of proprioception in these two aspects of agency, visual-proprioceptive congruence appears to enhance the low-level feelings of agency causing earlier, more effective adaptations to the motor command. As a consequence of this, proprioception also has an indirect influence the higher-level judgment. Therefore, the current findings, particularly for condition V0P1, suggest not only that proprioception is important for feelings of agency but also that it can contribute to enhancing those feelings opposed to a role limited for the detection of discrepancies only. However, in terms of higher-level judgments this may only be indirect process, via producing a more accurate reach, and does not necessarily support the existence of an independent visualproprioceptive comparison within the comparator model. In the explanation of the comparator model by Frith et al. (2000), it was suggested that afferent feedback is used, in addition to the formation of the estimated actual state, to fine-tune motor commands and thus contributes to the predicted consequences of the actions (predicted state representation). The results of the current study initially appear compatible with this explanation. In condition V1-P0 the motor commands are altered based on only visual feedback, whilst in condition V0P1 the motor commands are more affectively fine-tuned due to the succinct visual and proprioceptive signals (both affecting the motor commands in the same way). However, in condition V1-P1 the inaccurate proprioceptive feedback does not affect the motor commands at all (cursor demonstrates error levels equivalent to those in the unperturbed conditions at both 25% and 100% of the reach), possibly due to visual dominance, enhanced by the visual nature of the task. Visual-proprioceptive incongruence does, however, appear to have an affect on the verbal judgments, as previously discussed, this could be due the proprioceptive signals altering the estimated actual state sufficiently to result in a mismatch with the predicted state representation. The reason for proprioceptive signals lack of influence over alterations to the motor command could be because the desired state is to get the cursor to the target location for which the proprioceptive feedback is not essential. However, why then the predicted state representation should be so greatly affected by visualproprioceptive congruence in V0-P1 is less clear. For a thorough explanation of the current results the comparator model requires information from an additional component that determines the relevance of the incoming afferent feedback and may in turn also have an influence on higher-level judgments. An independent visual-proprioceptive comparison, which enhances low-level feelings of agency over afferent feedback, achieves this.

The Comparator Model and a Sense of Ownership

A further criticism made by Synofzik et al., (2007) is that the comparator model does not successfully account for a sense of ownership (recognition that it is my body moving) because a sense of ownership does not require efference. The addition of an independent visual-proprioceptive comparison within the comparator model, as described above, can account for this and as a result can directly associate the sense of ownership with the sense of agency. The similar

brain activations observed by Balslev et al. (2006) for detecting perturbations applied to both active and passive movements supports the relationship between a sense of ownership and a sense of agency. In the passive conditions participants had to detect temporal differences between their own finger moving and the presented visual feedback. In this circumstance participants do not produce a motor command and efference copy on which to form a predicted state representation. Therefore, the normal processes of the comparator cannot be functioning and judgments are over ownership of the movement opposed to agency. However, if the comparator also had an independent visual-proprioceptive comparison, which can function in the absence of the motor command, this aspect of the network would be activated with both passive and active movements. Balslev et al. (2006) found that there was a behavioural difference between the two conditions, in that participants produced more errors with passive movements. This is also compatible with this explanation because when the movements are passively made judgments are only based on the visual-proprioceptive comparison (ownership), whilst in the active movements there is additional information available from the predicted and estimated actual state, and the desired and actual state comparisons, on which to form a judgment (agency).

8.5: Conclusions

The current findings suggest that high-level self/other judgments are strongly influenced by end point accuracy, whether or not the action matches the intentions. However, visual-proprioceptive incongruence can increase other judgments for accurate visual feedback. Taking these results in conjunction

with those from the Chapter 7, in which reducing proprioceptive feedback increased self-judgments, suggests that proprioceptive signals have a negative affect on agency, alerting the high-level processes to discrepancies. In terms of low-level agency mechanisms visual-proprioceptive congruence enhances the response to the perturbation, which leads to a more accurate movement and thus a higher percentage of high-level self-judgments. Therefore, these results suggest a greater role for proprioception than is given credit in the comparator model, supporting the presence of a separate visual-proprioceptive comparison. Such a comparison within the comparator model would mean that parts of the same network would be activated with feelings of agency and ownership. This therefore explains the results of Balslev et al. (2006) in which they found no significant difference in neural activity when detecting perturbations of active (agency) and passive (ownership) movements.

The proceeding chapter will further attempt examine the interactions between high-level judgments and low-level motor responses in relation to endpoint accuracy and visual-proprioceptive congruence. Adaptation using incremental perturbations has been said to occur without conscious awareness (Michel et al., 2007) so that low-level changes to the motor commands are made without informing high-level processes. Therefore, applying incremental perturbations in a self/other judgment task can help to examine the relative importance of endpoint accuracy and visual-proprioceptive congruence to high-level judgments. The perturbed trials will be accurate, due to adaptation, but also have visual-proprioceptive incongruence. Exposure to unperturbed trials, however, will produce inaccurate visual feedback (adapted to the absent visual perturbation) whilst visual-proprioceptive congruence is maintained.

Chapter 9

Dissociating High and Low-level Agency Mechanisms

9a: Agency and Intentions

9a.1: Introduction

The comparator model account of agency (Frith et al., 2000) involves low-level mechanisms based around a forward model that compares the estimated actual state of the motor system to a pre-formed predicted state representation. Initially a representation is produced of the desired next state of the motor system that is based on prior intentions. Following, and based on this, the movements required in order to achieve that desired state are specified, and the motor commands for executing these movements are issued. Simultaneously an efference copy is formed of the motor commands, which is used to create a predicted state representation (representation of the predicted next state of the motor system) that can then be compared to actual next state that is estimated primarily on the basis of sensory feedback. Whilst minor discrepancies of these comparisons go on to inform further specifications of the motor commands as a normal part of motor learning, larger discrepancies are interpreted as actions that are controlled or influenced by another agent. Within this account of agency, however, there is no reference to how this comparator output is conveyed to, and interpreted by, the high-level conscious processes that produce the verbal judgement of agency, which is that measured in the current,

as well as in numerous previous (e.g. Farrer et al., 2003a, Farrer et al., 2003b, Tsakiris and Haggard, 2005), experiments.

A high-level account of agency has been described by Stephens and Graham (2000), who suggest that intentions and hence a sense of agency is only inferred over our actions retrospectively based on prior knowledge and behaviour in a similar way to how we infer the intentions of other people. This account, however, suffers a similar criticism as it fails to recognise input from any low-level agency mechanisms. More recently, researches have begun to link these two aspects together (Synofzik et al., 2007 and Gallagher, 2007) suggesting the experience of agency can be affected by top-down and bottom-up processes. However, it is as yet unclear how these mechanisms interact in order to produce normal, as well as specific examples of abnormal, experience of agency.

The results from Chapter 8 demonstrate empirical evidence for a distinction between high and low-levels of agency. Participants made unimanual-reaching movements whilst holding onto a robotic manipuladum. Similar to all the experiments in the current thesis, visual feedback (cursor) was provided of these movements that was either synchronous with their actual limb trajectory or was rotated by 4-degrees away from the limb. However, an additional manipulation was applied to the movements, the presence or absence of a physical perturbation, which shifted their actual limb trajectory by an equivalent 4-degree angle. Therefore, within Chapter 8 there were four experimental conditions; Unperturbed -when the feedback was veridical, an actual representation of their intended action that was accurate relative to the target (to which participants were aiming) and the visual feedback was

congruent with the true position of the limb (visual-proprioceptive congruence). Visually Perturbed – the spatial location of the cursor was inaccurate with respect to the actual limb position (no visual-proprioceptive congruence) and the target, being rotated away from the unperturbed limb trajectory by 4-degrees. Physically Perturbed – The cursor was accurate with respect to the actual limb position (visual-proprioceptive congruence), however, was perturbed by 4-degrees away from the target as a result of a 4degree perturbation being applied to actual limb trajectory. Visually and Physically Perturbed – The actual limb trajectory was perturbed by 4-degrees away from the target whilst a simultaneous opposing visual perturbation was applied so that the cursor remained accurate with respect to the target, yet there was no congruency between the visual and proprioceptive signals.

It was found that proprioceptive information was ignored by low-level mechanisms (measured by the degree of motor response to the perturbation) in the presence of accurate visual feedback, so that the cursor remained accurate relative to the target (as accurate as in the unperturbed trials) throughout the entire reach when both visual and physical perturbations were applied, despite the actual limb position being inaccurate with respect to the target. Similarly the reaches that only had visual perturbations applied (visually perturbed) remained inaccurate throughout the movement with respect to the target (cursor perturbed away from the unperturbed limb). Of particular interest were the results for the physically perturbed trials in which the cursor was perturbed by an equivalent degree away from the target as in the visually perturbed trials, but as a result of the perturbed limb trajectory and so maintaining visualproprioceptive congruence. In these trials, after showing initial inaccuracy, the

reaches became accurate at the end of the movement (equivalent to unperturbed reaches). This degree of correction leading to an accurate endpoint seemed to be in direct response to visual-proprioceptive congruence and occurred without reaching conscious awareness (evident by the high percentage of self-judgments given in response to these trials). As such it was argued that visual-proprioceptive congruence enhanced low-level motor responses, which resulted in the motor system implementing more effective correction mechanisms.

High-level judgments, on the other hand, as measured by the self/other verbal response, were found to predominantly correspond with high endpoint accuracy, in that the most accurate movements (cursor relative to target) yielded the highest percentages of self-judgments. However, the presence of visual-proprioceptive incongruence reduced the likelihood of a self-judgment to accurate visual feedback (visually and physically perturbed reaches).

Therefore, the results of Chapter 8 suggest that high-level judgments are mainly informed by end point accuracy (intentions), whilst only being negatively informed by proprioceptive feedback (detecting discrepancies).

Interestingly, there was also a low-level motor response in the visually perturbed conditions, in that similar correction mechanisms to that seen in the physically perturbed conditions were implemented. This attempt at correction was, however, not successful, these trials being the most inaccurate and thus yielding the fewest percent self-judgments. Nevertheless for the motor system to implement alterations to the motor commands in an attempt to correct the movement, they were, in effect, treating the feedback as self. Therefore demonstrating that actions that are judged by high-level processes to be other, can still be treated by the low-level components of the motor system as self.

Previous experiments have also demonstrated instances of low-level motor responses occurring in absence of high-level conscious awareness. For example, Goodale et al. (1986) conducted an experiment in which participants were required to reach towards a target, the spatial location of which was shifted during the course of the movement. The participants were found to make the necessary on line adjustments to their reach in order to be accurate to the target whilst remaining unaware of both the alterations made to their reaches and the movements of the target. Therefore, the information concerning the shifting target location must have been available to the low-level aspects of the motor system responsible for adapting the motor commands (in order to correct the movement), yet did not reach high-level conscious awareness.

In a later experiment conducted by Slachevsky et al. (2001) participants were found to remain unaware of relatively large alterations made to their actual movements by gradually introducing larger and larger visual perturbations. The participants were required to draw straight lines with a stylus on a graphics tablet, whilst perturbations were applied to the visual feedback of these movements that gradually increased in size over consecutive trials. Therefore, in order to produce the desired straight line, the participants had to make larger and larger alterations to their actual movements away from the straight line direction. At the end of each movement the participants were asked whether the movement that they actually produced matched that presented via the visual feedback. However, because these visual perturbations, and hence motor adaptations, were implemented incrementally, the visual feedback never deviated significantly from that intended. Consequently the participants did not become consciously aware of the perturbations until a mean perturbation angle of 14-degrees. These results also (in accordance with that found in Chapter 8) suggest the high-level judgments to be concerned with the goal of the movement whilst remaining unaware of the precise movements implemented in order to achieve that goal.

The reason that participants become aware of incrementally presented perturbations at all is likely to be a result of the grossly conflicting visual and proprioceptive information. In a study similar to that completed by Slachevsky et al. (2001), Fourneret et al. (2002) found deafferented patient G.L. to remain unaware of such visual perturbations, that she was able to successfully compensate for, even with an angle 40-degrees (the largest size perturbation tested in their experiment). Moreover, there have been many studies (including those in Chapter 7 of the current thesis) that have consistently shown that reduced or absent proprioceptive feedback impedes the detection of such perturbations (increases in self-judgments) (Farrer et al., 2003 and Balslev et al., 2006). Therefore, considering these results in conjunction with those discussed above from Chapter 8, lends further support to the role of proprioceptive feedback only having a direct effect on high-level judgments through the detection of discrepancies (detecting other movements).

Therefore, if high-level judgments are predominantly informed by the outcome of a given movement as opposed to the low-level precise motor responses, it should be possible to covertly adapt participants' reaches, via the application of incremental perturbations, so as to increase the percentage of self-judgments in response to perturbed visual feedback. The reason for this being that, due to the adaptation, of which the participants have little or no conscious awareness, it will be the perturbed rather than unperturbed reaches that produce accurate visual feedback. In addition to this, as the participants are unaware of the magnitude of their motor adaptations in response to perturbed visual feedback, when presented with a true representation of their actual, adapted movements (unperturbed) such trials should be more likely to elicit an other judgment, irrespective of the presence visual-proprioceptive congruence.

Therefore in the current experiment participants made self/other judgments over perturbed (other) and unperturbed (self) visual feedback of unimanual reaching movements toward a target. In one condition, perturbations were applied incrementally so that over the course of the experiment larger and larger alterations were made to the actual movements in order to produce accurate reaches (in response to the larger and larger perturbations). Throughout the experiment, however, participants were periodically exposed to unperturbed visual feedback, revealing the actual inaccurate trajectory of their limb. In a second condition, equivalent perturbations were applied but this time presented in a random order. It was predicted that participants would give a higher percentage of self-judgments over perturbed visual feedback and a lower percentage of self-judgments over unperturbed visual feedback with incrementally compared to randomly presented perturbations. Therefore, planned comparisons were conducted between equivalent perturbations sizes of the incremental and random conditions.

9a.2: Method

Participants

A sample of 12 participants consisting of 7 females and 5 males with a mean age 27 years (range 22 - 33 years) took part in the study. All had normal or corrected to normal vision and were right handed.

Materials

The visual feedback was displayed by the Mirage system (Chapter 2) so that participants could view real time video footage of their actual reaches from the same perspective as if viewing the actual hand. Participants sat at a 260 x 1220mm table with a 215 x 480mm mirror placed on a wooden surface that was suspended 320mm over the table top. 320mm above the mirror was a iMAC OSX 10.4.1, 2.8GHz computer positioned so that the image on the screen was reflected into the mirror so as to appear as if it was in the same spatial plane as the table top (actual movements). An additional mirror (230 x 390mm) was positioned underneath the first mirror so that the reflective surface was pointing down towards the table. A small monochrome Basler A601F firewire CCD (charge-coupled device) camera (sampling at 60 Hz) with a Tamron 6mm fixed focal length lens was positioned on the edge of the tabletop approximately in line with the participant's midline and the midline of each mirror. The camera lens was pointing up at an angle of 75-degrees so that it captured the images reflected in the down-facing mirror (see Figure 9.1).

The camera relayed these visual images back to the computer, which were displayed on the screen so that they were reflected in the up-facing mirror. This allowed real time visual images of the participant's reaching movements to be reflected in the up-facing mirror to appear in the same spatial location as the actual movements. The position and angle of the camera and mirrors allowed for the visual feedback to be presented of the participant's actual limb movements (video footage) from the same perspective as if actually viewing the hand. Relaying the images through the computer enabled the application of manipulations to the feedback. An infrared reflective marker was attached to the index finger of the reaching (left) hand and a short-range 8-diode infrared camera was positioned on top of the CCD camera. The infrared camera had 8 light emitting diodes positioned around the circular periphery and a small light sensor at the top. The light sensor was obscured in order for the camera to be used in the absence of complete darkness. This set up allowed the participant's movements to be monitored by tracking the brightest point on the image display (infrared reflective marker). Black cloth covered the surface on which the mirror rested and was also draped over the back of the computer.

The computer programme was written in LabVIEW 8.2 running on windows XP and an additional standard 15-inch monitor was attached so that the experimenter could observe the experiments progression. A plastic nut was positioned on the leading edge of the table in order to give the participant a proprioceptively defined start point.

Figure 9.1: Schematic representation of the experimental set up. The camera (a) was angled at a 75° angle pointing towards the down-facing mirror (d) so that it captured the participant's actual movements, which when presented on the computer screen were reflected in the up-facing mirror (c) so as to appeared in the same spatial location as the actual movements. The infrared diodes (b) allowed tracking of the infrared reflective marker (e) attached to the index finger of the reaching hand (brightest point of the image). The angle and positioning of the CCD camera (a) and mirrors (c) (d) allowed viewing of real time video footage of the actual reaches from the same perspective as if viewing the actual hand.

Procedure

Participants sat at the table and looked down into the mirror in which they could see a black screen (a reflection of the image from the computer). Participants placed their left index finger on the start point positioned on the leading edge of the table, just out of the view of the CCD camera. Their hand was positioned in a pointing posture, and they were required to return to the

same start position at the end of each trial. At the beginning of each trial a white circular target approximately 100mm in diameter appeared and there was a sound of a tone. The tone indicated to the participant to make a unimanual reaching movement towards the location of the target, which disappeared shortly after movement onset (disappeared as soon as the marker was detected). The target position varied between four possible locations that were 200mm or 220mm forward and 50mm or 150mm right of the start location. During the reach the participants saw a live (delay ~16.7ms) monochrome video image of their actual moving hand.

Of a total of 80 trials, in ten the image was unchanged from that captured by the computer (unperturbed). Whilst the remaining 70 trials were evenly divided between ten different sized (leftward) linear perturbations (1 - 10-degrees) so that for each perturbation size there were 7 trials. The perturbations were formed by rotating the image away from the actual limb trajectory as described in Chapter 2. At the end of each trial the participants were required to make a verbal judgment as to whether the feedback received was an accurate representation of their actual movements (self/unperturbed) or not (other/perturbed). The video image of the movements remained on screen for 750ms after disappearance of the target for the participant to complete their reach following which the screen turned blank and the participant was prompted for their verbal response.

All participants took part in two conditions, which were conducted on two consecutive days. The order of which the sessions were completed was counterbalanced between participants. In one condition the perturbed trials were ordered incrementally (see Figure 9.2a) so that within the experimental

block there were ten consecutive steps (one for each size of perturbation) running directly after each other, starting with a 1-degree perturbation and running in order to the 10-degree perturbation. Within each of these steps there were 8 trials, 7 of which were perturbed trials (all of the same size perturbation) and one unperturbed trial. An unperturbed trail was randomly assigned to one of the 8 trials within each step. In the other condition the order of all trials was random (Figure 9.2b). Importantly the trials within each condition were equivalent, with equal numbers of each perturbation size in both conditions and a mean perturbation size of 5-degrees. The fundamental difference being the order in which the trials were presented. At the beginning of each session participants took part in a practice block consisting of 20 unperturbed trials in order to get participants accustomed to the set up (seeing their own hand in the mirror) and the timing of the reaches.

Figure 9.2: Example of distribution of perturbations over trials for a) incremental and b) random conditions. The data in both graphs is equivalent, only differing by the order of the trials.

9a.3: Results

The data were converted into percent correct judgments and were separated into six bins per condition, bin ZERO contained unperturbed trials only (0degree perturbation) whilst bins ONE to FIVE each contained two (sequential) perturbation sizes (e.g. bin two contained responses to trials with 1 and 2degree perturbations whist bin three contained responses to trials with 3 and 4degree perturbations). These data were then entered in to a 2x6 repeated measures ANOVA with 2 factors; CONDITION, for which there were two levels, RANDOM and INCREMENTAL, and BIN NUMBER, for which there were six levels, ZERO, ONE, TWO, THREE, FOUR and FIVE.

There was no significant main effect of CONDITION (F(1,11)=0.96, p=NS). A significant main effect was found of BIN NUMBER (F(5,55)=16.15, p<0.001) for which bin ONE (1 and 2-degree perturbations) had the greatest percentage of self-judgments (85.88%) and bin FIVE (9 and 10-degrees) having the fewest percent percentage of self-judgments (58.93%). There was also a significant CONDITION * BIN NUMBER interaction (F(5,55)=10.54, p<0.01).

Planned comparisons (Figure 9.3) revealed a significant difference between RANDOM and INCREMENTAL for bins ZERO (F(1)=20.38, p<0.001), with RANDOM (67.22%) having a higher percentage of self-judgments than INCREMENTAL (40.19%), THREE (F(1)=5.55, p<0.05) with RANDOM (76.6%) having a greater percentage of self-judgments compared to INCREMENTAL (62.5%) FOUR (F(1)=4.14, p<0.05), with INCREMENTAL (66.01%) having greater percent self-judgments than RANDOM (53.89%), and

FIVE (F(1)=20, p<0.001) with INCREMENTAL (58.92%) having greater percent self-judgments than RANDOM (32,14%). No significant differences were found for bins ONE (F(1)=0.55, p=NS) or TWO (F(1)=2.34, p=NS).

Figure 9.3: Graph showing percent self-judgments for each BIN NUMBER of the RANDOM
(open circles) and INCREMENTAL (filled squares) conditions. Self-judgments were significantly fewer for the unperturbed trials (ZERO) when the perturbed trials were presented
in incremental steps (with an unperturbed trial embedded with in each step) than when all
perturbations (including 0-degree perturbations) were presented randomly. Small to medium
sized perturbations for both conditions produced a high percentage of self-judgments, whilst
for the larger perturbations a greater number of self-judgments were produced for the
incrementally presented perturbations compared to when randomly presented. Error bars
represent standard error and asterisks denote significant differences (*= p<0.05, **=p<0.001).

9a.4: Discussion

When the perturbations were applied to the reaches in an incremental (multistep) fashion the participants appeared to adapt their perception of self in accordance with the perturbations; significantly increasing their percent self-judgments for the larger perturbation sizes compared to when all the perturbations were randomly assigned across the trials. In addition to this, the

self-judgments to the unperturbed trials that were embedded within the steps of the INCREMENTAL condition were significantly reduced in comparison to the responses for to the unperturbed trials in the RANDOM condition. In fact, in the INCREMENTAL condition, participants gave other judgments more often than self-judgments in response to unperturbed (self) visual feedback. These results clearly demonstrate that by covertly adapting the low-level motor system to perturbed visual feedback it is possible to induce a false other judgment to unperturbed (self) visual feedback. These results support those from Chapter 8 suggesting that reach accuracy was the strongest predictor of a self-judgment. In order to produce an accurate reach with perturbed visual feedback, the actual reach trajectory was deviated away from the target. This meant that when the participants saw their actual movement it was inaccurate and thus they were more likely to give an other judgment.

Updating Low-Level Mechanisms

Interestingly it was noted that during the incremental part of the experiment, not only were participants more likely to give an other judgement in response to the unperturbed trials but also they appeared to be more likely to give an other judgment to the trials that immediately followed the unperturbed trials. For example, Participant 7 responded other to both the unperturbed trial and the trial immediately following the unperturbed trial on 8 out of 10 occasions.

On further examination of the reach trajectories it was discovered that despite having given an other judgment to the inaccurate unperturbed trial, (one participant frequently laughed at these trials exclaiming; “definitely other”) on the subsequent trial the participants misreached in the opposite direction (see Figure 9.4). This means that the participants were still making adaptations to their motor commands on the basis of the preceding trial despite having judged it to be other.

Figure 9.4: Hand paths from Participant 7 of the visual feedback on 3 consecutive trials in the INCREMENTAL condition. The first reach (black solid line) is the trajectory of a reach that was adapted to the perturbed visual feedback (10-degree perturbation) and was most accurate to the target (black circle) in response to which the participant gave a self-judgment. The second reach (grey solid line) is an unperturbed trial (participants saw their actual inaccurate movement) in response to which an other judgment was given. The third trial (dashed line) is the subsequent perturbed trial in which the participant misreached in the opposite direction and also gives an other judgement. Note: hand paths illustrated do not show reaches from a fixed start point as reaches are shown in relation to a fixed target location (actual target location shifted) and the experimental set up prevented recordings of the beginning of the reach.

Therefore, although high-level processes were judging the observed action to be other, low-level mechanisms were using information concerning the observed reach error of that same movement to update the motor commands. Therefore, in effect, treating the movement as self. As a consequence when the perturbations were reintroduced in the trials that immediately followed the unperturbed trials the participants were also inaccurate with respect to the target and as such were more likely to respond other compared to trials with equivalent perturbations.

To clarify this further the incremental data were re-plotted (Figure 9.5) this time segregating the data into just 5 bins (identical to bins ONE – FIVE in the original analysis, two consecutive perturbation sizes per bin) whilst also separating the unperturbed trials and then the trials subsequent to the unperturbed trials into equivalent bins. Therefore, the percentage of self-judgments were calculated for the perturbed trials at each step of the experiment, in addition to this, the percent self-judgments were also calculated for the unperturbed trials that corresponded to each step, and in a similar manner the percent self-judgments were calculated for the perturbed trials that immediately followed the unperturbed trials for each step. 95% confidence intervals were then calculated to examine whether the percentage of self-judgments for both trial types deviated significantly from the mean self-judgments at each step.

Figure 9.5: Re-plotted data of mean percent self-judgments for the perturbed trials (open circles) unperturbed trials (black crosses) and also incorporating data points for the perturbed trials that immediately followed the unperturbed trials (filled squares). Note that the crosses and squares follow a very similar pattern, both falling outside the 95% confidence intervals (error bars) calculated for the circles. Asterisks denote significant differences.

From the graph in Figure 9.5 it is clear that the percent self-judgments given in response to the trials immediately following the unperturbed trials closely follows the pattern observed for the unperturbed trials, both of which were significantly different from mean percent self-judgments at each bin as measured by 95% confidence intervals. This result demonstrates that although the participants made a high-level judgment of other over the unperturbed visual feedback, the low-level components of the motor system were still treating the feedback as self.

Presumably we all have an initial set of pre-learned forward models that allow us to accurately reach to objects in our environment. During prism adaptation, in which our visual environment is shifted relative to our body, these original forward models prove unsuccessful, as misreaches occur in the direction of the prismatic shift. Therefore the forward models are replaced by

adapting the motor system to the new visual environment and restoring accuracy to our reaches. However, the original forward models were never actually lost as following removal of the prismatic shift, so that our visual environment returns to normal, despite initial misreaches in the opposite direction, the motor system rapidly reverts back to the original forward models so that our reaches, once again, become accurate. In the current experiment the participants' original forward modes were adapted/replaced in accordance with the perturbed visual feedback, however, following presentation of unperturbed visual feedback, in which the participants were exposed to their actual (inaccurate) limb movement, the adapted forward model quickly reverts back towards its original state, hence misreaching in the same direction as the perturbation in the subsequent trial.

One reason for this rapid reversal in adaptation could be due to the original forward models being triggered by the presence of visualproprioceptive congruence. The results from Chapter 8 have already demonstrated that when feedback from these two modalities is in agreement it can have a profound effect on updating low-level correction mechanisms: adapting to perturbations that shift the visual feedback in conjunction with the limb faster and more effectively than perturbations that lead to inaccuracy of the visual or proprioceptive information alone.

Interestingly although more self-judgments were made to the perturbed visual feedback in the incremental condition, it is clear from the graph that self-judgments gradually decreased with increasing size of perturbation. This was likely to be a result of the increasing visual-proprioceptive incongruence, which has been found to increase the likelihood of an other-judgment to accurate visual feedback (Chapter 8). The responses given for the unperturbed trials demonstrated a similar pattern, in that the amount of self-judgments deceased with the progression of the experiment (increasing perturbation size of the surrounding trials). The reason for this is also likely to be because of endpoint accuracy, for larger perturbations, the participants actual movements would have to deviate further from the target location in order for the visual feedback to remain accurate. Therefore when presented with visual feedback of their actual movement (unperturbed trial) it would be more inaccurate compared to the preceding unperturbed trials earlier on in the adaptation (actual movements compensating for smaller perturbations). Therefore the number of self-judgments to unperturbed visual feedback are consistent with the relative accuracy of the movement, the more inaccurate the reach, the more likely the participant will give an other judgment. Similar results are also evident to the trials immediately following the unperturbed trials. The greater the error observed in the unperturbed trial, the greater the degree of correction implemented by the low-level mechanisms, so the greater the inaccuracy on the subsequent perturbed trial. These results suggest that endpoint accuracy is the strongest predictor of a self-judgment and, whilst visual-proprioceptive incongruence can increase the likelihood of an other-judgment to accurate visual feedback, visual-proprioceptive congruence appears to have little effect on directly contributing to a self-judgment.

Shifting the Perception of Self

Another point of interest observed in the current results is the pattern of self-judgments across the perturbation sizes in the RANDOM condition. Instead of

participants simply producing fewer self-judgments with increasing perturbation size (such as that found in the results for the experiment in Chapter 2 and also found by Farrer et al., 2003b) The point at which the participants gave the greatest number of self-judgments was shifted towards the mean (5-degrees). Similar to in the current study, participants in Chapter 2 made self/other judgments over actual and perturbed visual feedback of unimanual reaching movements. In Chapter 2, five perturbation sizes were used that were randomly assigned across trials and the number of trials for each

perturbation were equally divided between leftwards and rightwards direction. For example, there were 24 4-degree perturbations, 12 towards the right (+4degrees) and 12 towards the left (-4-degrees). For the original analysis in Chapter 2 the data were collapsed across direction, giving rise to a one sided slope in which the percentage of self-judgments decreased with increasing size of perturbation (Figure 9.6a). Therefore, on the basis of these results, a similar pattern would be expected in random condition of the current experiment, which also involves the application of randomly assigned perturbations to visual feedback of self-generated movement, however, this was not what was found (Figure 9.6b).

Figure 9.6: a) Original data from Chapter 2 with percent self-judgments collapsed across perturbation direction. The number of self-judgments decreases with size of perturbation so that the highest number of self-judgements was given in response to the smallest (0-degrees) perturbation. b) Predicted curve of self-judgements based original graph from

Chapter 2 (black line) and actual percent self-judgements from the current experiment (open circles). In the current experiment the highest number of self-judgments is found in bin TWO (3 and 4degrees) opposed to bin ZERO (0-degrees).

There was, however, a fundamental difference between the perturbations in the current experiment and those used in Chapter 2, that is, whilst Chapter 2 used equivalently sized leftward and rightward perturbations all those in the current experiment were always towards the left. This meant that in Chapter 2 the 0-degree perturbation was also the mean perturbation, whilst in the current experiment the mean perturbation was 5-degrees. When re-plotting the data from Chapter 2 so that each perturbation has a separate data point (Figure 9.7) this relationship becomes clearer as the graph now reveals a bell shaped curve (normal distribution) in which the highest percentage of self-judgments correspond with the mean (0-degree) perturbation size.

Figure 9.7: a) Data from Chapter 2 were re-plotted so that each perturbation has a separate data point (negative values refer to leftward perturbations, positive refer to rightward perturbations). The new graph reveals a normal distribution, it is clear from the graph that the highest number of self-judgments is given in response to the 0-degrees perturbation which is also the mean. b) RANDOM data from the current chapter. Peak self-judgments approaches the mean.

Previous studies on motor learning in response to unpredictable visual perturbations (similar to those in Chapter 2 and the random condition of the current study) have found that participants tend to learn the mean of the distribution from which the perturbations are selected (Körding and Wolpert, 2004). In these experiments the participants are most accurate with the mean perturbation size. If high-level self-judgments are more likely to be given in response to the most accurate reaches, which, with such a random array of perturbations are likely to be reaches with the mean perturbation applied, then it follows that the point at which participants give the highest number of self-judgments is also likely to be the mean. However, the highest percent self-judgments in the current experiment occurred in bin TWO consisting of 3-and 4-degree perturbations, whereas the overall mean was 5-degrees. Peak percent self-judgments may have been lower than the mean due to the relatively small number of trials (most motor learning experiments use in the region of 200

trials e.g. Scheidt et al., 2001) particularly as the aim of the task was not focused on accuracy. Alternatively, as the presence of visual-proprioceptive incongruence has been found to reduce the likelihood of a self-judgment to accurate visual feedback this may, therefore, have imposed a limit upon the peak of the curve.

Extending the Model

The current results help to further demonstrate that humans are largely unaware of the precise nature of their actions. As high-level conscious awareness, even in a task such as this, in which participants are required to look out for discrepancies between actual and visually presented movements, is more concerned with the outcome of an action rather the precise motor adaptations required to achieve that outcome. Relating this to the comparator model, the current results, in conjunction with those from Chapter 8, suggest that low-level feelings of agency that are associated with the forward model component of the comparator and measured by the motor response to the visual perturbations, are concerned predominantly with comparisons between the predicted and estimated actual state and between visual and proprioceptive feedback. High-level judgments, on the other hand, that are most likely associated with mechanisms outside the comparator and are measured by the verbal self/other judgments, are mainly concerned with comparator output deriving from the comparison between the desired and estimated actual states, whether or not an action achieves its goal. Therefore, on the basis of the current experiment in conjunction with results from the preceding chapters the following additions to the comparator are proposed (Figure 9.8).

Figure 9.8: The centre of the diagram is equivalent to the original comparator as described by
Frith et al. (2000) with the surrounding elements added on the basis of evidence from the
current thesis. High-level judgments are mainly informed by the desired-[estimated] actual
state comparison (solid black arrow) and negatively informed (dashed arrows) by low-level
mechanisms and the visual-proprioceptive comparison. Low-level agency mechanisms are
informed by the predicted-actual state comparison and the visual-proprioceptive comparison.
The visual-proprioceptive comparison is an integral part of the comparator model, under
normal circumstances there is no conflict and these signals form the estimated actual state.

Firstly, on the far left hand side of the diagram is the visualproprioceptive comparison. Under normal circumstance visual and proprioceptive signals are produced directly from the actual movements and as such, are largely in agreement. The information derived from these signals is then used to help create the estimated actual state, which is used for further comparisons within the model. Therefore, these signals and thus the visualproprioceptive comparison are interregnal components involved in the internal

workings of the comparator, even though under normal circumstances no conflict is produced. In prism adaptation and in the current experiments, however, a dissociation is introduced between the visual and proprioceptive signals in which case information concerning this conflict is fed directly into the high-level components of agency and can reduce the likelihood of a self-judgment.

High-level agency mechanisms (right hand side of the diagram) are conscious processes that are likely to be situated outside the main comparator. These mechanisms are predominantly concerned with the outcome of a given action being directly informed by the desired and actual state comparison, whilst there is only evidence that they are negatively informed by the visualproprioceptive comparison and low-level agency mechanisms i.e. reducing agency feelings. Low-level agency mechanisms refer to the forward model output of the comparator and so are directly informed by predicted-actual state as well as the visual-proprioceptive comparisons. These mechanisms can have a direct effect on the specification of movement that enables more efficient adaptation of the motor commands leading to a more accurate movement and thus in turn has an indirect effect on high-level judgments.

9a.5: Conclusions

There is evidence in the current thesis for direct and indirect bottom-up effects of agency, in that enhancing low-level feelings of agency can indirectly increase the likelihood of a self-judgment (as a consequence of producing more accurate movements, see Chapter 8) and also that reducing low-level feelings of agency (comparator mismatches) can directly increase the likelihood of an other judgment to accurate visual feedback. For example, the experiment in Chapter 5 found that disrupting low-level predictive mechanisms by rIPL TMS can increase the likelihood other judgment to unperturbed (self) visual feedback. However, evidence for a similar top-down effect on agency is less forthcoming. In the current experiment, following exposure to inaccurate unperturbed visual feedback (following adaptation), participants were more likely to produce a judgment of other, which is in accordance with that expected based on intentions, whilst their low-level mechanisms preceded to use the information from the inaccurate reach when planning the subsequent movement. Therefore, it appears that reducing high-level experience of agency has no effect on low-level processes. However, it has been proposed by Michel et al., (2007) that increasing high-level experience of agency for perturbed visual feedback can increase the low-level correction mechanisms required for adaptation (low-level agency mechanisms). In the following section this theory will be discussed alongside evidence from a single neglect patient.

9b: Agency in Neglect

9b.1: Introduction

Patients suffering from neglect have been found to exhibit enhanced adaptation to prismatic perturbations (e.g. Rossetti et al., 1998). Neglect is a disorder that has been associated with right parietal damage (Driver and Mattingley, 1998), characterised by the patient's failure to acknowledge objects on, or orient towards the contralesional (normally left) side. Prism adaptation has been used as a rehabilitative strategy for the symptoms of neglect, using optical prisms to shift the visual field initially further to the right (ipsiesional, non-neglected side) resulting in an aftereffect over to the left (contralesional, neglected side) (e.g. Serino et al., 2007 and Luaute et al., 2006). Interestingly whilst the aftereffects observed in neurologically intact individuals usually last only a few minutes, aftereffects observed with neglect patients have been found to last up to four days (Pisella et al., 2002) and, in addition, the magnitude of the aftereffect has been found to be greater than observed with controls (Rossetti et al., 1998).

Similar increased aftereffects have been reproduced in neurologically intact participants. Michel et al. (2007) used a multi-step adaptation paradigm (similar to the INCREMENTAL condition described above) to enhance prism adaptation aftereffects in comparison to those produced using a traditional single-step paradigm. In the multi-step condition the perturbations were implemented incrementally in 2-degree steps using a separate pair of prism goggles for each step (ranging from 2 -10-degrees), whilst in the single-step

In the single-step condition participants immediately showed surprise at the optical displacement, recognising that the goggles had affected their vision causing them to misreach. Participants in the multi-step condition, on the other hand, failed to notice the perturbation, even in response to direct questioning at the end of the experiment. Michel et al. (2007) claimed that by increasing self-attribution, prism adaptation aftereffects can be increased and therefore the more pronounced aftereffects evident with neglect patients may be a result of patients attributing perturbed actions to themselves (over self-attribution). This is supported by observations in neglect patients who also do not spontaneously, or following direct questioning, report awareness of the prismatic perturbations (e.g. Rode et al., 2003).

Michel et al. (2007) suggested that for prism adaptation at least, neglect patients exhibit what they referred to as ‘hypernosognosia’, and which they described as ‘self-attribution of the prism-induced errors’. However, this description is misleading, as if the patient felt as though the errors were self-produced it would be expected that they would attempt to apply a strategy in order to correct them, which they do not. A more accurate definition might be that the patients do not detect the prism-induced errors. In this explanation the neglect patients are, in effect, treating the perturbations as self, however, this is because they do not detect the perturbations opposed attributing the