Bangor University

DOCTOR OF PHILOSOPHY

Priming of reach trajectory when observing actions within and beyond peripersonal space

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Award date:
2010

Awarding institution:
Bangor University

Link to publication

Priming of reach trajectory when observing actions: Within and beyond peripersonal space

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This thesis is submitted in partial fulfilment of the requirements for
the degree of Doctor of Philosophy, completed in the School of
Psychology, Bangor University.

Acknowledgements

I would first like to thank Steve Tipper for his supervision, encouragement and support throughout my PhD. I could not have had a better supervisor. I have received much good advice and encouragement from the more experienced members of his lab, Andrew Bayliss and Patric Bach, with whom it has been a pleasure to work with. Thanks also go to Ralph Pawling for his feedback on my writing. I would also like to thank my second supervisor Simon Watt for his feedback on my work, and especially for all his help with the ProReflex system.

Research does not take place in isolation and Bangor University has been a vibrant and exciting place to study. I have gained much from the collaborative atmosphere, particularly from Paul Downing and his lab, who have shared their knowledge and insights in our joint lab meetings. I would also like to thank the administration staff and the members of the technical (IT) support team; carrying out my research would not have been possible without them.

A PhD is a long project and I would like to thank my friends, Chris, Zachary, and Glyn for encouraging me and keeping my spirits up. Finally, I would also like to thank my landlord and friend Cecil Condron for all his kindness and help throughout my studies here in Bangor.

This work was supported by a Wellcome Trust Programme Grant awarded to Steven P Tipper.

Parts of this work have been communicated as follows:

Experiments 2, 4, 5, 6, 7a, 7b, 8, 9, 10:

Griffiths, D., & Tipper, S. P. (2009). Priming of reach trajectory when observing actions: Hand centred effects. *The Quarterly Journal of Experimental Psychology, 62(12),* 2450-2470.

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Abstract

The aim of this thesis was to investigate whether observation of actions by others can affect the trajectory of a reach to an object, that is, the means by which that goal is achieved. This work has been inspired by the discovery of mirror neurons in primates and evidence that humans also possess a mirror system. The 13 experiments presented in this thesis used a reaching and lifting task involving obstacle avoidance to naturalistically manipulate the heights of reach trajectories. The results from these experiments provide strong evidence that people do simulate the specific kinematics of observed reaches, and that this affects the subsequent reach of the observer. Importantly, this demonstrates that the human mirror system is concerned with more than just behavioural goals, setting us apart from other primates. The effect was independent of viewing perspective, occurring both when participants sat next to and opposite each other. Action priming by observation did not occur in all circumstances. When participants viewed obstacle avoidance outside of peripersonal space priming did not occur. The final experimental chapter presents experiments that explored further the nature of the effect of peripersonal space, providing intriguing contrasts. In some circumstances the judgment of peripersonal space appears to be purely metric, rather than space that can be reached or acted within. The last pair of experiments, however, suggest that action priming may be affected by more than just the visual properties of the observed reaches, and that higher-level concepts, such as ownership, may effect priming.

CHAPTER 1:
INTRODUCTION

1.1 Mirror neurons in the macaque monkey

> "The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka!' (I found it!) but 'That's funny ...' "- Isaac Asimov.

One of the most exciting developments in neuroscience in recent years, and one which has been responsible for motivating many new directions of investigation, has been the discovery of mirror neurons in monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). These are a special class of neurons that fire both when the monkey engages in a motor behaviour as well as when observing that behaviour.

This fascinating discovery was, however, an accidental one. Di Pellegrino and his team were investigating area F5 of a monkey's brain, taking single cell recordings of neurons that fired whilst the monkey retrieved various objects. During testing it was noticed that some of these neurons also fired when the monkey observed an experimenter picking up and placing food. Some of the neurons were quite specific, only firing when the observed movement closely matched that of the motor act the neuron coded. A great deal of research has followed on from this initial discovery. What has become clear from this research, outlined below, is that these neurons are involved in the coding of abstract goals rather than the specific motor details of the action.

Gallese, Fadiga, Fogassi, and Rizzolatti (1996) investigated and categorised the properties of mirror neurons further. Those neurons that fired for a specific action, such as precision grasping, and observation of such specific actions were defined as “strictly congruent” and comprised 31.5% of the neurons tested. A larger group of neurons, 60.9%, were described as “broadly congruent”. Whilst the eliciting motor act for these neurons was highly specific the observed actions were less so. Some neurons, for example, would fire when the monkey observed various types of grip, others would respond to the experimenter carrying out different types of hand action, such as manipulation and grasping. Some neurons were indifferent to the effector, firing when observing both hand and mouth grasping movements, seemingly goal-orientated and indifferent to how that goal was achieved. 7.6% of neurons were termed “non-congruent” where no relationship appeared to exist between the motor act and the observed action.

Mirror neurons do not respond when monkeys observe objects being grasped with tools that they have not encountered before, for example, pincers (di Pellegrino et al., 1992) and importantly they also do not fire when actions are mimicked in the absence of a goal object. This study emphasises the necessary role of a goal in mirror neuron activation. One of the best demonstrations that mirror neurons are concerned only with goal directed behaviour, rather than specific details of a viewed action, comes from Umiltà et al. (2001). The monkey observed a number of trials in which the experimenter either reached for a peanut or mimed reaching. In some trials the end part of the action was hidden by a screen (see Figure 1.1, Panel C & D). Before the start of the trial the monkey was briefly allowed to see behind the screen, which revealed the presence or absence of the object. As well as activating during the full vision condition to the experimenter grasping the object (Panel A), the mirror cells also activated in the hidden condition (Panel C) when they had seen the presence of an object behind the screen, not however when the object was absent (Panel D). Visually the two occluded conditions (with and without an object, Panels C & D) are identical, however only the object present condition caused activation. This suggests that the monkey is able to imply the outcome of the action even in the absence of crucial visual cues, create a motor representation, and recognise the goal of the action.

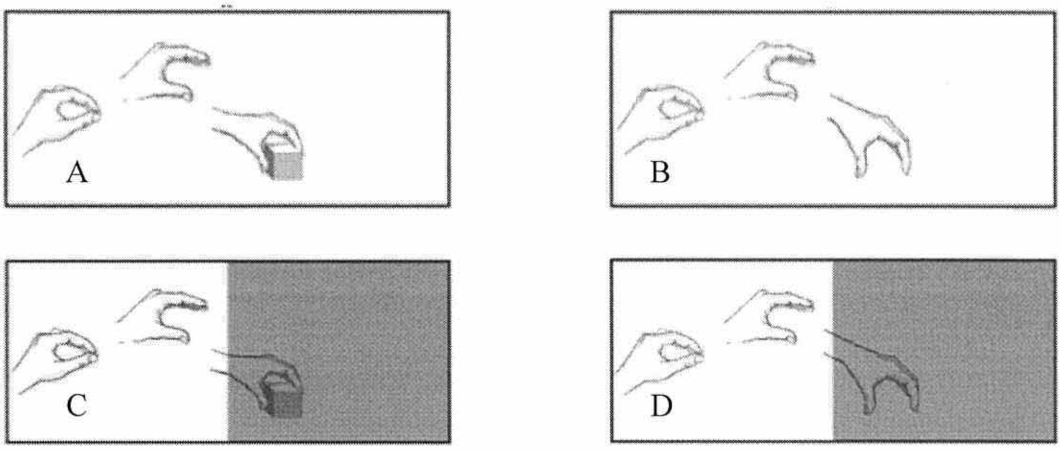


Figure 1.1. Umiltà et al. (2001).

Further evidence to suggest that mirror neurons are involved in understanding the goals of actions comes from Kohler, Keysers, Umiltà, Fogassi, Gallese, and Rizzolatti (2002). They discovered audiovisual mirror neurons in F5 that not only activated when the monkey observed or carried out a specific action but also when the monkey heard the sound of that specific action being carried out, for example cracking a peanut. This discovery again suggests that mirror neurons are coding the higher goal of an action rather than any more basic aspect, such as movement kinematics.

Even those mirror neurons that appear to code for specific movements, such as grasping, have been shown to code for the act of acquiring the object rather than the specific kinematics of the grasp itself. For example, Umiltà et al. (2008), while recording in F5, trained monkeys to use two types of pliers to grasp objects. The first type required the usual grasping and closure of the hand to pick up an object; the second required the reverse action, that the monkey must release the grip on the pliers in order to grasp an object. They found that neurons that fired during various phases of a grasping movement also fired during the same temporal phases of the grasp with normal pliers; further they found that the same neurons also fired during the same temporal phases using the reverse pliers, even though, for example, the equivalent final phase of the normal pliers gripping movement in the reverse pliers involved opening the fingers. The neurons were indifferent to the exact manner in which the goal was achieved.

Further research (Fogassi, Gallese, Fadiga, & Rizzolatti, 1998; Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005) has revealed that neurons in monkeys' inferior parietal lobe (IPL) also have mirror properties. Like the neurons in F5, most of the neurons tested coded for specific actions, such as grasping, however most of these neurons show marked differences in activation depending on the subsequent acts. Fogassi et al. (2005) trained the monkeys to carry out two types of action: First, reach and grasp and then to place the object in a container and second, reach and grasp followed by eating. Even though the initial reach-to-grasp stage was identical, most of the neurons responded either to grasping followed by placing or grasping followed by eating, but not to both. They also tested the neurons during observation of these motor sequences. Most of the neurons fired during action observation and most of them showed the same pattern of discrimination, that is some neurons fired preferentially for grasping acts followed by eating and some when the final act was placing the object. The monkey was aware at the initiation of action of its own movement and what its intentions were, that is the purpose of the grasp. The fact that the monkey's neurons also showed the same pattern of discrimination for an observed grasp indicates that it was aware, at some level, of the intentions or goal of the observed motor act.

In summary, mirror neurons in monkeys give them the ability to process observed actions in the areas of the brain that the monkey uses itself to plan and execute its own movements. These neurons seem concerned, not with the specific kinematics of how the observed action was achieved, but with deriving the intended goal of the motor act allowing the monkeys to go beyond the simple visually presented information, and indeed extract and anticipate the goal of an action in the absence of full visual information (Kohler et al., 2002; Umiltà et al., 2001). Additionally, these neurons are not activated by seeing a goal object alone, or by intransitive movements (movements in the absence of a goal). The neurons only activate when observed action is directed towards a goal.

1.2 A human mirror system

Since the discovery of mirror neurons in monkeys much work has investigated the possibility of a human mirror system, and the extent of its similarity to that of the macaque monkey. The first work, though, to indicate that humans might use the same area for action and observation of movement in fact predates the discovery of mirror neurons in monkeys. Gastaut and Bert (1954) measured electroencephalographic (EEG) recordings in subjects whilst they viewed human movements. They found that the mu rhythm, (alpha range: 8-12Hz) present at rest, is suppressed not only when the subject is performing actions but also when observing actions. Muthukumaraswamy, Johnson, and McNair (2004) have further shown that this suppression is even greater for object-directed grasps.

More recent evidence for a human mirror system has come from transcranial magnetic stimulation (TMS) studies. During TMS a magnetic field is applied, via a coil, close to the subject's motor cortex. The magnetic field induces a small current in the brain activating the motor cortex. This produces a small electrical potential, called an MEP (motor-evoked potential), which can be measured in muscles, such as the arm or hand. Studies have shown that MEPs are higher during action observation, selectively in muscles that would be used to self-produce the observed action (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Strafella & Paus, 2000; Gangitano, Mottaghy, & Pascual-Leone, 2001). Further, the muscle activation follows the same temporal pattern as self-produced movements, both for transitive (goal-orientated) and intransitive actions, suggesting that observed movements are simulated.

Various functional magnetic resonance imaging (fMRI) studies have sought to identify the human homologues of F5 and the IPL, and to assess to what extent other areas may be involved in the human mirror system. The inferior frontal cortex has been suggested as the human equivalent for F5, including Broca's area, BA44 and the ventral premotor cortex, BA6 (Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Binkofski, Buccino, Posse, Seitz, Rizzolatti, & Freund, 1999; see

Morin & Grèzes, 2008, for a review) Additionally Buccino et al. (2001) show that not only does observation of action activate the premotor cortex but that it does so in a somatotopic manner.

A number of studies have shown both observation and action activate the IPL (Hamilton & Grafton, 2006; Schmuelof & Zohary, 2006; Gazzola et al., 2007). Others have additionally shown activation in the superior parietal lobe (SPL) (Iacoboni et al., 1999; Filimon, Nelson, Hagler, & Sereno, 2007; Grèzes & Decety, 2001) as well as the intraparietal sulcus (IPS) (Filimon et al.; Grèzes & Decety). Buccino et al. (2001) again found that activation of the parietal lobe, for object related actions, was also somatotopically organised, with the IPL being active for mouth movements and the IPS for hand; the hand activations in that experiment matching closely with those found by Binkofski et al. (1999) when hands manipulated objects.

There has been some debate as to whether the activation of a particular area of cortex by both action production and action observation really reflects mirror cell activity (Gazzola & Keysers, 2009; Etzel, Gazzola, & Keysers, 2009). It is possible that within a region there are two completely distinct populations of cells, one encoding action production while another encoding action perception. There have been some recent attempts to find better evidence for the existence of human mirror systems (e.g. Etzel et al.). One particular study, Oosterhof, Wigget, Diedrichsen, Tipper, and Downing (2010), used multi-voxel pattern analysis (MVPA) techniques to look for common coding. This study demonstrated that a classifier trained to distinguish various produced actions was above chance in identifying the same actions when they were observed, and vice versa when training on viewed action and testing on produced actions. Interestingly they found that anterior parietal areas coded more for the goal of the action, whereas the postcentral gyrus coded more for the effector properties used in the action. These results demonstrate the existence of a common neural coding for the visual and motor aspects of action.

It is proposed that the mirror system in humans is involved in the understanding of actions of others (see Rizzolatti 2005; Rizzolatti & Craighero, 2004). It might be expected that if areas in the human brain are simultaneously involved in the execution of action and the simulation of the actions of others that damage to these areas, which might manifest themselves in difficulties in the execution of action should lead to deficits in understanding of the actions of others. Such evidence would be compelling causal evidence for a mirror neuron system in humans.

There are few studies that have established a connection between damage in brain areas associated with the mirror system in humans and deficits in action perception. Saygin (2007), for example, tested a large group of stroke patients for deficits in biological motion perception. His lesion analysis revealed that the superior temporal and premotor frontal areas were associated with deficits in biological motion perception. Another study, Pazzaglia, Smania, Corato, and Aglioti (2008), examined patients with limb apraxia and had difficulty performing gestures. They found that patients with damage to the opercular and triangularis areas of the frontal gyrus also had deficits in their ability to identify the correct execution of familiar actions.

The paucity of evidence from patients is surprising, however, one point to consider is that brain trauma and damage tends to occur in older adults. It is possible that some areas of the brain may be necessary to develop an understanding of observed actions and the goals of those actions. However, having developed a general understanding of action those areas may later no longer be necessary or of less importance in understanding actions.

It has also been suggested by some that a mirror system in humans may underlie the development of theory of mind (e.g. Gallese & Goldman, 1998). Whilst the ability to simulate the observed actions of other may facilitate the development of a theory of mind evidence from blind children would suggest that the ability to observe and simulate the actions of others is not necessary to develop a theory of mind. Peterson, Peterson and Webb (2000) show that while there are some developmental delays in acquiring a theory of mind (quite possibly due to more limited social interactions with their peers and a general lack of visual information) blind children do develop a theory of mind.

The idea that the mirror system in humans and mirror neurons in monkeys are involved in action understanding has often been raised (see for example Rizzolatti & Craighero, 2004; Gallese & Goldman, 1998). Kilner, Friston, and Frith (2007) point out that the details of how the mirror system might enable this to take place are not explicitly described. They draw upon the predictive or forward model account of motor control (Wolpert & Miall, 1996; see also Wolpert & Flanagan, 2001), to explain one very plausible way in which a mirror system might mediate action understanding. When we move this produces consequences. These consequences can be assessed using sensory feedback. However this feedback is slow and impractical for fast movements. Wolpert and Flanagan suggest that when we move our motor commands are used to predict or estimate the outcomes of our actions, which is much faster. However these estimates alone are not sufficient to produce accurate and effective movements. After sometime the actual consequence of movement may drift from the prediction. They propose that these estimates are then attenuated by sensory feedback. Extending this idea further they suggest that use a number of different forward models in a given situation and then select the model whose prediction most closely resembles the sensory feedback.

Kilner et al. (2007) suggest that that a mirror system could be involved in a reverse of this model, whereby the sensory visual input is used to generate a model predicting the ongoing consequence of the observed action. This prediction is then compared with the ongoing outcome of the observed action, the error in prediction is then used to attenuate the model of the ongoing action and change the prediction. Flanagan and Johansson (2003) have found support for this theory from their study which shows that eye movements of participants observing actions are predictive rather than simply reactive to the observed movements.

The studies discussed above provide strong evidence for the existence of a mirror system in humans, that is, a system where observed movements are simulated in the brain areas that are involved in the preparation and execution of movements. The techniques used though, are non-invasive and indirect, and provide no evidence for the existence of specific mirror neurons in humans. However, a very recent study published by Mukamel, Ekstrom, Kaplan, Iacoboni, and Fried (2010) (see also Keysers & Gazzola, 2010, for a discussion) has provided the first data to show that actual mirror neurons exist in humans. Normally the invasive technique of single cell recording is not possible in humans, however, patients with severe epilepsy sometimes have areas in their brain responsible for triggering their seizures removed. In order to identify the areas responsible for the seizures implants, which record cell activity, are placed in the brain and the patient monitored until seizures occur. Some of these patients volunteer to participate in experiments.

The patients observed and carried out four types of action, frowns, smiles, power grip and precision grip. The action instructions were words. Mukamel et al. (2010) were able to identify a number of neurons that responded to both action and observation of action. Some of those neurons exhibited selectivity for a particular action over another, for example showing significantly higher firing rates for the observation and execution of a power grip over a precision grip. The areas of the brain examined were not determined by areas most likely to be involved in mirroring activities but by clinical relevance. The further revelation from this study is that these mirror neurons were found outside areas that have so far been considered the most likely homologues to the monkey F5 and IPL, that is the human IPL and the ventral premotor cortex (PMv). The human mirror neurons were found in the medial frontal lobe (supplementary motor area) and in the medial temporal lobe (the hippocampus, parahippocampal gyrus, and entorhinal cortex).

While the majority of studies have provided evidence for a mirror system in the IPL and PMv, Keysers and Gazzola (2010) point out that there are studies that have given some hint that areas outside these regions may be involved in mirroring. Further detailed discussion of the precise geography of the brain areas that may form part of the mirror system in humans is beyond the scope of this thesis. Rather, the crucial point is that there is strong evidence for a mirror system in humans.

A number of these studies mentioned above show that intransitive actions and observations of such actions do activate areas identified as being part of the human mirror system, in contrast to the evidence from primate studies mentioned already. One key difference between humans and monkeys would seem to be the ability to imitate, and one could well expect this to be reflected in differences in the human mirror system. Furthermore, evidence from action imitation also seems to support the idea that mirror systems encode behavioural goals, and are not simply responding to specific forms of action. For example, Gergely, Bekkering, and Kiraly (2002) investigated imitation with 14 month-old infants. They wanted to know under what circumstances infants would imitate a new behaviour. The infants observed someone turning on a light box on a desk using their head to touch it. In one situation the demonstrator's hands were occupied holding a blanket around them, in the other the hands were free. The infants were far more likely to imitate the demonstrator in the hands-free condition (69%), using their heads rather than their hands, compared to the hands-occupied condition (21%). In the hands-occupied condition the infants seemed able to asses the rationale behind using the head, whereas in the hands free condition the actual action itself may have been seen to be a goal or certainly to have some unseen advantage over the hands.

One study (Filimon et al., 2007) has attempted to investigate whether observing and carrying out reach actions activates common areas of the brain, that is if there is a mirror system for encoding reaching. This fMRI study compared executing, observing and imagining reach actions. The study showed common activation in the dorsal premotor cortex, the superior parietal lobe (SPL), and the intraparietal sulcus. Certainly the SPL has been identified in other studies as being involved in reaching (Culham, Gallivan, Cavina-Pratesi, & Quinlan, 2008), however the intraparietal sulcus has been identified as being involved in grasping movements (Culham, 2004; Tunik, Frey, & Grafton, 2005; Rice, Tunik, & Grafton, 2006; see also Cohen, Cross, Tunik, Grafton, & Culham, 2009). One problem with this study is that the reaching conditions (execution, imagery, and observation) all involved the presence of objects. Participants observed a video of a reach towards an object (though the video stopped just before the grasp was made) and executed reaches toward an object that appeared on a screen. Even though no actual grasping took place it is not certain that activations found relate to the encoding of the actual *reach* trajectory. The activations may have related to the final implied *goal*, in the same way that monkey neurons activated even when the final goal was obscured (Umiltà et al., 2001, see Figure 1.1).

It is indeed a key issue of what exactly is encoded when observing actions. There are various hypotheses. It might be the case that highly specific motor processes are simulated, such as the path the hand takes to reach an object, and the specific patterns of the finger movements as they shape to grasp the target. On the other hand, it is possible that the mirror system's primary role is to understand the goal of the action, with little concern for the specific way the goal is achieved. Thus, to understand current, and be able to predict future behaviour, it may be necessary only to understand the goal of the action, such as picking up a glass to drink, and not the specific properties of how the hand reached the glass. There is clear evidence to support the latter idea that the action simulation processes are concerned with encoding the behavioural goal, rather than the low-level specific properties of the action. To date there have been no studies that have truly attempted to separate the means by which goals are achieved from the goal itself and to assess whether or not the mirror system in humans simulates this aspect of action.

1.3 Action priming

Actions can be primed by a number of things. One of the most well known action priming effects is the Simon Effect (Simon, 1969). When spatial location, for example an object appearing on the left or right, is irrelevant to a task it can still prime a congruent response in the respective left or right responding hand. Visuomotor priming was first demonstrated using objects by Craighero, Fadiga, Umiltà, and Rizzolatti (1996). They found that participants responded faster to initiating a grip when they had been primed by a picture of the to-be-gripped object (see also Craighero, Fadiga, Rizzolatti, & Umiltà, 1998). Other action priming effects have shown that the actions evoked by an object are automatically computed. For example, when viewing a coffee cup whose handle is oriented towards the right hand, right-hand responses in object classification tasks are speeded. Importantly these action-affordance priming effects are produced even though participants do not have to grasp the object at any time, suggesting they are automatic (e.g., Ellis & Tucker, 2000; Tucker & Ellis, 1998).

Other studies have revealed that numbers, for example, can prime actions. Badets, Andres, Di Luca, and Pesenti (2007) had participants judge if they could grasp a rod between their thumb and index finger. When the judgment was preceded by a small number, participants underestimated their grasp, whereas they overestimated their grasp when the rod was preceded by a large number. In the same vein Moretto and di Pellegrino (2008) found numbers primed different grips. Participants saw a number and had to either make a precision or power grip depending on whether the number was odd or even. Larger numbers primed a faster response for a power grip and smaller numbers primed faster precision grips. Similarly, task irrelevant words have been found to prime the size of grip aperture (Gentilucci & Gangitano, 1998; Glover, Rosenbaum, Graham, & Dixon, 2004), as have odours associated with small and large objects (Tubaldi, Ansuini, Tirindelli, & Castiello, 2008).

1.3.1 Action priming from previous actions

One important type of action priming is the effect of a person's previous action on their current action. Rabbitt and Vyas (1970), for example, looked at reaction times (RTs) during sequences of key presses. Participants were asked to make keystrokes in response to one of four digits that appeared on screen. They responded using either their left or right hand, and either their middle or index finger. Fastest RTs occurred when the previous action used the same finger on the other hand and the slowest responses when the other finger had been used on the other hand. Keystrokes using the different finger on the same hand gave an intermediate RT. Not only is this evidence that previous actions affect current actions but also, along with studies such as that from Rosenbaum, Weber, Hazelett, and Hindorff (1986), evidence for reuse of motor plans.

Rosenbaum et al. (1986) theorised that the priming and interference effects observed in actions such as typing sequences, finger tapping, and letter recital is a result of motor plan recycling. They suggested that when carrying out a sequence of similar actions, rather than discarding an enacted motor plan and then creating another, it is more efficient, in computational effort and in time, to take the existing plan and modify only those aspects that differ between the two actions. Actions that differ significantly may require a new action plan altogether, as well as discarding the old one, creating a time cost, but perhaps not affecting other aspects of the action such as shape of grasp.

The idea of reusing and being affected by one's own previous actions is important. The mirror system hypothesis predicts that observed movements are simulated in the same areas that are involved in planning and executing an action. If one's previous actions prime one's current actions, then it might be expected that observation of action also primes one's subsequent actions. The aim of this thesis is to investigate whether observed reach trajectories are simulated. One way to investigate this is to first establish that a person's current reach is affected by their previous reach and then to investigate if observing a reach can affect a person's subsequent reach.

The following section presents a number of experiments that have used action priming to demonstrate that observed goal-directed actions, such as grasping, and intransitive finger movements are simulated and effect the observer's subsequent movements.

1.3.2 Action priming by observation of action

Action observation has been found to affect various aspects of subsequent movement execution. For example, one of the first studies to investigate action priming by observation was Brass, Bekkering, Wohlschläger, and Prinz (2000). Participants were required to lift either their index or middle finger on their right hand in response to seeing a mirrored hand lift the appropriate finger or seeing a hand with a cross on the nail of a finger. There were three types of trial in each condition, baseline, congruent, and incongruent (see Figure 1.2). In the finger movement condition the baseline was a video of finger movement without a cross on any finger (see Figure 1.2, Panel A). In the latter two trial types, in addition to viewing the movement, a cross appeared on the fingernail either on the moving finger or the stationary finger (Panels C & D). In the spatial finger cue baseline condition a photograph of a hand with no fingers lifted appeared and the cross indicated which finger should be lifted (Panel B). In the congruent and incongruent trials for this condition they saw a finger being lifted, which they were to ignore. That finger was either the same or different to the finger with the cross (Panels C & D).

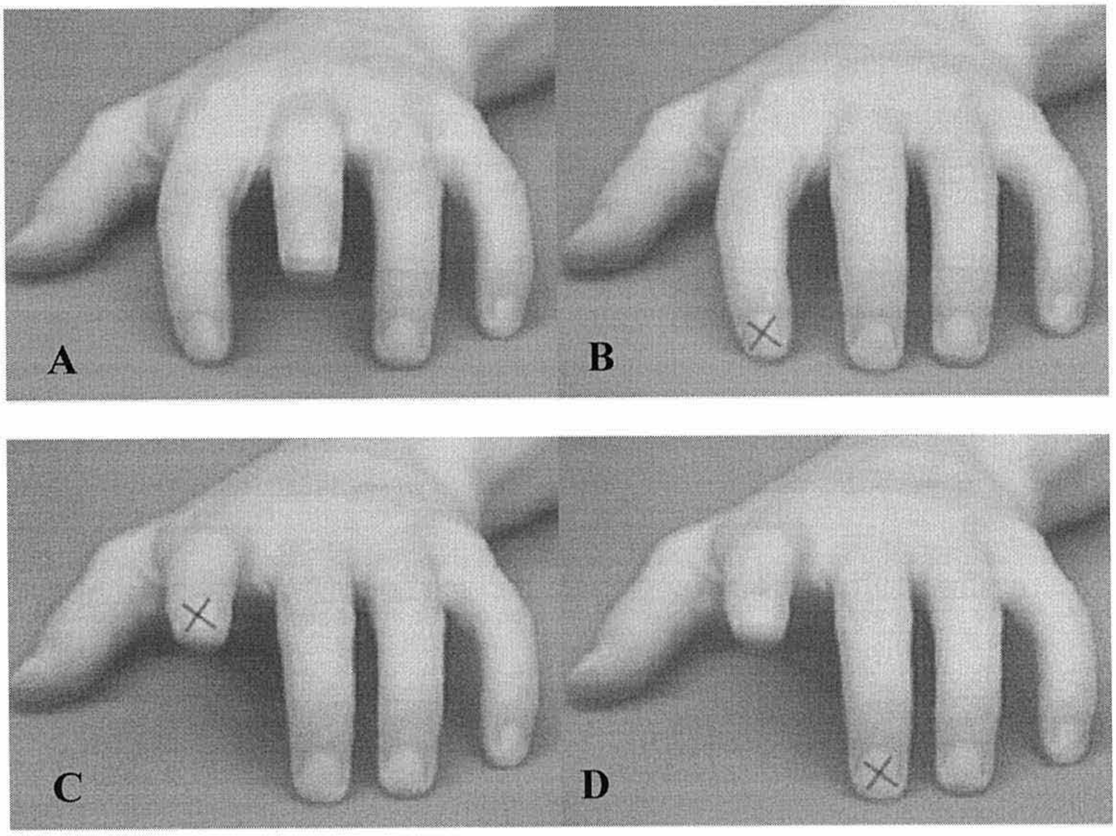


Figure 1.2. Brass et al. (2000). Participants responded to either the finger movement or the position of the cross.
Panel A: Baseline trial, finger movement. Participants saw a video of a finger moving with no cross marked.
Panel B: Baseline trial, cross. Participants viewed a photograph of a finger with a cross marked.
Panel C: The congruent trial for both the finger movement and cross condition.
Panel D: The incongruent trial for both the finger movement and cross condition.

Brass et al. (2000) found that finger movement stimuli produced faster RTs than the cross on the fingernail. In addition there was a significant effect of irrelevant finger movement in the cross condition, where finger movement significantly interfered with or facilitated RTs. However the presence of the cross in the finger movement condition only affected the incongruent condition and this effect was smaller. A further experiment from this study used the same stimuli but instead required the participants to respond with a tapping movement. In this experiment the observation of finger lift gave no RT advantages for the finger tapping condition compared to the spatial finger cue, nor was there any facilitation when the finger movement in the spatial cue condition was congruent. There was however an effect in both conditions in the incongruent trial types.

These experiments were carefully designed and it can be concluded that the finger movements themselves interfered with and facilitates movement in addition to any spatial compatibility effects that might be present. In addition these results showed that mere observation of movement is not sufficient for facilitation but that the observed movement should be similar in type to that of the executed action.

Brass, Bekkering, and Prinz (2001) replicated and extended the results of the previous experiments and investigated the possibility that the effects previously described may be due to dynamic spatial compatibility. In their first experiment participants made blocks of responses, either lifting their finger or tapping their finger. Within a block they saw both lifting and tapping movements, creating compatible and incompatible conditions. RTs were faster in the compatible compared to incompatible conditions, confirming the previous results that movement must be compatible in order for facilitation to take place and that non-identical movements interfere with movement execution. It could be argued that this effect was being created by a dynamic spatial compatibility, that is, the mere movement of a stimulus, any stimulus, upward was priming the RT advantage in the finger lifting condition, and vice versa in the tapping condition. The second experiment therefore included additional stimuli to that of the first one. In these stimuli squares moved up and down as the fingernail did, but with no view of the hand. The compatibility effects when viewing the moving finger were significantly greater than when viewing the moving square, demonstrating that the finger movements were producing effects over and above the priming of the spatial dynamics.

Aspects other than RTs, such as the kinematics of movement, have also been investigated. Castiello, Lusher, Mari, Edwards, and Humphreys (2002) examined the effects of priming on grasping movements. Participants viewed someone grasping either a small or large object. Their sight was obscured whilst a large or small object was placed in front of them and they then had to reach for the object. In valid trials, where participants viewed the grasping of the same object that they then acted upon, Castiello et al. found that time to peak grip aperture was longer and that the grip aperture itself was smaller. In addition time to peak velocity of movement was longer on valid trials. These results occurred both in trials where the chances of a valid trial were 80% and 50%.

As part of the same study participants also saw a robot hand grasping objects. On these trials the validity of the priming trial had no effect. It should be noted, though, that the robot hand did not match the kinematics of the human demonstrator, exhibiting no differences in grasping the two sizes of objects.

Edwards, Humphreys, and Castiello (2003) carried out a follow on study using the same paradigm. This later study differed in two ways. The chances of a valid trial were reduced to 20% and on some of the trials the observation of an action on the object was replaced by only the presentation of the object. In this study trial validity did not affect peak grip aperture, compatibility effects were only observed in the time to peak velocity of the reach and time to peak grip aperture. As with the previous study no affect of RT was found. The striking result from this experiment was that the presentation of the object alone also produced priming results, leaving doubt as to whether action priming had taken place at all in these experiments, and that any priming might be accounted for by object priming. However the observation of the robot hand produced no priming, which is surprising as it would have been expected that the objects presence would have some priming effect, suggesting that biological motion may have made some contribution to the priming.

Clearly seeing an object by itself can make a powerful contribution to action priming. It is not clear, though, whether all of the priming is accounted for by the mere observation of the object and that there was no contribution from action observation. The studies by Brass et al. (2000, 2001), however, would strongly suggest that action priming can take place and that that action must be matched to the action to be performed for there to be an advantage rather than interference.

Unlike the studies from Brass et al. (2000, 2001), who looked at intransitive actions, Dijkerman and Smit (2007) looked at the effect of observation of goal-orientated action during a grasping task. While participants grasped a cube they simultaneously observed an experimenter grasp or point to a cube that was the same, smaller, or larger than the participant's cube. In addition, participants observed trials where the experimenter made grasping or pointing movements without a cube. Observation of pointing actions towards the cube and both the pointing and grasping in the absence of an object had no effect on participants' movements. Only in the grasping condition where the cube was a different size to the participants' cube was any interference observed. The maximum grip aperture was larger when the participants viewed grasping of an object larger than their own than when they saw the same sized object being grasped. Whilst there was no action-absent (cube only) condition, only the comparison of two human action conditions, the fact that only the identical action (grasping) produced priming suggests that action observation had primed subsequent movements.

Interestingly the observed movement did not affect any of the reaching kinematics, that is, the movement time, time to peak velocity, peak velocity, and time to maximum peak aperture, suggesting that in previous studies where reach kinematics have been affected (Castiello et al., 2002; Edwards, et al., 2003) this could have been the effect of object priming rather than by the observed movement. There is certainly evidence for the dissociation of the reach and grasping components of prehension (Jeannerod, 1988; Chaminade, Meltzoff, & Decety, 2002) and that evidence so far has only suggested that grasping components are affected by observation of goal-orientated action. This would certainly fit with theories that mirror neurons and the mirror system in humans is concerned with the goal of an action rather than the means, specific kinematics, by which this goal is achieved.

Another study that investigates action priming by observation, but controls for the effect of the object or goal acted upon, was carried out by Massen (2009). She investigated the contribution of both action observation and observation of the movement of a physical device. A device was designed so that the arm of the device could be moved to touch one of two targets, near or far. The device (see Figure 1.3) could pivot either on the right or the left so that an identical movement of the device, say toward the far target, could be produced by an arm movement away from the body (left pivot) or toward the body (right pivot). The participants were in two groups, those who observed a movement using the right handle and those who observed a movement made with the left handle. To produce the movement in the device shown in Figure 1.3 the left handle would be pulled and not pushed. Thus the Masson was able to manipulate a change in hand direction, target, and device/bar movement independently. Neither the observation of the same hand movement (push/pull) alone or the same movement of the device alone produced RT advantages, only when the hand movement observed and the device movement observed were the same was a RT advantage seen. This experiment demonstrated that there was a contribution both from the device (goal object) observed and the biological motion observed to the priming of subsequent action. This result is somewhat different from those obtained in primate studies such as Umiltà et al. (2008). In that study the mirror neurons were indifferent to the exact manner in which the goal was achieved, activating to both the squeezing and release of pincers to obtain the goal. Massen's study hints that in humans embodiment of observed actions may include information additional to the goal achieved.

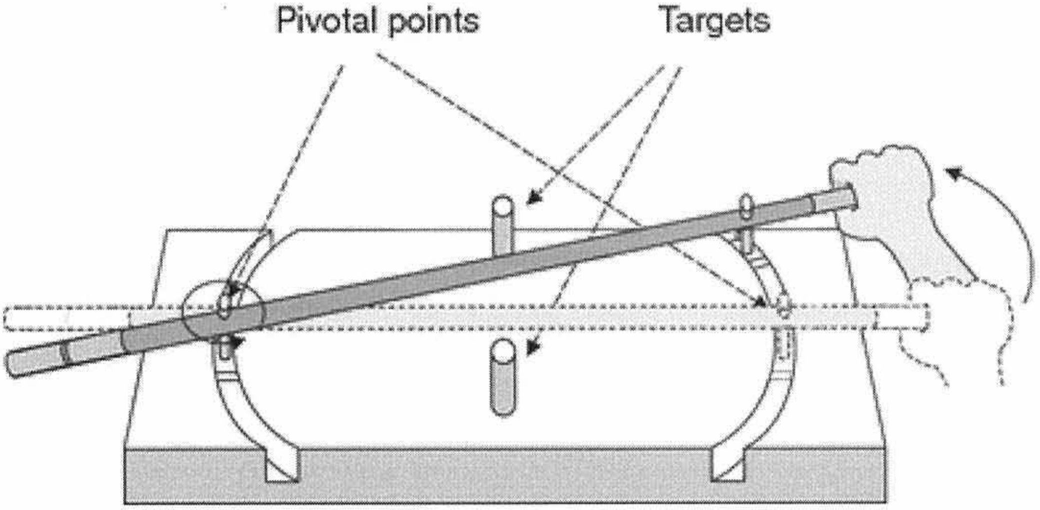


Figure 1.3. Massen (2009). This figure shows the device used. Participants had to push or pull the bar to touch one of the targets. The device could be set to pivot on either the left (as shown here) or the right. When the device pivots on the left-hand side participants must push forward to reach the far target. When the device pivots on the right participants must bring the bar towards them to reach the far target, and vice versa for the near target.

If movement observation in humans activates the same brain areas that are used to execute and plan movements then action observation whilst simultaneously producing an action would be expected to cause interference if that action is not the same. In their studies Kilner, Pauligan, and Blakemore (2003) and Kilner, Hamilton, and Blakemore (2007) required participants to make up-down or left-right movements while observing another person making the same or different movement. There was significant variance in participant's movement when they viewed incongruent but not congruent movements. If humans used two separate systems, one involved in action generation and another involved in understanding the action of another it might be expected that observation of action would not affect the execution of action, or that observation of action, being an additional cognitive load, would affect execution, but that that effect would occur regardless of the type of observed action. This differential effect dependent on the type of action observed suggests that observation and execution of movement are using the same system and that identical observed movements cause less or no interference because they match the motor plan for the currently enacted movement.

Further evidence for action priming comes from Jonas et al. (2007) who used a slightly different approach and explored the effects of observed behaviour on inhibition of return (IOR). Inhibition of return is the suppression or inhibition of processing of a location where the viewer's attention has been recently drawn. Jonas et al. presented participants with a photo of a resting hand with a dot on the index and little finger. In the cueing condition the participants saw either a finger lift (with the dot remaining on the nail) or the same still hand but with the dot moved further up the finger. This was followed by a short delay and then another photograph instructing which finger was to be lifted. There was an overall IOR effect, that is, where the finger or dot in the cue photograph matched the instruction finger RTs were significantly slower. This IOR was significant for both the dot movement cue and the finger movement cue, however in addition they found that the finger cue produced significantly more IOR. This study provides evidence of action simulation and that it can lead to, in addition to IOR, an inhibition of action. If observed actions are simulated in a mirror system the question of why people do not imitate every action seen must be accounted for. This study provides evidence that simulation does take place and that inhibition also occurs when that action is not required. The suggestion of inhibition resulting from action observation fits in with other findings by Mukamel et al. (2010) who also found human neurons that fired when executing actions but that showed inhibition when observing those same actions.

1.4 Conclusion

This introduction has reviewed the literature including those from both fMRI and action priming studies. Research to date has so far only found evidence to suggest that in goal-orientated actions it is the goal and actions directed upon the goal object (such as grasp aperture) that are simulated. Some researchers, such as Filimon et al. (2007), have attempted to investigate areas of the brain that might encode the reach component of prehensile action. The experimental design, however, does not rule out the possibility that in fact it is the goal that has been encoded in the observation and execution conditions, rather than the reach.

Priming studies have examined aspects of reach kinematics (Castiello et al., 2002; Edwards et al., 2003) but again they have not provided definitive evidence that the priming that took place was not in fact the result of mere exposure to the goal object, and it therefore cannot be said that reaching kinematics of the observed action have been encoded and simulated. Whilst studies such as those of Kilner et al. (2003, 2007) have examined intransitive actions without a goal object, and found the kinematics of the movement to be affected, these actions might better be classified as a goal in themselves. These are not incidental or unconscious movements to reach a goal, but consciously produced actions that may in themselves be considered a goal.

It is therefore unresolved whether the means by which a goal is achieved, for example the path of a hand taken to reach a cup, is simulated when actions are observed. The purpose of this thesis is to present a number of experiments which investigate whether in fact reach trajectories, the reaching component of prehensile action, are simulated. Demonstration of this will not only extend the knowledge of how the human mirror system works but require previous assumptions, that our mirror system is only concerned with the goals and final intentions of actions, to be laid aside. It will also provide further evidence of another element of behaviour that sets humans apart from close primate relatives.

1.5 Overview of experimental chapters

As stated earlier, if an aspect of observed movement is simulated in the brain in the same areas that are involved in action execution then it would be expected that this action would affect subsequent movement. Therefore the methodology that will be used in the following studies will be a priming paradigm, to examine whether reach kinematics are simulated and affect subsequent behaviour.

In order to establish a paradigm that will be expected to produce priming from observed action it must first be established that the action when carried out by an individual first primes their own behaviour. If an individual's own previous actions do not prime their subsequent actions it cannot be expected that the observation of the actions of others would have an effect on their subsequent actions. Therefore the first experimental chapter, Chapter 2, will present two experiments that establish an experimental paradigm that produced a carry over effect from previous actions that affect subsequent reach path trajectories towards a goal object. The third experiment in this chapter extended the within-person priming effect to show that the effect is independent of the final action carried out on the goal object.

Chapter 3 introduces the methodology for a two-person experiment that allows priming of action by observation to be assessed. In the first two experiments participants were seated opposite each other, viewing actions from an allocentric perspective. These experiments produced no priming by action observation. In the third experiment in this chapter participants were seated next to each other, viewing actions from an egocentric perspective. In this experiment participant were significantly affected by viewing the reach trajectory of another. Chapter 3 ends with a discussion about the possibility that the priming effects found were mitigated by viewing perspective.

Having established that reach path action priming can occur from an egocentric perspective Chapter 4 explores this further with two experiments where the participants sat at 90° to each other. Additionally these experiments also explore the effect of sharing an obstacle or a target object. These two experiments did not deliver a reduced effect, compared to the egocentric perspective, which would have been expected if the effect was contingent upon the angle of action observation. Based on Tipper et al. (1992, 1997) work it was theorised that perhaps the effects were hand-centred, that is, that observed actions were only embodied when the observed actions took place in peripersonal space. With this idea in mind the third experiment in this chapter was designed with participants again seated opposite each other (allocentric perspective) but this time closer together, with the observed obstacle avoidance taking place within the peripersonal space of the observer. This experiment produced a significant priming effect by action observation.

As discussed at the beginning of this section actions can be facilitated by many different stimuli, including smell, spatial location and an object's affordances. In any given experiment more than one of these may be contributing to any observed action priming, or indeed account for all of the observed priming. The experiments in this chapter provide strong evidence that action priming of reach trajectory took place. It was, however, important to carefully design experiments to eliminate the possibility that the behaviour had not been primed, for example, by the goal object or obstacle. Therefore the final experiment in Chapter 4 investigated whether the priming found in the previous experiments is attributable to the presence of the obstacle or goal object alone. The presentation of blocks alone, in the absence of action, did not elicit any priming effects.

Chapter 5 reports on two experiments that sought to further explore the effects of peripersonal space. The first experiment in that chapter examines whether the priming effect in peripersonal space can be extinguished when participants are unable to act upon the other participant's blocks. A Perspex® screen was employed to separate participants, allowing them to see the other participant's blocks but not to act on them. The presence of the Perspex® screen did not, in fact, eliminate the action priming effect. The final pair of experiments replicated the effect that observation of trajectory reach paths do not prime actions when the action observed is outside peripersonal space, at 90° perspective. They further explore whether the sense of peripersonal space can be extended by inspiring a sense of ownership of the objects being used outside peripersonal space. The use of shared blocks and workspace produced a significant priming effect, despite the fact the observed actions were outside peripersonal space.

In the final Chapter an overview of the main findings of the thesis are outlined. The work has shown for the first time that the kinematics of another person's reach path are internally represented in an observer. This representation influences subsequent reach path, where similar curved trajectories are produced. The key variable as to whether such reach path priming effects are detected appears to be that the observed action be within the peripersonal space of the observer. However, the final study suggests some limits to the peripersonal space account, as ownership/possession of acted upon objects can produce effects beyond peripersonal space, suggesting higher cognitive processes may be involved. Further studies to investigate such issues in the future are discussed.

CHAPTER 2:

SINGLE-PERSON PILOT STUDIES

2.1 Introduction

The introduction to this thesis presented and discussed some of the research that has considered the nature and the question of whether humans posses a mirror system, that is, a system that processes observed actions in the same areas of the brain that deal with the planning and execution of actions. The evidence is compelling and that humans have a mirror system is widely accepted in the scientific community. What is still in question is the nature of that system, how it differs from that of primates and what aspects of movement are simulated during action observation.

Monkey mirror neurons appear only to code for observed goal-directed actions, not intransitive or mimed actions, and what is encoded is related more to the goal of the action rather than specific kinematics of the movement (e.g., Kohler et al, 2002; Umiltà et al. 2008). In humans there is strong evidence that, in addition to coding for goal directed actions, intransitive actions such as mimes are also coded. There is to date no evidence that the kinematics of observed reaches, the means by which a goal is reached, is encoded in any way.

The purpose of this thesis is to investigate whether humans encode the kinematics of other's reaches. If this is the case, it is expected that encoding will take place in areas of the brain that encode a person's own reach kinematics. In order to develop a method by which the effect of other's movements can be investigated it is first necessary to establish that a person creates a kinematic plan to reach a target, rather than guiding their movement to an object online, that is, whilst the movement is in progress. If a reach to a goal is guided online it is unlikely to be affected by previous observation of others' actions, or indeed their own previous actions.

If the kinematics of the reach trajectories of others are encoded and effect a person's subsequent movement it should also be expected that a person's own previous reaches affect their subsequent reach. If a particular methodology does not produce within-person priming it is unlikely to yield priming by observation of another's reach. Therefore this first experimental chapter contains three experiments which investigated within-person reaching, with a view to establishing a methodology to investigate the effects of observation of reaching on reach kinematics.

Investigations by Gergely et al. (2002) have shown that actions following observation can depend on how that action is presented. Participants can easily become aware of the purpose of an experiment and what factors are being manipulated. It is therefore undesirable that the nature of the reach trajectory should be obvious, to ensure that any encoding is of an implicit nature. It was therefore necessary to design an experiment that manipulated reach trajectory covertly, presenting the most ecologically valid scenario. The most natural reason to deviate one's reach is to avoid an obstacle.

Therefore participants in the first series of experiments were required to simply reach out and pick up a target object, which was sometimes presented alone and other times in the presence of an obstacle. The nature of previous trials was manipulated. It was predicted that if a prior reach leaves a representation in memory, a subsequent reach trajectory might be influenced by it. Thus a previous reach around or over an obstacle could evoke more curved reaches on the next trial even if no obstacle is present.

2.2 Experiment 1: Single-person, reaching horizontally around an obstacle

2.2.1 Method

2.2.1.1 Participants

All of the participants in each of the studies reported in this thesis gave informed consent and participated in return for course credits. All of the experiments received the approval of the School of Psychology's ethics committee. Each participant had normal or corrected-to-normal vision and was right handed. In this experiment there were 14 students (3 male) with a mean age of 20.1years.

2.2.1.2 Materials and apparatus

All the experiments that will be described in this thesis involved motion capture of hand movements. The movements were recorded using a retro reflective marker that was placed on the back of each participant's wrist, approximately between the scaphoid and lunate bones. In addition a marker was placed on the work surface as a reference point. Participants' movements were tracked using a Qualisys ProReflex motion capturing system (Qualisys AB, Gothenburg, Sweden). The data were recorded using Qualisys Track Manager (QTM) software. Data was sampled at 200Hz by two ProReflex cameras suspended approximately 2m above the work surface. Each sample produced three coordinates, x, y, and z, which identified the position of a marker in 3D space.

The cameras were calibrated prior to each experiment. This data was then processed in MatLab by programs written by the author.

The wooden target block was 9 cm high, with a base 3 x 2 cm. The wooden obstacle block to be avoided was 18 cm high, with a base 4.5 x 4.5 cm.

2.2.1.3 Procedure and design

In all experiments participants sat at a desk with the chair adjusted so that the arm to be used to reach the target rested comfortably on the desk with the forearm at right angles to the upper arm and the hand approximately 20 cm from the trunk. The far edge of the target block was always 40 cm from the starting position of the participant's reaching hand. The near edge of the obstacle, when present, was 20 cm from the hand (see Figure 2.1).

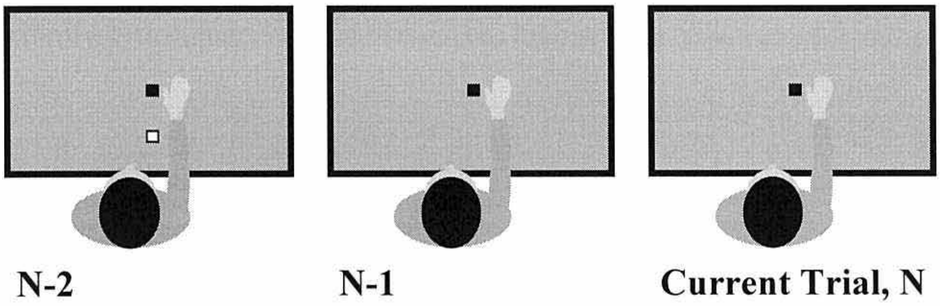


Figure 2.1. Single-person reaching. This diagram shows an example series of reaches, where the same person performs on every trial. N-1 is the trial that preceded the current trial. N-2 is the last but one trial. The black square is the target; the white square is the obstacle. This example shows an O-No-No trial sequence.

Participants were asked to reach for, lift up, and replace the target block back on its marker, using normal speed with their right hand. The experimenter demonstrated the movement speed required and all participants carried out 10 practice movements before the start of the experiment. Too slow a movement would have been unrepresentative of naturalistic actions. Acting as quickly as possible, as is required in some types of response experiments, would have produced many more collisions with the blocks, reducing data collected, and again not be representative of typical everyday reaches. On 50% of the reaches there was an obstacle present. In Experiment 1 participants were asked to avoid the obstacle by reaching around it in the horizontal plane.

At the beginning of the experiment the participant was asked to close their eyes. The experimenter then set up the blocks and gave the instruction to the participant to open their eyes. This was the cue for the participant to initiate their action, reaching, lifting the block and placing it down again on the same spot. They then brought their hand back to the start position and closed their eyes. The experimenter then rearranged the blocks for the next trial. It was important for the participant not to be able to see the experimenter rearranging the blocks. If observed action does in fact affect the observer's subsequent action it was important that the experimenter's movements did not have an influence. When the obstacle block was not in use it was kept out of sight.

The purpose of these initial three experiments was to establish a paradigm that could be adapted to examine between-person effects. The experiments in this chapter will consider the effect of the previous two reaches on the current trial. The relevance of considering two previous trials will be discussed later in relation to the two-person experiments. The current trial, previous trial, and trial before last will be referred to as n, n-1, and n-2 trials respectively.

Considering the current reach and those of n-1 and n-2 gives eight possible trial orders. A trial may have an obstacle, henceforth referred to as O (Obstacle trial) or have no obstacle, NO (No Obstacle).

The eight possible trial orders:

n-2	**n-1**	**n**
NO	NO	NO
O	NO	NO
NO	O	NO
O	O	NO

n-2	**n-1**	**n**
NO	NO	O
O	NO	O
NO	O	O
O	O	O

Each of these trial orders occured 10 times in random order for each participant, giving 80 trials plus two initial trials to establish the n-2 history for the first relevant trial (which were disregarded). It should therefore be noted that the previous trials were of no predictive value to the current trial.

2.2.2 Results

For each trial the maximum deviation to the right, from a line envisaged between the starting point and the target object, was calculated for the outward reach. An average of the ten trials for each of the eight trial types, mentioned above, was calculated (see Table 1 in Appendix A). Trials where participants knocked over a block were excluded, as were the two trials that followed it. If previous trials affect the current one it is important to remove trials following collisions. A number of trials were also excluded where part of the trajectory was not properly tracked by the equipment. In this experiment 3.13% of trials were excluded. The excluded trials did not occur significantly more for a certain trial type.

This experiment used real objects, and it was found that participants were careful to avoid knocking over the obstacle block by clearing it with as wide a margin as possible. This meant that during obstacle reaches there was very little variation in the maximum width. The obstacle trials had significantly smaller standard deviations than the no-obstacle trials, [*F*(1,13) =16.18, *p*=.002]. Due to this lack of variability no effects of the presence or absence of an obstacle on the previous trials (n-1 and n-2) were found when the current trial was an obstacle trial. Though, as can be seen from Table 1b in Appendix A, the averages do show the same directional pattern as the non-obstacle trials. Therefore only the current trials without an obstacle will be discussed in the results sections. Table 1b, in Appendix A, shows the means of the obstacle trials of each experiment in the thesis. Table 1a shows the means of the non-obstacle trials.

Figure 2.2 represents the results. The widths were analysed using a two-way within-subjects analysis of variance (ANOVA), with two factors: n-1 trial type (with or without obstacle) and n-2 trial type. This analysis revealed a main effect of both the n-1 trial [*F*(1,13) =7.30, *p*=.018], and the n-2 trial [*F* (1,13)=25.27, *p*=.039]. That is, participants' reaches were significantly wider if the previous trial (n-1) or the trial before last (n-2) contained an obstacle, than if the previous trials had not contained obstacles. There was no significant interaction between n-1 and n-2 [*F*(1,13)=0.29, *p*=.600]. Figure 2.2 also shows the results of planned comparisons between conditions. These comparisons compared the baseline No-No-No condition with O-No-No (obstacle on n-2 trial) showing the n-2 effect to be significant [*t*=2.42, *p*=.031], and No-No-No compared to No-O-No showing that the n-1 effect was also significant [*t*=2.89, *p*=.013]. All of the *t* tests presented in this chapter are two-tailed.

When questioned afterwards none of the participants guessed the purpose of the experiment and were not aware of having made wider reaches following obstacle trials.

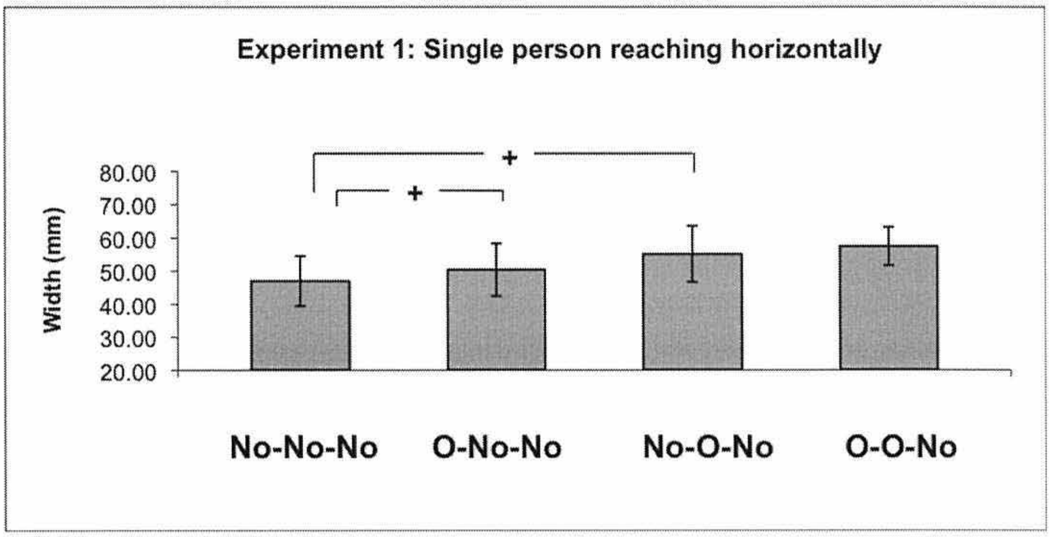


Figure 2.2. Means of the maximum width deviation for non-obstacle reach trials (trial n), with their standard errors. The bars marked + show a significant *t* test result at *p*<.05. These are two-tailed *t* tests, as are those in the following experiments in this chapter. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

In this experiment and those that follow the dependent variable selected is maximum height. As noted in the discussion of experiments such as Castiello et al. (2002) and Edwards et al. (2003) in Chapter One, there are many different variables that can be obtained which provide information about a trajectory. These include the time to peak velocity, total movement time, time to initiate action, and measures such as initial angular offset (the angular difference between the direct path and the initial path taken). Unfortunately the limitations of the equipment (the use of only two cameras) meant that in a large number of trials the initial part of the reach was not recorded. Participants' hand movements at the start of trials often occluded the wrist markers from at least one of the cameras, preventing the calculation of the markers position in 3D space. It would have been possible to have independently recorded the starting and finishing times of the movements, however it was felt that it was important that participants did not feel that their movement times were being explicitly recorded, which might have caused more rushed, less natural movements.

2.2.3 Discussion

These results show that a person's current reach kinematics can be primed by their previous reaches. On trials where no obstacle was present reaches toward the target were more curved than they needed to be if they had followed obstacle trials. Furthermore the current reach is affected not just by the last trial but also the trial previous to that (n-2). The persistence of the priming effect over at least two trials indicates that obstacle avoidance is a good paradigm choice to examine the effects of reach trajectory priming by action observation between two people alternating trials. This paradigm allows the investigation of the effect of action observation from the previous trial (n-1) as well as the effect of an individual's own previous action (n-2).

2.3 Experiment 2: Single-person, reaching vertically over an obstacle

2.3.1 Introduction

The objective of these first experiments was to establish a protocol that could be used with two participants to examine the effect of observing another's previous actions on a participant's subsequent action. The first experiment established that participants are affected by their previous actions when reaching around obstacles in the horizontal plane. On further consideration however, it was decided that this movement was not ideal for a two-person experiment. Consider, for example, two right-handed persons seated opposite each other. If one participant is primed by viewing the reach of the other what aspect of the reach will they embody? They may translate the movement to their own perspective and produce wider reaches (reaching further out to their right) after seeing the other participant reach around an obstacle. They may, however, having seen the other participant's right hand reach out further to the viewing participant's left, make a *less* wide reach to the right. Both these aspects may in fact influence the subsequent reach. It was therefore decided that observing actions reaching *over* an obstacle in the vertical plane would reduce the possible variables of reach kinematics that may influence the observer. It was a consideration that reaching over an obstacle requires slightly more energy to lift the hand against gravity, therefore a single-person experiment to examine whether vertical reaching also produced within-person priming effects was carried out. This experiment was in all other ways identical to Experiment 1, except that participants were given the instruction to reach over the obstacle and not around it.

2.3.2 Method

2.3.2.1 Participants

A total of 24 students (four male), with a mean age of 20.3 years, participated in this study.

2.3.2.2 Materials and apparatus

The materials and apparatus are the same as in Experiment 1.

2.3.2.3 Procedure and design

The procedure and design are identical to Experiment 1 except that participants are instructed to reach over the obstacle.

2.3.3 Results

A number of trials were removed (2.08%) where participants knocked over blocks and where the full trajectory of the reach was not recorded by the equipment. For each trial the maximum height above the table of the wrist on the outward reach was calculated. As with Experiment 1 it was found that participants cleared the obstacle with as much space as possible, and again the reaches in the obstacle trials showed significantly less variation than in the non-obstacle trials [F=(1,23)=41.05, $p< .001$]. The results were analysed as in Experiment 1, using a two-way within-subjects ANOVA on the data from the non-obstacle trials. There was a main effect of both the n-1 trial, [$F(1,23)= 14.57$, $p< .001$], and the n-2 trial, [$F(1,23)= 10.36$, $p< .004$]. Participants reached higher on trials that followed trials where they had had to avoid an obstacle, than if they had not had to avoid an obstacle. There was no significant interaction between the effect of the last reach (n-1) and the reach before last (n-2) [$F(1,23)= 2.39$, $p=.136$]. Figure 2.3 illustrates the results as well as results of the planned comparisons. The comparison between the baseline No-No-No condition and O-No-No showed a significant n-2 effect [$t = 2.13, p = .044$], as did the comparison between the baseline and the No-O-No condition [$t = 2.52, p = .019$].

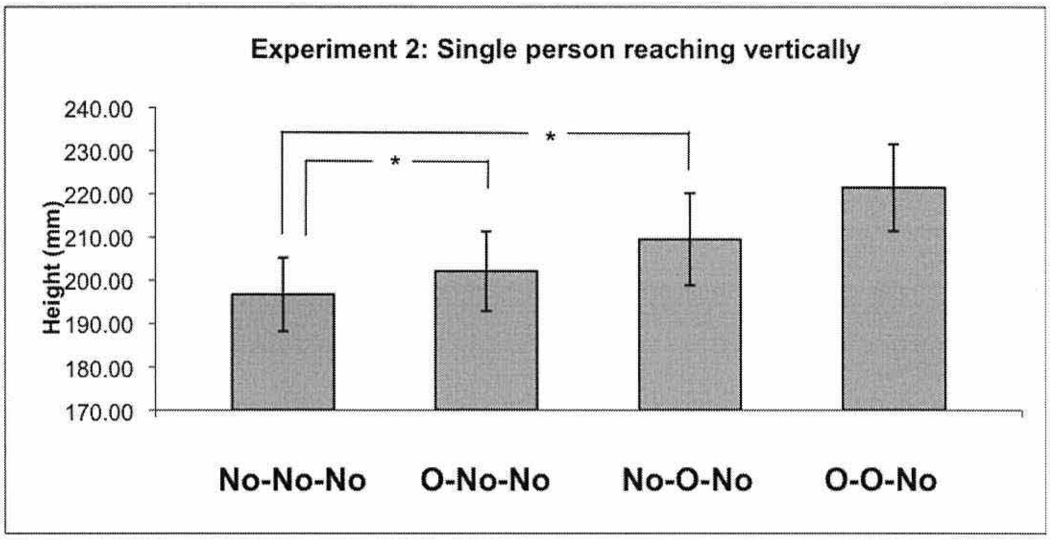


Figure 2.3. Means of the maximum height for non-obstacle reach trials (trial n), with their standard errors. The bars marked + show a significant *t* test result at *p*<.05. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

2.3.4 Discussion

Though the movement required to avoid obstacles in this experiment differs from that in Experiment 1, this methodology still produces action priming over at least two trials. This confirms that an individual's reaching kinematics are affected by their previous actions.

After completion of these experiments Jax and Rosenbaum (2007) published their work on action priming of reach trajectories. Their work on within-person priming is broadly similar to that presented here. The most notable difference is that rather than using actual blocks in a naturalistic setting they chose to use a virtual environment. In their experiments participants moved a manipulandum, which forced their movements to remain in the horizontal plane. Participants' movements were relayed to a screen as a stick figure. From a central starting position they moved their hands to a target in one of twelve positions (presented on the screen) around the central starting point. On some trials participants would have to curve their arm around to avoid a virtual obstacle which appeared on the screen.

Jax and Rosenbaum (2007) measured initial angular offset (IAO) and curvature index. IAO was the angle between the direct path from the starting position to the target and the actual initial path direction. The curvature index was the maximum perpendicular distance of the hand from the direct path between the starting position and the target, divided by the straight line distance between the starting and end points and then multiplied by 100. Their results essentially confirm those reported in Experiments 1 and 2 of this thesis. They found that the curvature index, which is a similar measure as the maximum width in Experiment 1, was significantly larger following obstacle present trials but only when the current trial was without an obstacle. IAO was greater following obstacle trials both when the current trial contained an obstacle and when it did not. Unlike the experiments presented here, the target location varied. Jax and Rosenbaum found effects even when the previous reach was to a target at a different location. Thus the effect generalised across the workspace.

In their second experiment they compared three groups of participants. For one group the obstacle randomly appeared. The other two groups had a predictable sequence of O O No No O O (O-obstacle; No-obstacle absent); one group was informed of this in advance, the other not. They found no significant difference between any of the groups. This suggests that the priming effect is not based on the expectance of the obstacle being present or absent.

The first two experiments in this chapter find the same results as the work of Jax and Rosenbaum (2007) and extended it into a more ecologically valid setting by using actual blocks, where participant made more naturalistic movements. Both studies provide strong evidence that within-person action priming is a robust effect. The purpose of these experiments was to establish an experimental paradigm that would lend itself to studying the effect of observing reach trajectories of one individual on subsequent reach trajectories of another. This methodology meets this criterion.

2.4 Experiment 3: Single-person, reaching with two different targets

2.4.1 Introduction

This experiment was designed to look at whether the influence of previous trials was linked to the particular goal, or whether the priming was indifferent to that goal and the manipulation necessary on that goal. Studies investigating priming of the grasp component of a reach have found that grasping can be primed by the mere presentation of an object (Edwards et al., 2003; Craighero, Umiltà, Fadiga, & Rizzolatti, 1996; Craighero et al., 1998). If priming is the result of merely seeing the goal or linked to the previous actions on a particular goal then the alternation of different goal objects and different actions on those goal objects should not produce action priming at n-1. Research however suggests that the reach and grasp components of a prehensile action are processed by two separate circuits (e.g. Tanné-Gariépy, Rouiller, & Boussaoud, 2002; Cavina-Pratesi, Ietswaart, Humphreys, Lestou, & Milner, 2010). This separation, first proposed by Jeannerod (1981), predicts that the reach toward an object would be largely unaffected by the preparation of the hand to act on that object. It was therefore expected that this experiment would produce both an n-1 and n-2 effect.

2.4.2 Method

2.4.2.1 Participants

A total of 14 students (3 male), with a mean age of 20.4 years, participated in this study.

2.4.2.2 Materials and apparatus

The materials and apparatus are the same as in the previous experiment, except that there are two goal objects, one yellow and one blue. Both goal objects are 9 cm high, with a base 3 x 2 cm. The blue block had a 1 cm^3 piece of foam placed on top and was fixed to a thin 10 cm^2 wooden base (painted black to match the table surface) to prevent the block from falling when pressed.

2.4.2.2 Procedure and design

The procedure and design of this experiment are the same as Experiment 2 except as follows: the goal object and action on that object alternated between trials. When the yellow block was presented participants were instructed to reach, lift the block with a pincer movement, and place it down in its original position. When the blue block was presented they were instructed to reach out and use their index finger to press down on the foam attached to the top of the object and return their hand to its starting position. As with the previous two experiments there were eight trial orders of obstacle and no-obstacle trials. With the two different types of actions this produced sixteen different trial types:

Push **n-2**	**Lift** **n-1**	**Push** **n**
NO	NO	NO
O	NO	NO
NO	O	NO
O	O	NO
NO	NO	O
O	NO	O
NO	O	O
O	O	O

Lift **n-2**	**Push** **n-1**	**Lift** **n**
NO	NO	NO
O	NO	NO
NO	O	NO
O	O	NO
NO	NO	O
O	NO	O
NO	O	O
O	O	O

O = Obstacle trial No = No obstacle trial

Each trial type occurred ten times, a total of 160 trials. The trials were split into two blocks of 82, 80 trials plus two initial trials to establish the n-2 history for the first trials of relevance.

2.4.3 Results

Trials where participants knocked over blocks and where the full trajectory of the reach was not recorded by the equipment were removed (2.32%). For each trial the maximum height of the wrist above the table on the outward reach was calculated. The heights were analysed using a two-way within-subjects ANOVA for each person's results. There were two factors, n-1, the effect of the differing action (with or without obstacle), and n-2, the effect of the same action previously carried out. The analysis revealed main effects for both n-1, the effect of the previous reach with a different action [$F(1,13)=12.15$, $p=.004$] and n-2, the effect of the previous reach with the same action [$F(1,13)=15.04$, $p=.002$]. There was no significant interaction between n-1 and n-2 [$F(1,13)=0.11$, $p=.746$]. Figure 2.4 shows the results collapsed across action type. The chart shows the planned comparisons between the No-No-No condition and No-O-No which was significant [*t*(1,13)=2.24, *p*=.043], as was the comparison between No-No-No and O-No-No [*t*(1,13)= 2.45, *p*=.029].

Overall the participant's current reach trajectory is affected by not only the previous reach using the same action on the same goal object (n-2) but also by the previous reach (n-1) where the final action and the previous action were different.

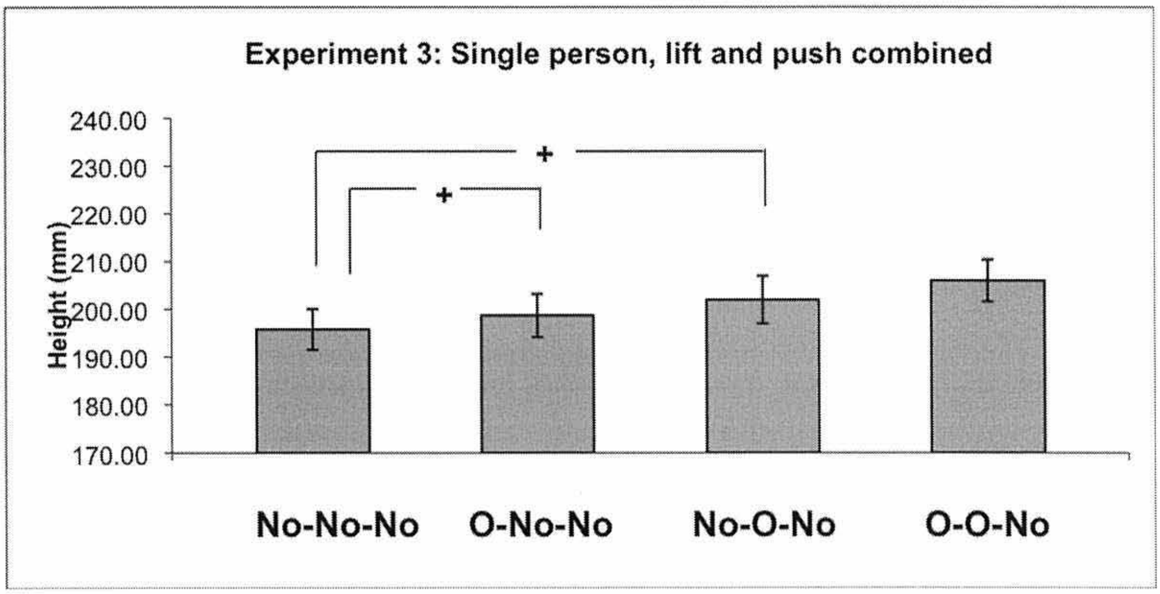


Figure 2.4. Means of the maximum height for non-obstacle reach trials (trial n), with their standard errors. The bars marked + show a significant *t* test result at *p*<.05. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

2.4.4 Discussion

The purpose of this experiment was to investigate whether the priming effect of a previous action on the reach path was linked to the goal object and the action on that object or whether the reach path priming effect was independent of the goal and final action. The results from this experiment are very clear. Reach trajectory is primed when an obstacle is avoided on the previous trial (n-1) even when the current and previous actions and objects are quite different. This result rules out notions that retrieval of prior reach trajectory is determined by goal or goal action identity. That is, if the reach was linked to an action plan involving the final goal-orientated action (that is a separate plan for each action, lift or push) then it would be expected that the n-1 reach would have no influence at all on the current reach. The fact that the n-1 reach action influences the current reach trajectory suggests that priming can occur independently of the final goal action.

This result fits in with the literature which suggests that the transport component of prehensile action is largely processed separately from the final action on a goal, though this theory is still controversial. Jeannerod (1981) first proposed a model that suggested a reach-to-grasp movement could be split into two separate components or channels, transport of the hand to the object and the grip or manipulation to be carried out on that object.

This theory finds support from both monkey and human studies. Two particular inactivation studies have provided evidence that the ability to grasp and manipulate a goal object can be impaired whilst accurate reaching remains intact. Fogassi, Gallese, Buccino, Craighero, Fadiga and Rizzolatti (2001) and Gallese, Murata, Kaseda, Niki, and Sakata (1994) temporarily deactivated two areas of the macaque monkey brain, F5 and anterior intraparietal area (AIP) respectively using muscimol injections. Both studies found impaired hand shaping to grasp objects, but no deficit in reaching accuracy. The role of the AIP in manipulating objects is also confirmed by Sakata, Taira, Murata, and Mine (1995) who found the majority of neurons in this area coded for specific object manipulations. Conversely Fattori, Kutz, Breveglieri, Marzocchi, and Galletti (2005) have carried out single-cell recording in area V6A of the macaque monkey, finding that neurons here show selectivity for different phases of a reach, reach directions and spatial locations. Inactivation studies on V6A in monkeys significantly affected reaching speed and showed misreaching to locations (Battaglini, Muzur, Galletti, Skrap, Brovelli, & Fattori, 2002). Other single-cell recording studies have also found area F2 (the dorsal premotor cortex - PMd) to be involved with direction and distance of reach (Kurata, 1993; Messier & Kalaska, 2000). Further areas, in the superior parietal lobe (SPL), involved in reaching include the medial intraparietal area (MIP) (Johnson, Ferraina, Bianchi, & Caminiti, 1996), which is involved in arm movement and direction, and an area described as the parietal reach region (PRR) by Batista and Andersen (2001) involved in reach planning, which may include part of the MIP and V6A (Gail & Andersen 2006; Snyder, Batista, & Anderson, 2000).

It is proposed that two separate circuits exist in the monkey brain, a dorso-lateral circuit consisting of the AIP (in the inferior parietal lobe - IPL) and F5 (ventral premotor cortex - PMv) for goal directed grasping (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), and a dorso-medial circuit area V6A, MIP (in the superior parietal lobe SPL) and F2 (PMd) dealing with reaching (Tanné-Gariépy et al., 2002). Tanné-Gariépy et al. tested the degree of separation of these two paths in a within-monkey tracer study. They injected the monkeys with retrograde tracers in the PMv and PMd and did in fact find the projections to these areas from the IPL and SPL, respectively, to be largely segregated. Monkey research allows researchers, particularly in the case of single cell recordings, to gain a great deal more information about how areas of the monkey brain function compared to the research carried out on human participants. Whilst primate brains do differ from the human brain, many of the landmarks and structures are similar. The research on monkey brains provides valuable insight and can help guide investigation into the functioning of the human brain.

A number of studies, using various techniques, provide evidence for human homologues of the areas described above, showing the same anatomical separation of areas, that is SPL and PMd involvement in reaching and IPL and PMv involvement in grasping.

The human homologue to the AIP is the anterior intraparietal sulcus (aIPS). Hamilton and Grafton (2006) carried out a repetition suppression fMRI experiment and found that the aIPS was sensitive to viewing repeated goals but not when viewing repeated reach trajectories. Culham (2004) also found aIPS activation for grasping in her fMRI study (see also Culham, Danckert, DeSouza, Gati, Menon, & Goodale, 2003; Frey, Vinton, Norlund, & Grafton 2005). TMS applied to the aIPS region is found to disrupt the formation of grasping movements whilst the reach component was unaffected (Tunik et al., 2005; Rice et al., 2006; see also Cohen et al., 2009). This result also fits with the findings that patients with lesions in the aIPS have deficits in finger coordination, but few problems with reaching (Binkofski et al., 1998). This same study found that control subjects showed activation in this area when grasping. The human homologue for the other area demonstrated in monkeys to be involved in grasping (F5) is the ventral premotor cortex which includes Brodmann's area 44. PET studies have shown this area to be activated when grasping objects (Rizzolatti et al., 1996; Grafton, Arbib, Fadiga, & Rizzolatti, 1996).

Several areas in the human brain have been identified as being involved with reaching and potentially corresponding to the monkey MIP and V6A in the SPL. Connolly, Andersen, and Goodale (2003) carried out an fMRI study which examined areas involved in pointing movements and planning to point (versus planning a saccade) and found activation in the SPL, anterior to the parieto-occipital sulcus (the superior parieto-occipital cortex – SPOC) in an area anatomically similar to the monkey V6A. As Connolly et al. point out, this anatomical similarity parallels that between the monkey (AIP) and the human (aIPS) grasping area. In an interesting double dissociation with the patients studied by Binkofski et al. (1998), Cavina-Pratesi et al. (2010) reported on an optic ataxia patient who has impairments in reaching but under some circumstances does not show difficulties in gripping. Optic ataxia patients typically show gripping impairments as well as reaching difficulties. Cavina-Pratesi et al. suggest that this occurs where damage extends beyond reach regions to include the aIPS, and is a secondary rather than a primary symptom of optic ataxia.

Culham et al. (2008) also identified the SPOC as being involved with arm transportation movements. Additionally, when passively viewing locations, it is more active for those locations within reach, that is within peripersonal space. Filimon, Nelson, Huang, and Sereno (2009) also found the SPOC active during reach, but that it was more active for visual than non-visual reaching. They also found activations for reaching in the SPL's anterior precuneus (Brodmann's Area 7a, Scheperjans et al., 2008) and medial intraparietal sulcus (mIPS), present with and without vision.

These studies provide evidence of the involvement of the areas described in reaching and grasping. Evidence to support relative separation of reaching and grasping processing of prehensile action comes from Cavina-Pratesi et al. (2010). They asked participants to reach and grasp or reach and touch (with the knuckles) various objects at various locations. The results from the fMRI showed activation in the SPOC region and SPL for the transport, but not for the grip component of the movement. Conversely the grip component, and not the reach component, of the movement was found to activate the PMv and aIPS areas of the brain. This dissociation in activation is consistent with the areas other studies have described as being involved in these components. Additionally they found common regions of activation in the SMA and PMd areas, suggesting these areas may be involved in integration of the information from the two streams, helping coordinate the reach and grasp movements. Cavina-Pratesi et al., though, do not rule out that there may be some "cross-talk" between the two streams.

The studies discussed above provide some support for Jeannerod's (1981) proposal that there are two separate channels involved in a prehensile movement: one dealing with the transportation of the hand towards the object and the other controlling the final actions to be carried out on that object. This theory provides a good explanation for the results of Experiment 3, why it is possible for previous reaches to affect current trajectories even though the final goal object and action on that goal were different. Later chapters will discuss this evidence and the anatomical layout of the human parietal cortex further, particularly with respect to the SPOC. This is a key area involved in reaching and planning actions to particular locations as well as encoding peripersonal space. It will be suggested that this may explain why the later research in this thesis demonstrates that action priming by observation of the reach trajectory is linked to peripersonal space whereas there is, as yet, no evidence to suggest that action priming by observation of grasping is dependent on observation of grasping in peripersonal space.

Finally this experiment provides evidence that the reach trajectory is not being primed by the visual presentation of a particular goal object, but rather by the previous actions. Further evidence that trajectory priming is the result of previous actions rather than any other aspect of the visual scene is presented in Chapter 4, Experiment 9. In that experiment participants alternate between acting on the blocks and simply viewing the blocks set up but not acting on them. This experiment clearly demonstrates that the visual scene and the objects therein do not contribute to the priming of the reach trajectory.

CHAPTER 3:

ALLOCENTRIC vs EGOCENTRIC PERSPECTIVE

3.1 Experiment 4: Seated opposite, same hands

The experiments in Chapter 2 established that an individual's reach kinematics are affected by their previous reaches. Participants' reaches are significantly higher following trials where they reached over obstacles. This effect was robust, occurring with both horizontal and vertical movements. It therefore provided an excellent paradigm with which to investigate the effects of observing another's reaching actions in two-person experiments.

The following three experiments in this chapter therefore focus on the main question of the thesis. That is, whether another person's reach path is simulated by the observer. If motor programmes for reaching are activated when observing another person reach to a target, then it is predicted that the observer's subsequent reach path will be affected by this prior observation. Further, if action observation activates the motor systems of the observer, as if they themselves had produced the reach, then reach path priming effects should be similar to those reported in Chapter 2.

3.1.1 Method

3.1.1.1 Participants

A total of 24 right-handed students (17 female), with a mean age of 18.9 years, participated in this study in return for course credits. None of the pairs of participants were acquainted with each other.

3.1.1.2 Materials and Apparatus

The materials and apparatus are the same as in Experiment 1.

3.1.1.3 Procedure and design

Experiment 2 established that vertical reaching over obstacles elicited a within-person priming effect. This procedure was modified for use with two participants. The two participants were seated opposite each other, giving the participants the best view of each other's actions. Figure 3.1, Panel A shows the seating arrangements for the participants. The participants shared the target block, which was, as in Experiment 2, 40 cm away from the starting position of each participant's hand (marked by a black square in Figure 3.1, Panel A). The obstacle block (shown as a white square), when present, was 20 cm away from the participant whose turn it was to move. The obstacle block appeared 50% of the time. On non-obstacle trials the obstacle was removed from view. Participants alternated reaches. They started the experiment with their eyes closed. The experimenter placed the blocks and then spoke the name of the first participant. This was their cue to open their eyes, reach out, lift the block and replace it back down, returning their hand to the starting position and closing their eyes. The other participant was instructed on hearing the name to open their eyes, observe the scene, and to close their eyes again when the first participant had finished their action.

The experiment was designed to investigate the effect on the current participant's reach, n, of observing a reach, n-1, and of the participant's previous reach, n-2. As described previously, there are eight trial orders of obstacle and non-obstacle trials. Each person carried out each type of trial 10 times. This experiment was divided in to two halves, with 80 trials in each half, plus two trials to establish condition history.

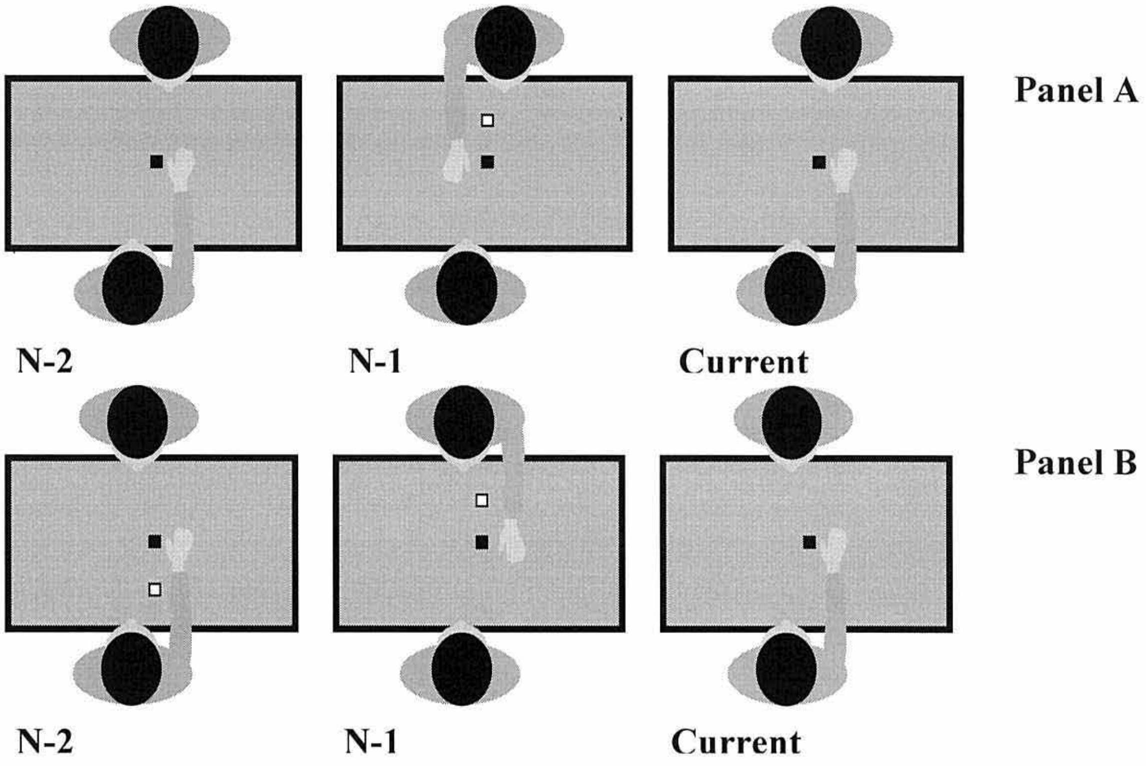


Figure 3.1. Two-person reaching, seated opposite. Panel A shows the arrangement for Experiment 4, with both participants using their right hands. Panel B shows the arrangement for Experiment 5, with one participant using their left hand and the other using their right hand. The diagrams show two example series of reaches, with the participants alternating moves. N is the current trial. N-1 is the trial that preceded the current trial and was carried out by the second participant. N-2 is the last but one trial, where the current participant last moved. The black square is the target; the white square is the obstacle. These examples show No-O-No (Panel A) and O-O-No (Panel B) trial sequences.

3.1.2 Results

As previously described, error trials (e.g., collision with blocks) were removed from the analysis (0.99% of trials). Furthermore, where participants failed to open their eyes on an observation trial their following action trial was removed.

The heights were again analysed using a two-way within-subjects ANOVA for each person's results, with two factors: n-1 trial, the effect of the other person's reach; and n-2 trial, the effect of their own movement (each factor being with and without obstacle). This analysis revealed no main effects for the within-subject n-2 effect [*F*(1,23)=2.33, *p*=.140], the between-subject n-1 effect [*F*(1,23)=0.64, *p*=.433], or the interaction [*F*(1,23)=.01, *p*= .814]. Figure 2.2 shows the graph of height means. Further analysis with *t* tests (two-tailed) comparing the baseline condition (No-No-No) with an obstacle at n-1 (No-O-No) and the baseline condition with an obstacle at n-2 (O-No-No) revealed no significant effects [*t*(23)=0.43, *p*=.669 and *t*(23)=0.78, p=.443, respectively].

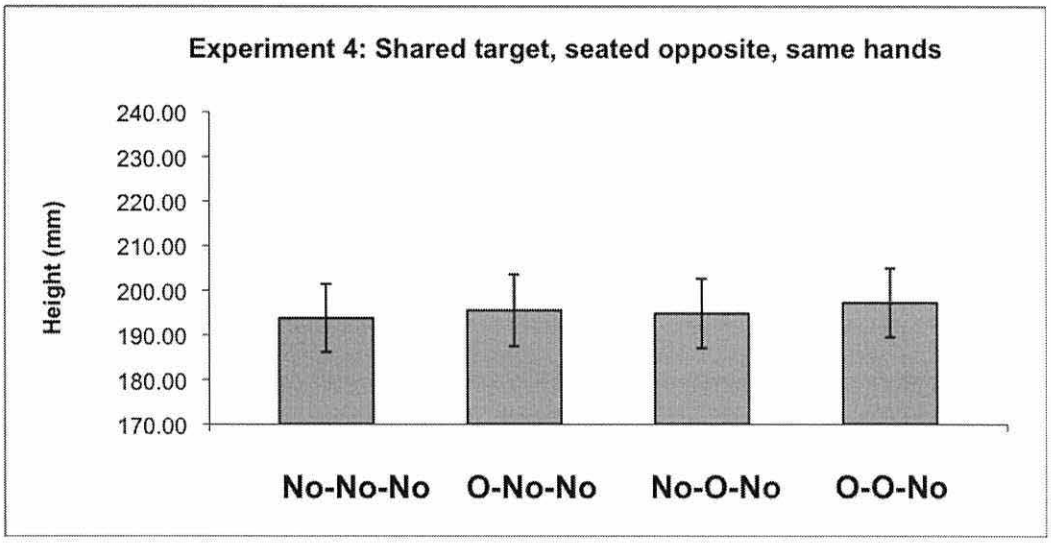


Figure 3.2. Means of the maximum width deviation for non-obstacle reach trials (trial n), with their standard errors. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

3.1.3 Discussion

Somewhat surprisingly, no evidence was found to support the idea that the reach trajectory of an observed reach is simulated. That is, there is no evidence that a participant's reach is higher just after they have observed another person reach over an obstacle. This lack of obstacle priming effect between people could be taken as evidence that indeed action simulation processes are somewhat abstract. Motor systems represent the goal of the action, in this case grasping the wooden block, but the specific manner of the action is not encoded. Such a result would be in line with previous work where mirror systems can encode goal-directed actions even when they are not directly observed (e.g., Umiltà et al., 2001).

A second finding from this experiment is that the person's own prior reach has no significant effect on their subsequent reach path. That is, n-2 effects are not observed, which suggests that observation of another person undertaking the reach-to-grasp task interferes with the representation of one's own previous action.

One experiment, of course, is not sufficient to establish that priming of reach trajectories by another person cannot take place. It may be that specific attention needs to be drawn to the reach. Bach, Peatfield, and Tipper (2007) have demonstrated that attention can play a key role in embodiment of action. Therefore perhaps participants pay less attention to another person's reach path than to their own. Hence effects are not detected during action observation.

Additionally it should be noted that in this experiment each participant used their right hand. Research by Koski, Iacoboni, Dubeau, Woods, and Mazziotta (2003), for example, has shown that when participants imitate a mirrored hand from a third-person perspective (viewing a left hand but responding with the right) it produces higher activation in the inferior frontal mirror area than when viewing an anatomically matched image (viewing a right hand and responding with the right hand). Similarly Alaerts, Heremans, Swinnen, & Wenderoth (2009) used TMS to investigate motor-facilitation of the left primary motor cortex (M1) and found that viewing videos of left hands from a third-person perspective produced greater facilitation than videos of the right hand (see also Maeda, Kleiner-Fisman, & Pascual-Leone, 2002). Developmental studies also show that early in life children tend to imitate as in a mirror, copying another person's right-hand actions with their own left hand (e.g. Bekkering, Wohlschläger, & Gattis, 2000).

Another very interesting fMRI study from Shmuelof and Zohary (2008) showed differences in activation between viewing hand actions from an egocentric (their own) and from an allocentric (third-person) perspective. When participants observed from an egocentric perspective this activated contralateral areas in the anterior SPL. That is, observing a right hand from an egocentric perspective activated the left hemisphere, and vice versa. These results occurred regardless of whether the actions occurred in the left or right visual fields. The opposite pattern was found when observing actions from an allocentric perspective. When participants observed a right hand carrying out an action this activated the right hemisphere, and vice versa. If a participant's actions with their right hand activate the *left* hemisphere and observation of a right hand, from an allocentric perspective, activates the *right* hemisphere, that is a different area of the brain, it would seem logical that observation of the action with the right hand would not produce any priming. It was therefore decided that a second two-person experiment would be carried out, but this time one of the participants would use their left hand and the other their right hand. It was hoped that this matching would produce priming effects.

3.2 Experiment 5: Seated opposite, mirrored hands

Experiment 4 examined whether the observation of another's reach could affect the trajectory of subsequent reaches. The results from Experiment 4 showed no effects of observation. In that experiment both participants had sat opposite each other and used their right hands. Evidence, discussed in section 3.1.3, suggests that viewing actions carried out by the left hand from an allocentric perspective, rather than the right hand, may be more likely to lead to that action being embodied and activating the area of the mirror system that deals with the participant's own right-handed actions. Experiment 5 was carried out to investigate this possibility.

3.2.1 Method

3.2.1.1 Participants

A total of 24 right-handed students (18 female), with a mean age of 20.2 years, participated in this experiment in return for course credits. All participants had normal or corrected-to-normal vision.

3.2.1.2 Procedure and design

This experiment was identical to Experiment 4 except that one of the participants in each pair was randomly assigned to use their left hand (see Figure 3.1, Panel B).

3.2.2 Results

In this experiment 1.72% of trials were removed. As in Experiment 4 there were no significant main effects of observing another person's reach path at n-1 [*F*(1,23)=2.10, *p*=.162], or the participants own n-2 reach [*F*(1,23)=0.42, *p*=.525] and no interactions [*F*(1,23)=0.07, *p*=.793]. Thus, consistent with the previous experiment, neither the participant's own previous actions (n-2), nor the observed actions (n-1), affected their current action (see Figure 3.3). Further analysis (two-tailed *t* tests) comparing the baseline No-No-No to the O-No-No and No-O-No conditions revealed no effects [*t*(23)=0.49, *p*=.631 and *t*(23)=1.39, *p*=.179, respectively]. To increase the power, the data from Experiments 4 and 5 were combined. This confirmed the lack of n-1 [*F*(1,47)=0.19, *p*=.665] and n-2 [*F*(1,47)=1.68, *p*=.202)] effects and any interaction [*F*(1,47)=0.13, *p*=.722].

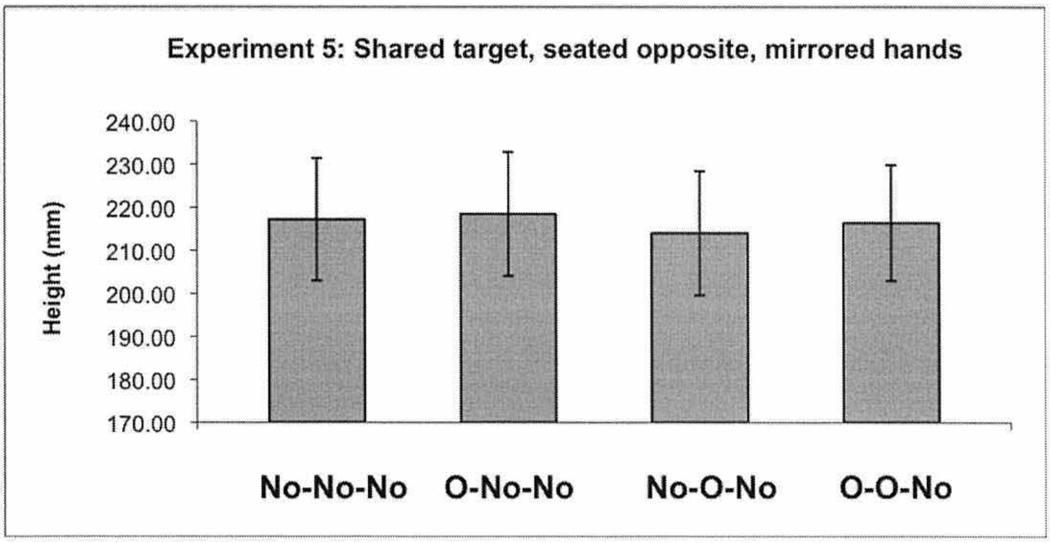


Figure 3.3. Means of the maximum width deviation for non-obstacle reach trials (trial n), with their standard errors. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

3.2.3 Discussion

This experiment replicated the results of Experiment 4 and seemed to provide evidence that, as might be the case with the monkey mirror neuron system, the reach trajectory by which a target is approached is not encoded. However, it is necessary to be cautious in generalising the results from any given set of experiments, and concluding that observed reach trajectories are never encoded could have been premature. Certainly under the conditions described in these two experiments trajectory is not encoded, and the fact that in both experiments the person's own carry-over effect (n-2) also disappeared gave concern. If the observation of the action was having no effect at all it might be expected that the effect of the participants' own previous actions would still be seen. The results from Experiments 4 and 5 were unexpected and did not show the expected action priming effect, however the results still left unanswered questions, which justified further investigation.

The participants in both Experiment 4 and 5 observed the actions from an allocentric rather than an egocentric perspective. The discussion from Experiment 4 considered a number of studies that suggested observing actions from an allocentric perspective was different from observing actions from an egocentric perspective. Alaerts, et al. (2009), for example, examined MEPs for two muscles in the right forearm. Participants observed movements from allocentric and egocentric perspectives of both left and right hands. When observing egocentric actions right-handed movements showed greater facilitation than left-handed movements. This pattern was reversed for movements seen from an allocentric perspective; movements of a left hand, for example, produced greater activation than right-handed movements (and vice versa). Additionally, however, the observed allocentric movements produced less motor-facilitation than egocentric movements. Allocentric left-hand movements were not equivalent in magnitude to egocentric right-hand movements, demonstrating a quantitative difference in activation caused by allocentric and egocentric perspectives.

Other studies have demonstrated that allocentric and egocentric views may be dealt with quite differently. FMRI studies by Chan, Peelen, and Downing (2004) and Saxe, Jamal, and Powell (2006) examined the effect of viewing bodies and body parts, such as hands and feet (images but no action), from egocentric and allocentric perspectives. The parietal cortex showed greater activation for egocentric perspectives compared to allocentric perspectives. Interestingly they found that the extrastriate body area showed a preference for allocentric perspectives.

Jackson, Meltzoff, and Decety (2006) investigated imitation and action observation from both an egocentric and allocentric perspective in their fMRI study. They found that for both imitation and observation, activity was greater in the sensory-motor system for egocentric compared to an allocentric perspective. They suggest that because the allocentric perspective requires a visual transformation, to match it to the perspective from which one's own actions are seen, that the allocentric perspective is less strongly associated with the sensory-motor cortex.

These studies suggest that there may be differences in the way actions from different perspectives are processed. It was possible that the non-significant results in Experiments 4 and 5 arose because the activation from observing actions from an allocentric perspective is not great enough to cause action embodiment and thus priming. This failure is specific to reach trajectory, and not grasp and action goals. The large number of studies confirming the existence of mirror systems using single unit recording work in monkeys (e.g., di Pellegrino et al., 1992; Gallese et al., 1996) and the extensive fMRI studies with humans (e.g., Iacoboni et al., 1999; Gazzola et al. 2007; Oosterhof et al., 2010, see Grèzes & Decety, 2001 for a review), have presented actions from the allocentric perspective. Nevertheless it was felt that it was worthwhile to investigate whether simulation of reach path was dependent on viewing perspective and that perhaps actions viewed from another perspective, which is closer to an egocentric view, may produce action priming.

3.3 Experiment 6: Seated adjacent, same hands

Experiments 4 and 5 did not produce any significant results. Participants' trajectories were unaffected by the observation of another's movements over obstacles. In these experiments participants viewed actions from an allocentric perspective while they sat opposite one another, it was theorised that actions observed closer to an egocentric perspective might be more likely to engage the mirror system. Experiment 6 was devised in order to investigate this possibility.

3.3.1 Method

3.3.1.1 Participants

A total of 24 right-handed students (17 female), with a mean age of 18.9 years, participated in this study.

3.3.1.2 Materials and apparatus

The materials and apparatus are the same as in Experiments 4 and 5.

3.3.1.3 Procedures and design

The procedure in this experiment is the same as in Experiments 4. Both participants carried out actions using their right hand. The only difference was the seating arrangements. In this experiment participants sat next to each other (see Figure 3.4), facing the same direction. Each participant reached for their own target presented directly in front of them and also reached over their own obstacle. As in all of the experiments, the target block was 40 cm from the starting position of each participant's hand, and the obstacle 20 cm away. The other participant's obstacle was 40 cm from the observer's hand.

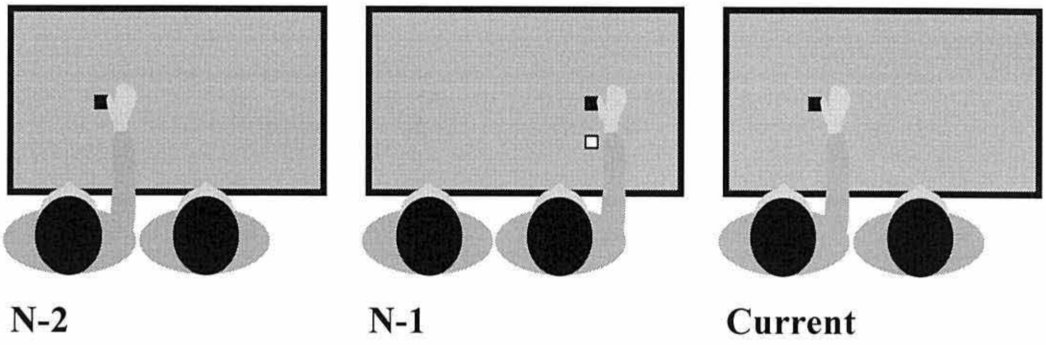


Figure 3.4. Two-person reaching, seated adjacent. This figure shows the arrangement for Experiment 6, with both participants using their right hands. The diagrams show an example series of reaches, with the participants alternating moves. N is the current trial. N-1 is the trial that preceded the current trial and was carried out by the second participant. N-2 is the last but one trial, where the current participant last moved. The black square is the target; the white square is the obstacle. This example shows a No-O-No trial sequence.

3.3.2 Results

A number of trials were removed due to obstacle collision and incomplete trajectory recordings (1.62%).

Unlike Experiment 4 and 5, this experiment showed a significant main effect for the influence of other participant's action on their current reach [n-1: $F(1,23)=8.43$, $p=.008$], showing that the priming effect, previously observed only with a participant's own previous actions, had transferred between people. Interestingly, in contrast to Experiments 4 and 5, observing an action does not remove the effect of a person's own previous reach [n-2: $F(1,23)=6.55$, $p=.018$] (see Figure 3.5). These two effects, within and between people, appear to be independent and no interaction was found [$F(1,23)=0.15$, $p=.700$]. Further two-tailed t tests between the baseline condition (No-No-No) and each of the single obstacle conditions (obstacle at n-1, No-O-No; obstacle at n-2, O-No-No) were significant [*t*(23)=2.38, *p*=.026 and *t*(23)=2.37, *p*=.026, respectively].

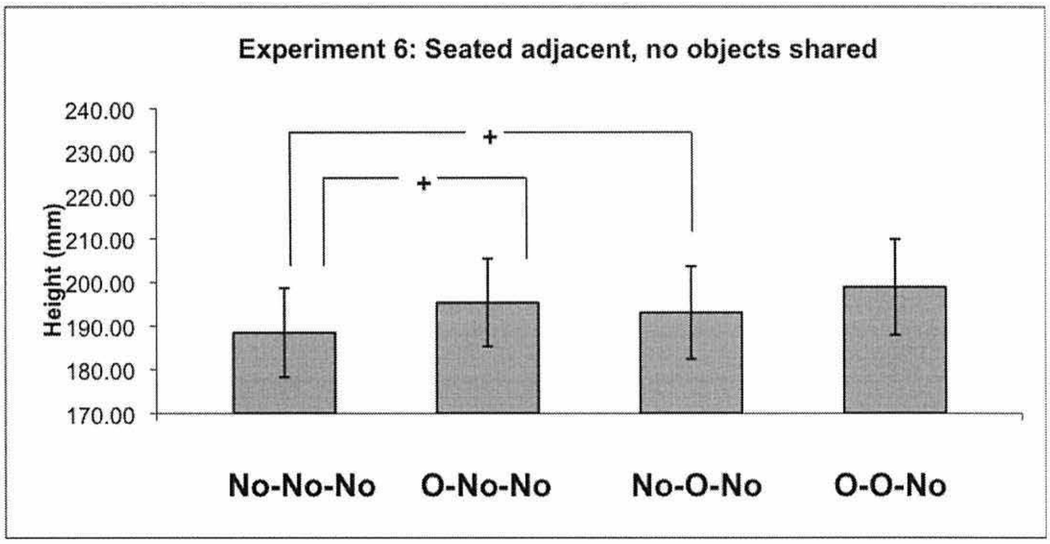


Figure 3.4. Means of the maximum width deviation for non-obstacle reach trials (trial n), with their standard errors. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The bars indicated by + show a significant *t* test result at *p*<.05. The error bars represent the standard error of the mean (S.E.M.)

3.3.3 Discussion

These results show for the first time that observing another person's actions appears to evoke simulations of the reach path of the hand. Thus, after observing another person reach over an obstacle, the observer's subsequent reach is higher. Such an effect implies that the prior activation of a reach simulation remains active, or can be retrieved from memory, to affect a subsequent reach. These results also show that participant's movements remain affected by their own previous movements (n-2), and that this appears to be independent of the effect of observing another's action in between movements.

The most noticeable difference between this last experiment and Experiments 4 and 5 is one of perspective. In Experiment 6 the participants' view of the observed action is very similar to the view that they see when moving their own hand, that is, an egocentric perspective. In the other two experiments participants sat opposite each other, an allocentric perspective, and would have to mentally rotate the observed action in order to visualise it from the same perspective as their own actions.

The results from these three experiments seem to be compatible with the research investigating perspective. Studies such as Chan et al. (2004), Saxe et al. (2006) and Jackson et al. (2006) show that bodies, body parts and actions seen from an egocentric perspective activate areas in the parietal lobe more than when seen from an allocentric point of view. Various areas of the parietal lobe may be involved in the human mirror system. The observed differential in parietal lobe activation could be theorised to explain why actions observed from an egocentric, and not allocentric perspective, are simulated.

If perspective mitigates whether or not the observed action is simulated, and thus is able to prime subsequent action, what is the nature of the effect of perspective? How do varying perspectives affect this priming effect? It is possible that such an effect would only occur at viewing angles very close to the egocentric perspective. Another possibility is that, rather than a sharp cut-off, there is a gradual diminishing of the effect at angles between egocentric (0°) and extreme allocentric perspective (180°) viewpoints. The following chapter will present the experiments that were designed to investigate these questions.

CHAPTER 4:

THE ROLE OF PERIPERSONAL SPACE

4.1 Introduction to Experiments 7a and 7b

Experiment 6, in Chapter 3, demonstrated for the first time that observation of the reach trajectory of a grasp can prime one's own reach trajectory. In that experiment participants' reaches were higher as a consequence of having observed another's reach over an obstacle. Experiments 4 and 5 did not produce action priming. This suggested that simulation, necessary to produce priming effects, does not take place in all cases of action observation.

There were a number of differences between Experiments 4 and 5, and Experiment 6. In the latter experiment, for example, participants did not share the obstacle or target block. The most notable difference, however, was the perspective from which participants viewed the other's action. As discussed in Chapter 3, there is some evidence to suggest that these two perspectives, allocentric and egocentric, are processed differently. The egocentric perspective is similar to the view that a person sees when their own hand and arm carry out an action, whereas the allocentric view may need to be rotated in order to match the egocentric perspective.

The purpose of the first two experiments presented in this chapter was to investigate the hypothesis that perspective mitigated action priming, and further, to explore the boundary conditions that determine when action priming of reach trajectory will and will not occur. When participants sat opposite (180°) each other in Experiments 4 and 5 there was no effect; when they sat adjacent (0°), in Experiment 6, there was an effect. The first question to explore was what would happen at intermediate angles. It is possible that priming will only take place at angles close to 0°. It is also possible that there will be a gradual reduction of effect as the angle of observation approaches 180°. In order to test these possibilities Experiments 7a and 7b were designed with participants sitting at the intermediary angle of 90°. Additionally, these experiments also examined the role sharing either the obstacle or target block might play in priming. Therefore in Experiment 7a participants shared the obstacle and in Experiment 7b they shared the target block.

4.2 Experiment 7a: Shared obstacle, seated at 90°

4.2.1 Method

4.2.1.1 Participants

A total of 24 right-handed students (17 female), with a mean age of 21.6 years, participated in this study in return for course credits. All participants had normal or corrected-to-normal vision.

4.2.1.2 Materials and apparatus

The materials and apparatus are the same as in Experiment 4.

4.2.1.3 Procedure and design

Both participants used their right hands. They were seated at 90° to each other on two sides of a table (See Figure 4.1, Panel A). Participants shared the obstacle, which was in the same position on the table for both of them. As in all previous experiments the obstacle was 20 cm from the hands' starting position. Participants responded to separate targets, which were 40 cm from the reaching hand. The experiment consisted of two blocks, each of 82 trials, as previously described.

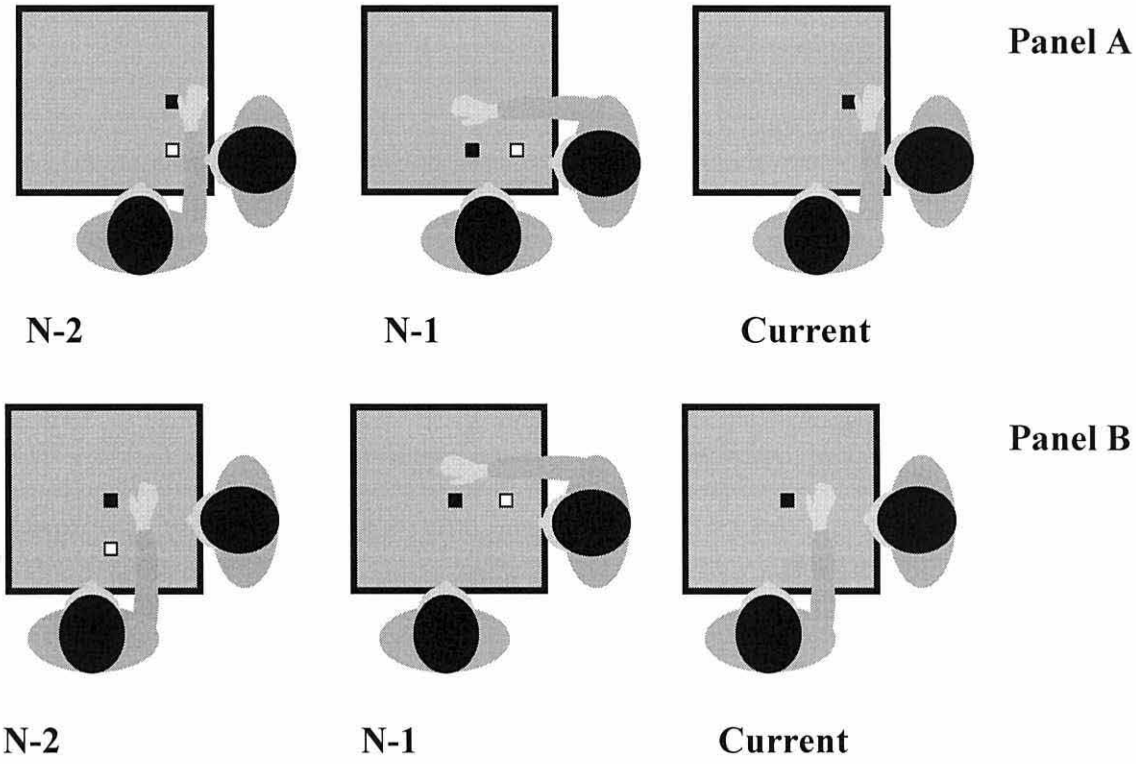


Figure 4.1. Two-person reaching, seated at 90°.
Panel A: Experiment 7a: shared obstacle.
Panel B: Experiment 7b: shared target.
In Experiment 7a participants avoided the same obstacle. In Experiment 7b participants grasped the same target. The diagrams show two example series of reaches, with the participants alternating moves. N is the current trial. N-1 is the trial that preceded the current trial and was carried out by the second participant. N-2 is the last but one trial, where the current participant last moved. The black square is the target; the white square is the obstacle. These examples show O-O-No sequences. In both experiments the obstacles and targets are within reach of the participants.

4.2.2 Results

A number of trials were removed (0.68%) due to collisions, failed trial recordings, and when participants had failed to open their eyes on the previous observation trial.

As in previous experiments, the maximum height of the wrist on the outward reach toward the target was calculated. The heights were again analysed using a two-way within-subjects ANOVA for each person's results, with two factors: n-1 trial, the effect of observing the other person's reach; and n-2 trial, the effect of the participant's own previous movement. The results are shown in Figure 4.2, Panel A. There was a main effect for n-1, the influence of the other participant's reach [$F(1,23)= 9.09$, $p=.006$], and for n-2, the influence of the individual's previous reach [$F(1,23)= 7.40$, $p=.012$]. The interaction between n-1 and n-2 is close to significance [$F(1,23)= 4.05$, $p=.056$]. Further planned contrast *t* tests (one-tailed) showed that conditions with obstacles at n-1 and n-2 were significantly higher than the baseline (No-No-No) [that is No-O-No, $t(23)= 3.53$, $p=.001$; O-No-No, $t(23)= 3.37$, $p=.002$, respectively]. From the pattern of results shown in Figure 4.2, Panel A, it appears that whilst a single obstacle at n-1 (No-O-No) or n-2 (O-No-No) produces significantly higher reaches than the baseline (No-No-No) the presence of an obstacle at *both* n-1 and n-2 (O-O-No) does not produce much more priming than either the No-O-No or O-No-No conditions, resulting in an interaction that is close to significance.

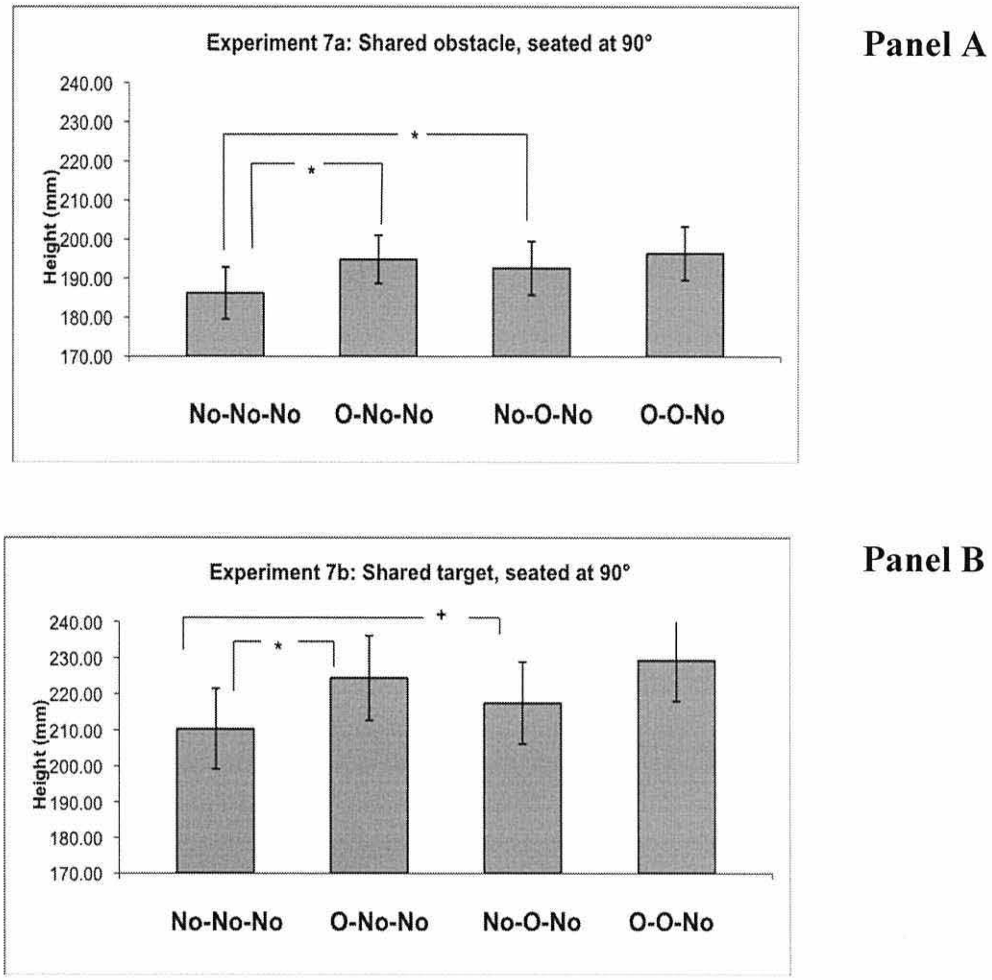


Figure 4.2. Means of the maximum width deviation for non-obstacle reach trials (trial n), with their standard errors. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The bars indicated by * show a significant *t* test result at $p < .01$; + represents a *p* value < .05. The error bars represent the standard error of the mean (S.E.M.)

4.2.3 Discussion

The results of this experiment are discussed at the end of Experiment 7b.

4.3 Experiment 7b: Shared target, seated at 90°

4.3.1 Method

4.3.1.1 Participants

A total of 24 right-handed students (16 female), with a mean age of 21.0 years, participated in this study in return for course credits. All participants had normal or corrected-to-normal vision.

4.3.1.2 Procedure and design

Both participants used their right hands. They were seated at 90° to each other on two sides of a table. They both shared the target object, which was 40 cm from each of their hands and in the same table location for both of them. Their separate obstacles were 20 cm from their reaching hands (see Figure 4.1, Panel B).

4.3.2 Results

A number of trials were removed (0.57%) due to collisions, failed recording trials, and where participants had failed to open their eyes on the previous observation trials. There was a significant main effect for the influence of the other participant's reach [n-1: $F(1,23)=8.54$, $p=.008$] and of the individual's own previous reach [n-2: $F(1,23)=46.03$, $p<.001$] (see Figure 4.2). There was no significant interaction between these two factors [$F(1,23)=0.13$, $p=.718$]. Further planned contrast t tests (one-tailed) revealed that reaches in the No-O-No and O-No-No conditions were significantly higher than those in the baseline condition (No-No-No) [that is $t(23)= 1.85$, $p=.039$ and $t(23)= 3.76$, $p<.001$ respectively].

4.3.3 Discussion

The results from Experiments 4, 5, and 6 suggested that perspective played a role in whether or not priming by observation would take place. Participants seated opposite to each other (180°) were not primed by the observation of the other's reach, whereas those who sat next to each other (0°) were. It was hypothesised that if perspective influenced priming then participants sat at angles larger than 0° would show reduced priming by observation or no priming at all. Experiments 7a and 7b were designed to examine these possibilities. However the results did not show any reduction in the size of the priming effect from action observation. The mean height increase for the condition with an obstacle at n-1 (No-O-No) compared to the baseline (No-No-No) for Experiments 7a and 7b are in fact higher than in Experiment 6 (6.44 mm, 7.20 mm and 4.56 mm respectively). These results suggested that other differences between the design of Experiments 4 and 5, and 6 might account for the differing outcomes.

As noted in Chapter 3, Experiment 6 did not involve participants sharing either the obstacle or target object, whereas participants in Experiment 4 and 5 did. This difference seemed unlikely to be the cause of differing results, however this possibility was also addressed by the design of Experiments 7a and 7b. In Experiment 7b, as in Experiments 4 and 5, participants shared the target block, and yet the results in this experiment showed significant effects of the n-1 and n-2 reaches. The experiments carried out up to this point strongly suggest that neither perspective nor the presence or absence of block sharing accounted for the differences in results obtained. The designs of the five experiments carried out to this point were re-examined.

Table 4.1 shows a summary of information from each of the experiments, noting the distances between the hand's resting position (which is 20 cm from the trunk) and the other participant's hand, obstacle, and target. Distances of 40-45 cm were within the reach of all participants, whereas distances over 50 cm were beyond the reach of all but a few participants. The table shows that in Experiments 6, 7a and 7b the other participant's obstacle was within reach, that is within peripersonal space, not always however the other participant's hand or target object. In contrast, in Experiments 4 and 5 the other person's target object was within reach but not so their obstacle. That is, without further actions, such as leaning forward and raising the upper body, a reach action to the other person's obstacle could not be achieved. Certainly, a reach over the other person's 18-cm-tall obstacle was not possible.

		Distance (cm)		
Experiment	Angle	Other's Hand	Other's Obstacle	Other's Target
4 & 5	180°	80	60	40
6	0°	35	40	54
7a	90°	28	20	28
7b	90°	57	42	40

Table 4.1. This table shows a summary of the distances between the observing participant's hand and the other participant's hand, obstacle, and target in Experiments 4-7b. The shaded figures show distances outside peripersonal space, that is distances beyond reach.

As noted, Experiments 4 and 5 did not produce obstacle avoidance priming effects, whereas Experiments 6, 7a and 7b have produced such effects on reach trajectory. When considering Table 4.1 it would appear that it is the distance of the other person's obstacle during action observation that may be the key variable. That is, when effects were not observed the obstacle was distant from the observer's hand, whereas when effects were observed the obstacle was consistently closer across all experiments. The other variables, such as viewing angle, other's hand and other's target, do not seem to have the same level of consistency.

Therefore, having reviewed the designs of the two-person experiments, it was hypothesised that perhaps the observation of avoidance of an obstacle outside peripersonal space (Experiments 4 & 5), on which the participant could not act, might have made the action less relevant. This lack of relevance could have prevented the activation of simulation processes. Previous research has indeed shown that during selective reaching tasks, the distance of an irrelevant to-be-ignored distracter object from the reaching hand was critical for the obtained interference and priming effects. For example, Tipper et al. (1997; Tipper et al., 1992) revealed action-centred selection processes in a selective reaching task. That is, when reaching for a target, distracters closer to the hand produced significantly higher interference and negative priming.

There is evidence from both monkey and human studies that peripersonal space (the area around us that we can reach with our hand without moving) involves specialised areas in the brain, distinct from those that encode far space (space beyond reach). Clear evidence for the existence of separate coding of peripersonal space comes from studies of neuronal activity in monkeys. There are three areas involved in processing information in peripersonal space. The ventral intraparietal sulcus (VIP) is involved in ultranear space, to approximately 20 cm (Colby, Duhamel, & Goldberg, 1993; Duhamel, Colby, & Goldberg, 1998; Graziano & Gross, 1995). Colby et al. (1993) found that neurons in the

VIP not only selectively responded to areas within the monkey's peripersonal space but were also highly selective for direction and speed of moving stimuli.

The VIP has projections to the ventral premotor cortex, F4 (Luppino, Murata, Govoni, & Matelli, 1999) and F4 itself has projections to the primary motor cortex (Barbas & Pandya, 1987; Graziano & Gross, 1998). The neurons in F4 respond to both somatosensory and visual stimuli within reach (Fogassi et al., 1992, 1996; Graziano, Yap, & Gross, 1994). The neurons in this area code the visual stimuli in arm-centred coordinates (Graziano & Gross, 1995), that is, as the arm moves so does the visual receptive field. Interestingly the neurons in F4 respond to objects in peripersonal space even if the monkey is anaesthetised (Graziano, Hu, & Gross, 1997). Neurons in the MIP also respond to stimuli within reach of the monkey (Colby & Duhamel, 1991) and respond to somatosensory stimuli on the hand.

Areas that are believed to be involved in coding far space in monkeys include the lateral intraparietal area (LIP) (Colby & Goldberg, 1999) and area 8, the frontal eye field (FEF). Rizzolatti, Matelli, and Pavesi (1983) found that lesions to the FEF in monkeys produced far space neglect, conversely when they lesioned F4 they found inattention to stimuli in peripersonal space. Whilst the involvement of the LIP and the FEF in representing peripersonal space cannot be completely excluded, there is clear evidence that areas such as the VIP, the MIP, and F4 seem exclusively involved in the representation of near space.

The representation of peripersonal space is, however, a flexible one. There is evidence from both monkey and human studies that, under certain circumstances, the representation of peripersonal space can be extended. One of the best examples of this is tool use. Iriki, Tanaka and Iwamura (1996), for example, found that the receptive visual field for neurons in the intraparietal sulcus was extended beyond the area the monkey could reach to include space that could be reached by a rake the monkey had been trained to use.

As discussed later, there is evidence from patient studies that show a dissociation between near and far space (Vuilleumier, Valenza, Mayer, Reverdin, & Landis, 1998; Halligan & Marshall, 1991). Berti and Frassinetti (2000) discuss one such patient, P.P., who shows neglect in near but not far space in line bisection tasks. However when the patient performed a line bisection in far space using a stick their neglect then extended into far space, implying a remapping of far space as near space. Such a remapping has also been shown in healthy participants.

Longo and Lourenco (2006) tested healthy participants in a line-bisection task in near and far space. Normal participants show a small left bias in bisecting lines in near space and a rightward bias in far space. The leftward bias was shown to extend into far space when participants used a stick to carry out the task in far space. Lourenco and Longo (2009) have also provided evidence that it is possible, not only to extend the representation of near space, but also to contract it. When their participants carried out line bisections with wrist weights, increasing the effort involved in the task, they found that participants showed a rightward rather than leftward bias in near space locations. These studies indicate that whilst there is evidence that near and far space are coded separately, the representations of near and far space are flexible.

That the human brain makes a distinction between peripersonal and extrapersonal space has been part of a number of theories. Previc (1998), for example, has proposed distinct cortical networks dealing with near and far space. He proposes that the dorsal visual pathway is involved with peripersonal space and actions carried out within it, whereas the ventral processing stream is concerned with extrapersonal or far space. Similarly, the results of imaging studies by Weiss and colleagues (Weiss et al., 2000; Weiss, Marshall, Zilles, & Fink, 2003) support the differential involvement of these two streams. That near and far space might be dissociable is further indicated by the patients of Vuilleumier, et al. (1998) and Halligan and Marshall (1991), the former having a patient who suffered from lateral neglect in far but not near peripersonal space, and the latter showing neglect for peripersonal near but not far space.

The fundamental importance of object distance for action is clear. That specific neural systems are dedicated to encoding peripersonal space, which enable immediate reach-to-grasp actions, while other systems encode objects in far space that require other motor processes (e.g., walking) before action can be produced, makes sense in terms of computational efficiency. It therefore remains a reasonable hypothesis that simulation processes of observed action may also be influenced by the distinction between peripersonal and far space.

To test this hypothesis Experiment 4, where participants sat opposite each other but their obstacles were outside peripersonal space, was redesigned. Experiment 8 replicated the allocentric perspective of Experiments 4 and 5, but crucially the participants share the obstacle, bringing it into the peripersonal space of both participants.

4.4 Experiment 8: shared obstacle, seated opposite

4.4.1 Method

4.4.1.1 Participants

A total of 24 right-handed students (18 female), with a mean age of 23.2 years, participated in this study in return for course credits. All participants had normal or corrected-to-normal vision.

4.4.1.2 Procedure and design

Both participants used their right hands and sat opposite to each other. The participants shared the obstacle, which was in the same location for both of them and as in all previous experiments the obstacle was 20 cm from the reaching hand. However, the obstacle was now in the peripersonal space of both participants. In this new task the participants now reached for separate target objects, which were 40 cm from their reaching hand, as in all previous studies (see Figure 4.3), with the other person's target now 5 cm from their hand.

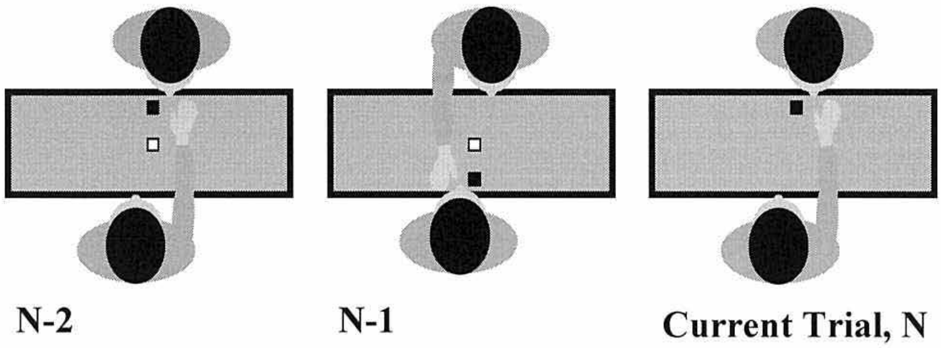


Figure 4.3 Shared obstacle, seated opposite. Participants avoided the same obstacle. The diagrams show two example series of reaches, with the participants alternating moves. N is the current trial. N-1 is the trial that preceded the current trial and was carried out by the second participant. N-2 is the last but one trial, where the current participant last moved. The black square is the target; the white square is the obstacle. This example shows O-O-No sequences. The obstacle and targets are within reach of both of the participants.

4.4.2 Results

Trials where collisions had occurred, there had been a recording failure, or where the participant had failed to open their eyes on the previous observation trial were removed (1.20%).

In Experiment 4, participants sat opposite each other, and the other participant's obstacle was outside the observer's peripersonal space. In that experiment there were no priming effects. In sharp contrast, unlike Experiment 4, the current Experiment 8 showed a significant main effect for the influence of the other participant's action on their current reach [n-1: $F(1,23)=14.98, p=.001$], showing that the priming effect had transferred between two people viewing each other from an allocentric perspective (see Figure 4.4). Again, in contrast to Experiment 4, observing an action from an allocentric point of view did not remove the effect of a person's own reach [n-2: $F(1,23)=13.26, p=.001$]. No interaction between n-

1 and n-2 was found [*F*(1,23)=1.21, *p*=.284]. Further planned contrast *t* tests (one-tailed) revealed that reaches in each of the single-previous-obstacle conditions were significantly higher than the baseline no-previous-obstacles (No-No-No) condition [that is, O-No-No, *t*(23)=2.80, *p*=.005; No-O-No, *t*(23)=2.86, *p*=.005].

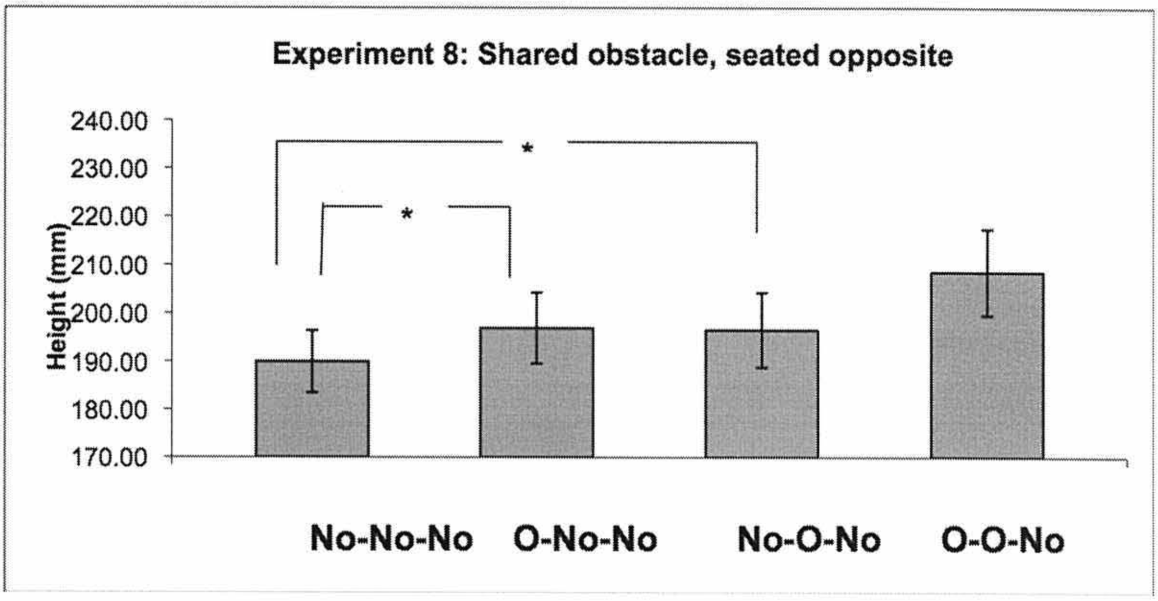
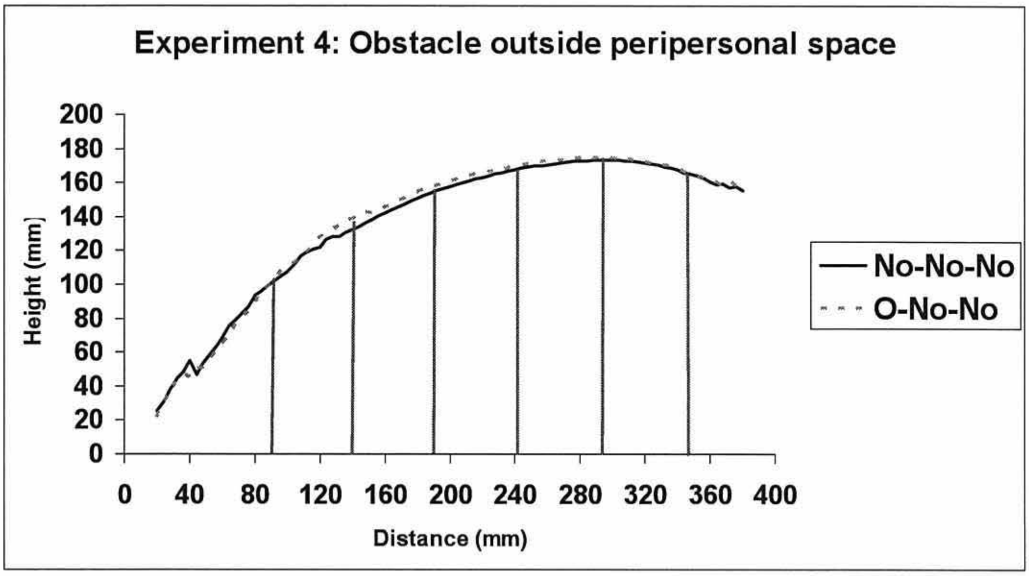


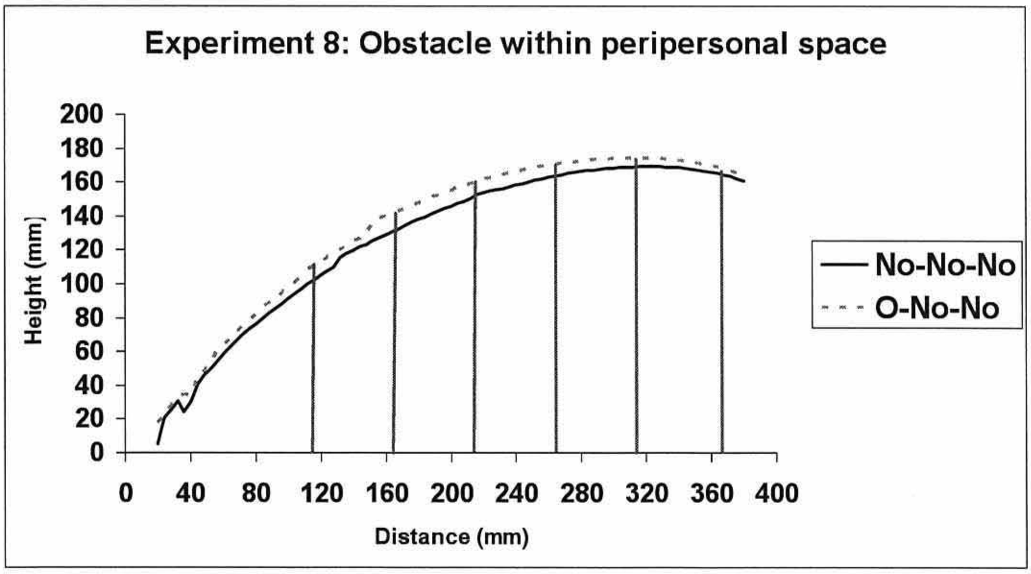
Figure 4.4. Shown here are the means of the maximum height reached for non-obstacle reach trials (n), with their SE for Experiment 8. The bars indicated by * show a significant *t* test result at *p*< .01. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials, and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

In addition to the analysis mentioned above, the results from this experiment were compared to Experiment 4, using a mixed two-way ANOVA. This analysis revealed a significant interaction between experiment and n-1 action priming [*F*(1,46)=7.19, *p*=.010], and between experiment and n-2 priming [*F*(1,46)=6.42, *p*=.015]. These results further confirmed the distinction between the results of this experiment, where both observation of another person's action and the participant's previous action primed the current reach, and those of Experiment 4, where no priming effects occurred.

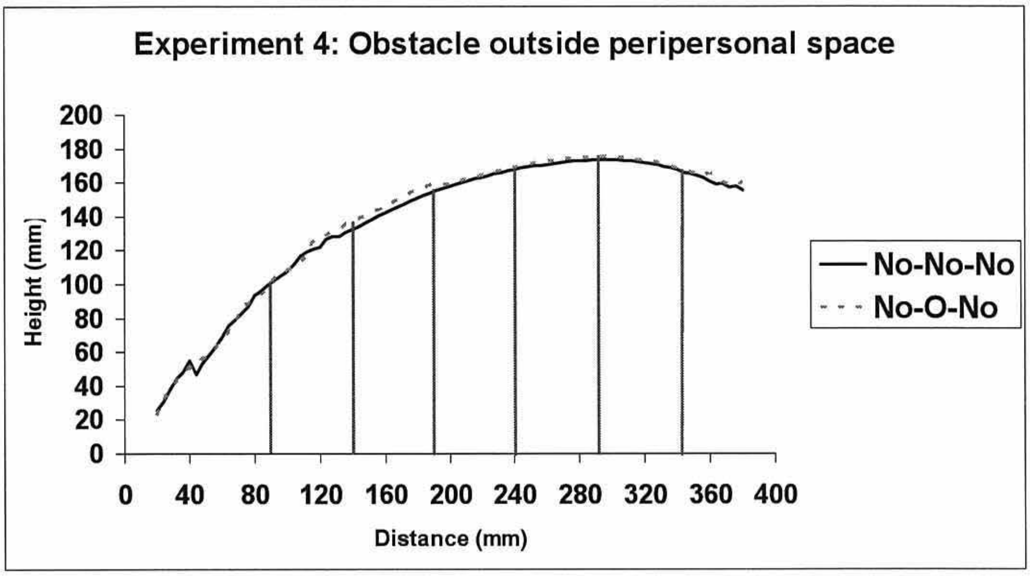
In Experiments 4 and 8 participants saw the other's action from an identical perspective and yet priming effects were only observed in Experiment 8. To further investigate the nature of the trajectory differences between these experiments, further analysis was carried out on several points along the trajectories, in addition to the comparison of maximum heights previously described. The Panels in Figure 4.5 illustrate the effect of an obstacle at n-2, that is, the comparison between No-No-No versus O-No-No trials (Panels A and B), and the effect of an obstacle at n-1, that is, No-No-No versus No-O-No trials (Panels C and D). These figures show the qualitative distinction between the experiments. The vertical lines show the points of comparison along the trajectories where the analysis was carried out in a 2 (obstacle condition) x location (6 loci at 5-cm steps) ANOVA. For Experiment 8 there was a significant obstacle priming effect at n-2 [$F(1,22)=19.96$, $p<.001$], which, as would be expected, interacted with location [$F(1,22)=8.99$, $p<.001$], declining as the hand approached the target. A similar pattern of effects was observed for n-1 obstacle priming effect [$F(1,22)=14.85$, $p<.001$], and interaction with location [$F(1,22)=3.63$, $p<.01$]. Confirming previous findings, there was no significant obstacle avoidance priming effect in Experiment 4.



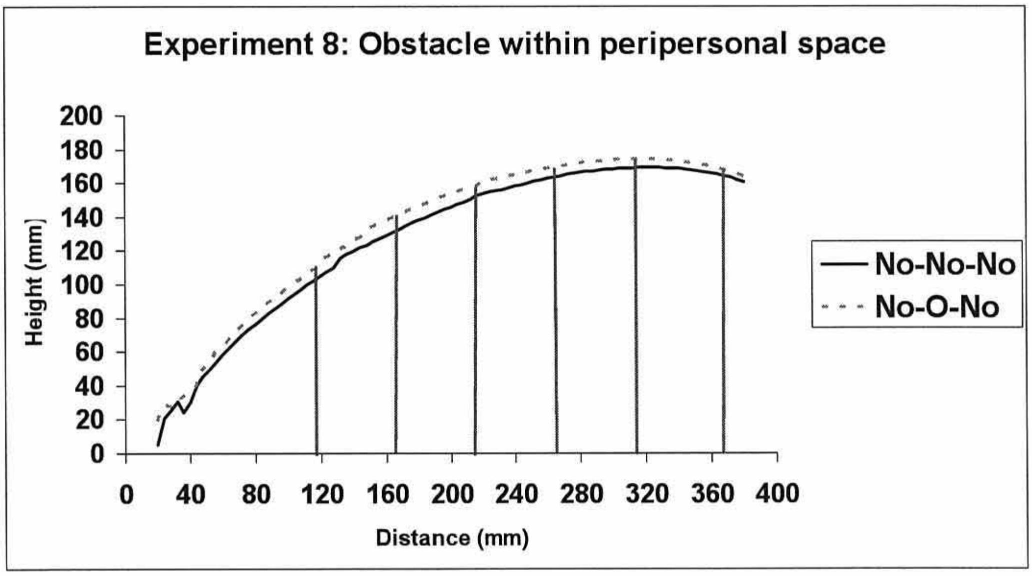
Panel



Panel B



Panel C



Panel D

Figure 4.5. Panel A: Experiment 4: Shared target, seated opposite, No-No-No vs O-No-No trials.
Panel B: Experiment 8: Shared obstacle, seated opposite, No-No-No vs O-No-No trials.
Panel C: Experiment 4: Shared target, seated opposite, No-No-No vs No-O-No trials.
Panel D: Experiment 8: Shared obstacle, seated opposite, No-No-No vs O-No-No trials.

The trajectories shown are the aggregate of each participant's average reach in that condition. The last 5 cm of the reach path have been removed due to the amount of noise at the end of the reach as participants adjust their hand for grasping. The vertical lines mark the points of the curve used in the ANOVA analysis described in the results section of Experiment 4. The far left of the curve was not analysed due to missing data from some participants from the early part of their reaches. (For further details see Appendix B)

4.4.3 Discussion

The evidence from this experiment supports the hypothesis that the priming of reach trajectories by observation is mediated by the distance of the avoided obstacle from the hand of the observer. The effect is robust and has been shown to occur in a number of different scenarios. It is unaffected by the perspective from which the action is observed, present when viewing from both allocentric and egocentric perspectives. Interestingly priming occurs regardless of the relationship between the observer and the other participant's blocks, having been shown to take place when the obstacle or target block are shared, as well as when no blocks are shared.

These experiments reveal an important difference between the encoding of observed actions on a target object, such as grasping, and those of the reach kinematics. There are no experiments that have demonstrated that priming of grasping movements by observation of action is affected by the proximity of the object and action to the observer. Whilst the experiments presented here cannot shed any light on why this difference may exist it is possible to speculate.

Actions carried out on goal objects are generally invariant to the distant that object is from the observer. Any planned action upon an object will remain a valid proposal from different distances. A thumb and forefinger to grasp a grape will be the appropriate action whether that grape is 5 cm or 30 cm away. Preparing a plan to grasp and then subsequently implementing it when the grape is in reach is efficient. Similarly, observing how another person grasps an object will provide useful information about the object and appropriate action, whether or not the object is currently within peripersonal action space.

In sharp contrast, the particular reach trajectory and path to reach that grape will vary depending on the position of that grape and the objects around it when it comes within reach. It would not seem efficient to make an action plan to reach the grape until a final position within reach is achieved and the relative distances of objects from the hand can be calculated. Thus any information regarding the trajectory of an observed reach is far less useful if the action or any object avoided is not in the viewer's peripersonal space. It would seem inefficient to be constantly encoding information regarding observed trajectories that is likely not to be useful.

The differences between reaching and acting upon a goal object may be explained in terms of the processing within the brain. Chapter 2 presented a number of studies that provided evidence for the segregation in processing of reaching and grasping into two separate streams. It is proposed that the stream dealing with grasping is dorso-lateral, consisting of the AIP (in the IPL) and F5 in the PMv (Jeannerod et al., 1995); whereas reaching involves a dorso-medial circuit consisting of V6A, MIP, and other areas in the SPL, and F2 (PMd) (Tanné-Gariépy et al., 2002).

Further sub-components in the action system have been noted above. For example, in fMRI studies such as Weiss et al. (2000, 2003) evidence has been found to support Previc's (1998) theory of distinct cortical networks dealing with near and far space, a dorsal visual pathway for peripersonal space and a ventral processing stream for extrapersonal space. Further evidence has also been provided by Bjoertomt, Cowey, and Walsh (2002). They found that repetitive TMS to ventral stream areas produced pseudo-neglect in far space for normal subjects, whereas TMS to dorsal areas produced neglect in near space. The evidence suggests that areas dealing with the processing of reaching are closely linked to areas involved with processing peripersonal space. This is, of course, efficient and logical. One can in fact only reach in peripersonal space, and information about peripersonal space is necessary to successfully manoeuvre the hand. What also seems to be the case is that areas dealing with grasping, such as the AIP (in the IPL) and F5, are less close to and less connected to areas that may deal with coding peripersonal space. For example, Gallivan, Cavina-Pratesi, and Culham (2009) have identified the superior parieto-occipital cortex (SPOC) region in the SPL to be more active for targets within reach and this area was found by Cavina-Pratesi et al. (2010) to be active for the reaching component, but not the grip component, of a movement. It may be that areas in the brain dealing with grasp planning, and thus affected by the observation of another's grasp, do not process, or receive input from areas dealing with the coding of peripersonal space and thus may be indifferent to this dichotomy of the world.

4.5 Experiment 9: Single-person, control

The experiments presented so far in this thesis provide strong evidence that when observing a reach to an object the kinematics of that reach can be encoded and effect the observer's subsequent actions. This is the first evidence to date that anything other than the final stages of an observed action, such as the grasp, are encoded. There has been much work investigating priming of such actions as grasping. It seems clear from studies carried out by those such as Dijkerman and Smit (2007) and Castiello et al. (2002) that observing another person grasp an object can prime the observer and affect their grasping actions. However, as discussed in Chapter 1, there is also a large amount of evidence that other stimuli are able to prime grasping, such as written object names (Gentilucci & Gangitano, 1998), numbers (Badets et al., 2007) and even odours (Tubaldi et al. 2008). Of most importance for the work presented here is that fact that the mere exposure to objects is able to prime actions (Craighero et al., 1996; Tucker & Ellis, 1998) particularly grasping (Edwards et al., 2003).

The evidence that objects alone can prime grasping raises the question of whether the priming effects on reach kinematics presented in this thesis are the result of the mere presence of objects (which can be acted upon) rather than the observed action towards those objects. The purpose of Experiment 9 was to investigate this possibility. The layout and structure of Experiment 8, which produced priming, was chosen. In place of observing a reach at n-1, the participants in this experiment alternated their reach with simply viewing the scene of blocks at n-1 as it had been laid out in the two-person experiment. The prediction is that even though target and obstacle objects are viewed, there will be no priming effects when an action is not observed.

4.5.1 Method

4.5.1.1 Participants

A total of 24 right-handed students (19 female), with a mean age of 20.5 years, participated in this experiment in return for course credits. All participants had normal or corrected-to-normal vision.

4.5.1.2 Procedure and design

The procedure was almost identical to Experiment 8, with the exception that this was a single-person experiment. The participant alternated between carrying out a reach and observing a scene with blocks in, as they were set up for the second participant in experiment 8. However, there was no second participant and they observed no movement (See Figure 4.6, Panel B). The participants were told that they would alternate reaching and viewing the scene, and that on the viewing trials they should just look at the scene until they were instructed to close their eyes. The participants started with their eyes closed and were then instructed to open their eyes. In the movement trial they reached, lifted up the target block and placed it down again. The participant was then given the instruction to close their eyes. On the viewing trial they opened their eyes and after 3s (the approximate time the other person's trial took) they were instructed to close their eyes. When the participant's eyes were closed the scene was rearranged.

As in all previous experiments, on the reach trial the participant's obstacle was 20 cm from their hand's starting position and the target block was 40 cm away. There were two blocks of 82 trials.

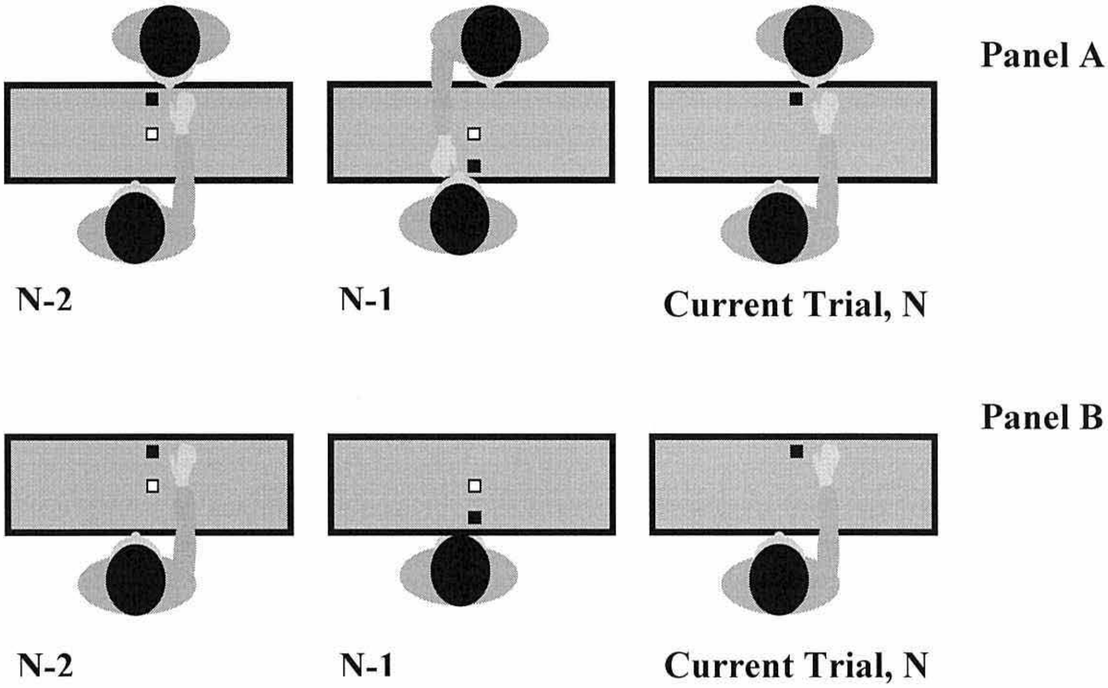


Figure 4.6. This figure shows the similarities and contrasts between Experiments 8 and 9. Panel A shows a series of reaches from Experiment 8, where participants alternated reaches. Panel B shows the arrangement for Experiment 9, where the participant alternates between reaching and simply viewing the scene.

4.5.2 Results

A number of trials were removed due to collisions and recording failure (0.72%). The results were analysed, as in previous experiments, using a two-way within-subjects ANOVA. The two factors were: n-1 trial, the effect of viewing a scene with blocks; and n-2 trial, the effect of the participant's previous movement (each factor being with and without obstacle).

The analysis revealed no main effect of viewing a scene with the blocks alone, that is, a scene with no action upon the blocks [n-1: $F(1,23)=0.01, p=.927$]. There was a main effect of the participant's previous reach [n-2: $F(1,23)=13.40, p=.001$]. There was no interaction [$F(1,23)=0.45, p=.509$]. See Figure 4.7 for the graph of height means. This figure also illustrates the results of planned (one-tailed) comparisons between the baseline, No-No-No, with the O-No-No (obstacle in the previous reach), which shows a significant effect [$t(23)=3.93$, $p<.001$]. A comparison between the baseline and the No-O-No condition (obstacle in the previously viewed scene) shows no significant effect [$t(23)=0.23$, $p=.400$].

In addition to the analysis mentioned above, the results from this experiment were compared to Experiment 8, using a mixed two-way ANOVA. This analysis revealed a significant interaction between experiment and n-1 action priming [$F(1,46)=5.54$, $p=.023$]. This confirmed the difference between this experiment, where the participant was not primed by simply viewing the blocks, and Experiment 8, where the participant was primed by the observation of the other person's reach, confirming that observing the reach is critical to the priming effect. There was no significant interaction between experiment and n-2 [$F(1,46)=0.03$, $p=.861$], confirming that the within-person priming is the same in each experiment.

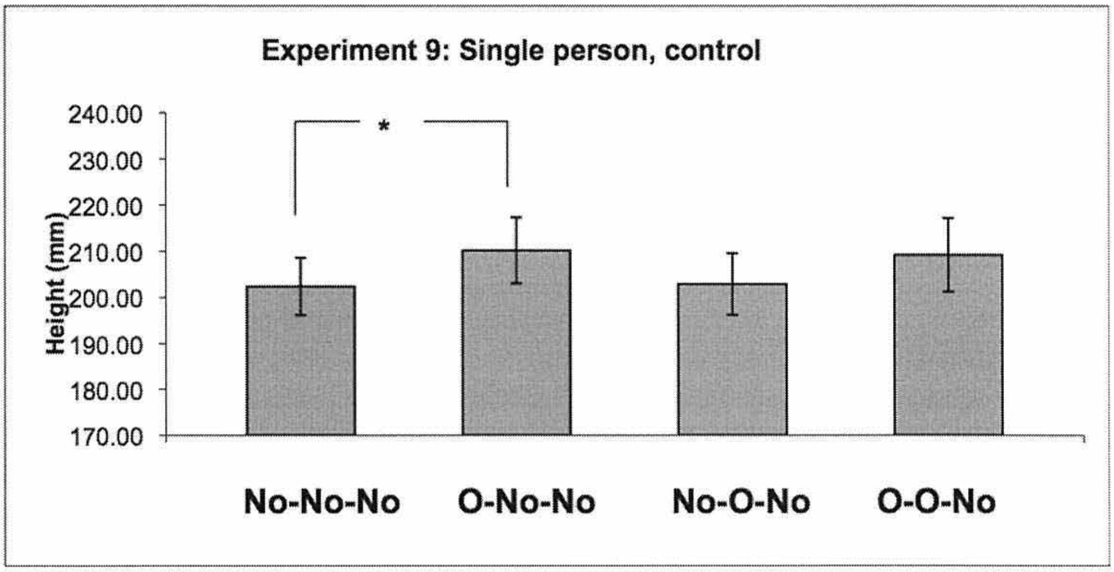


Figure 4.7. Shown here are the means of the maximum height reached for non-obstacle reach trials (n), with their SE for Experiment 9. The bars indicated by * show a significant *t* test result at *p*< .01. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials, and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

4.5.3 Discussion

The results from this experiment revealed no effect of merely viewing blocks between reaches. This confirms that the priming effects reported here are the result of observing another person's action, rather than any priming from the mere observation of the target block or obstacle.

This result demonstrates another distinction between the priming effects of observing grasps and the priming effects of observed reach trajectory. Edwards et al. (2003) demonstrated that grasping actions could be primed by the presentation of an object alone as well as being primed by observation of action upon an object. In contrast, the current results suggest that for reach trajectory priming to take place action observation may be necessary, providing further evidence that reaches and grasps may use different networks in the brain (as discussed in Chapter 2).

It is also interesting to note that participants are affected by their previous (n-2) reaches in Experiment 9. In contrast, recall that in Experiments 4 and 5, where action priming did not take place because the observed obstacles were outside peripersonal space, the participants were not primed by their previous grasps, that is, there was no n-2 effect. It is not clear why the n-2 effect disappeared in Experiments 4 and 5. Perhaps the maintenance and retrieval of prior reach trajectories is undertaken while relevant to the on going task. However, when a participant observes a reach over an obstacle that is outside peripersonal space, and hence is never an object they have to reach over, retrieval is vetoed. In this experiment it is clear that viewing the blocks in a scene does not in anyway interfere with the ongoing maintenance of their reach plan.

Experiment 6 in Chapter 3 was the first experiment to show that viewing others reach higher to avoid an obstacle leads to priming of the observer's own subsequent reach. This priming however, did not occur in all circumstances. The initial hypothesis from the results in Chapter 6 was that the priming effect was mitigated by the angle at which the observer viewed the obstacle avoidance. The first two experiments in this chapter, experiments 7a and 7b, were designed to confirm and explore this hypothesis further. However the results from these two experiments, whilst replicating the priming effect, did not show a reduction in the effect, as had been predicted. These results lead the author to re-examine the design and evidence from the experiments that had been carried out up to that point.

Examining the data and design of the experiments revealed that the common feature of those that showed the priming effect, but not those in which no effect was found, was that the obstacle which participants had observed being avoided was within their reach, that is, within their peripersonal space. This finding lead to a second hypothesis: that it was necessary for the obstacle being avoided to be within the peripersonal space of the observer. Experiment 8 tested this hypothesis. Participants in this experiment sat opposite each other, as in Experiment 4 (where no priming was found). However unlike Experiment 4, the participants sat much closer to each other so that the observed obstacle avoidance took place within the peripersonal space of the viewer. Experiment 8 produced significant results and participants were primed by both action observation, n-1, and their own previous actions, n-2, supporting the peripersonal space hypothesis.

The results from the experiments in this chapter have replicated the action priming effect reported in Chapter 3. The results have also revealed that peripersonal space is an important boundary condition in reach trajectory priming, in contrast to goal-directed actions. And finally, Experiment 9 has demonstrated that the action priming effects reported in this thesis are in fact dependent on action observation and cannot be elicited by the mere presence of objects alone (that can be avoided or acted upon).

CHAPTER 5:

EXPLORING THE LIMITS OF PERIPERSONAL SPACE

5.1 Experiment 10: Seated adjacent, transparent barrier

So far this thesis has presented a number of experiments that have explored reach trajectory priming by observation of action. These experiments have established that observing another person reach over an obstacle affects the subsequent reach of the observer, priming them to reach higher than they would naturally do so in the absence of an obstacle. This priming does not always occur and seems dependent on whether the observed obstacle avoidance takes place within peripersonal space, that is, within the reach of the observer.

Chapter 4 presented a number of studies that support the theory that the brain processes peripersonal space and extrapersonal space (space beyond reach) differently. It was suggested that the separate mechanisms dealing with reaching were anatomically close to those dealing with peripersonal space. Further, as it is only possible to reach within peripersonal space, the experimental results seem quite logical and plausible. It seems inefficient to encode the movements made by others to avoid obstacles that are outside of one's reach and that one is unable to interact with.

Studies from monkeys suggest that reaching space is calculated, not as fixed coordinates around the body, but in reference to the position of a monkey's arm. Graziano and Gross (1995) showed that as the monkey moved its arm so the visual receptive field surrounding the arm, represented in F4, moved. This type of coding suggests that peripersonal space is a representation of space that can be reached physically rather than a specific metric distance from the body. Following on from this it could be hypothesised that if the hand is prevented from reaching into a certain part of near space, by for example a barrier, that this space would no longer be coded as peripersonal space, because the viewer could no longer act on objects within this space. If peripersonal space is coded as space within which the hand can act rather than space that is a specific metric distance from the hand, then it might be expected that if an action took place within close proximity of an observer but the hand of that observer was unable to act on that space, any observed action that took place would not be encoded and therefore not prime the observer's subsequent reach.

This idea is supported by evidence from the studies carried out by Meegan and Tipper (1999) and Tipper, Meegan, and Howard (2002). They found that when reaching for target keys to be depressed, irrelevant to-be-ignored distractors interfered with (slowed) response to the target and were associated with inhibition, as measured via negative priming effects (Tipper et al., 1992). These distractor interference and negative priming effects were hand-centered, in that they were larger when the distractors were closer to the participant's reaching hand. They argued that such hand-centered effects were due to the near distractor winning the race for the control of action. This race model predicted that if it were possible to slow down response encoding of the distractor, while maintaining the same visual information, interference and negative priming effects would be reduced. To this end they presented transparent obstacles over the distractor object, which made the key depression response to them, when they were targets on other trials, more difficult. The results were very clear. Although the visual properties of the distractor were held constant, making the response more difficult with the transparent obstacle placed over the key greatly reduced how much the distractor interfered, and it abolished the inhibition associated with it.

Experiment 10 was designed to test whether it was simply the metric distance of the obstacle to the participant's hand that determines whether simulation of reach path is evoked or if it was dependent on the participant's ability to act on the obstacle. In Experiment 6 participants had sat adjacent to each other. They did not share any blocks and each participant's obstacle was within reach of the other. In the current Experiment 10 the arrangements were the same as that of Experiment 6, except that the participant's were separated by a clear Perspex® barrier. This gave each participant a clear view of the other's actions but prevented them from reaching towards each other's blocks. With this arrangement it was predicted that even though the other person's reach over an obstacle could clearly be seen, because it was not a potential obstacle for the viewing participant, the action would not be simulated and hence would have no effect on the participant's subsequent reach.

5.1.1 Method

5.1.1.1 Participants

A total of 24 right-handed students (14 female), with a mean age of 24.4 years, took part in this experiment in return for course credits. All participants had normal or corrected to normal vision.

5.1.1.2 Procedure and design

The seating arrangement and block design was identical to those in Experiment 6, with participants seated adjacent to each other. In this experiment however, the participants were separated by a clear Perspex® screen (see Figure 5.1). The screen was 50 cm high and 55 cm long. The screen extended from the table, between the participants, by 5 cm. The screen was 5 cm from the blocks of the participant on the left side. The distance between a participant's hand and the other participant's obstacle was visually 40 cm, however the barrier made reaching the other's obstacle impossible. As with previous two-person experiments, participants carried out two blocks of 82 trials.

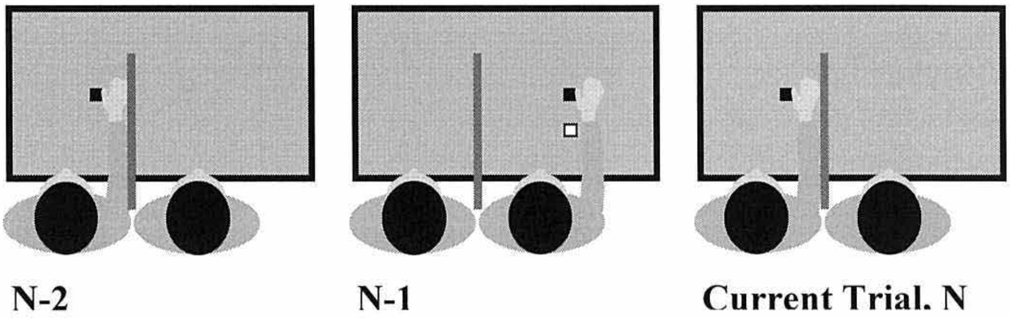


Figure 5.1. Experiment 10: seated adjacent, Perspex® barrier. The black square is the target and the white square is the obstacle. The barrier is marked in blue. It was 50 cm high and 55 cm long, extending over the edge of the table by 5 cm.

5.1.2 Results

A number of trials were removed (1.24%) due to collisions, failed recordings, and where participants had failed to open their eyes on the previous observation trial.

The results from this experiment are broadly similar to those from Experiment 6. There was a main effect of the participant's previous reach [n-2: $F(1,23)=8.09$, *p*=.009] and of the other person's movements [n-1: *F*(1,23)=4.99, *p*=.036] on the current reach trajectory (see Figure 5.2). There was however a significant interaction between n-1 and n-2 [*F*(1,23)=4.38, *p*=.048], revealing that the presence of an obstacle at both n-1 and n-2 did not have a significantly greater effect than if an obstacle had occurred singly at either n-1 or n-2. This is most probably due to the slightly weaker effects of n-1 in this experiment. Further planned (two-tailed) contrast *t* tests revealed that the presence of an obstacle at n-1 (No-O-No) compared to the baseline (No-No-No) lead to significantly higher reaches [*t*(23)=3.18, *p*=.004]. This is also the case with an obstacle at n-2 (O-No-No) compared to the baseline [*t*(23=3.66, *p*=.001]. These results clearly show that a participant's reach is affected by both the observation of the other's reach as well as their own previous reach.

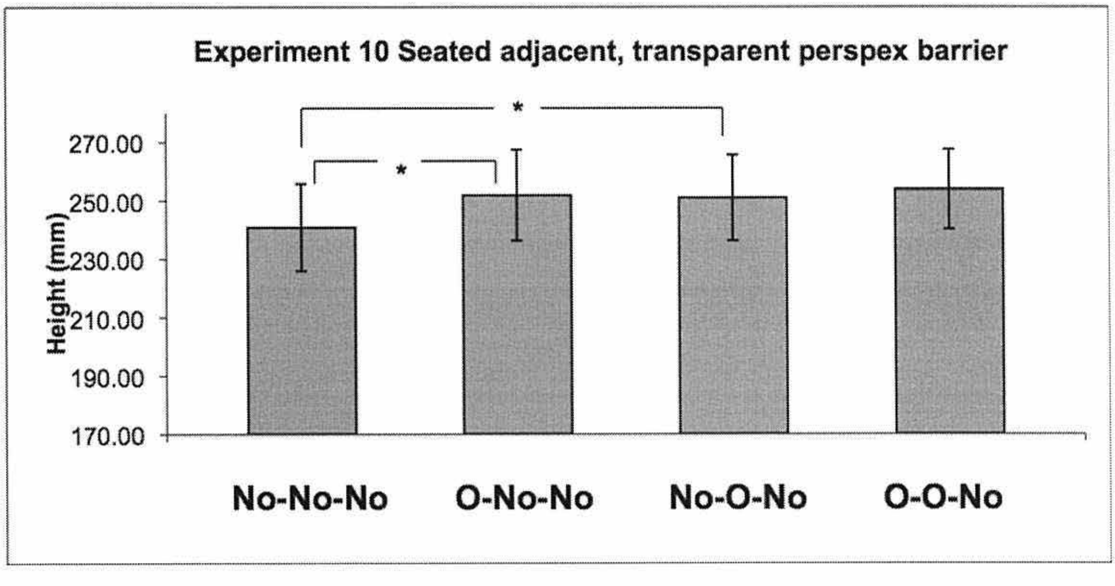


Figure 5.2. Experiment 10: seated adjacent, Perspex® barrier. Means of the maximum height reached for non-obstacle trials, with their standard errors. The bars indicated by * show a significant *t* test results at *p*<.01. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

5.1.3 Discussion

This experiment tested two alternative accounts of the between-person obstacle priming effect. The first account is that the potential for action is encoded. Thus, although the obstacle avoidance of the other person's reach could easily be seen through the transparent barrier, because the obstacle could not be directly acted upon by the viewer the simulation processes would not be activated. The alternative hypothesis is that the metric distance of the obstacle from the participant's responding hand is computed, and if this is perceived to be within peripersonal space, simulation of the other person's obstacle avoidance processes would be activated whether or not a direct action could be produced.

The expectation was that the former account would be supported, that is, when viewing the other person's reach over an obstacle, through a transparent barrier, simulation would not take place, and hence no n-1 reach path priming effects would be detected. Clearly this was not confirmed, as a significant n-1 obstacle priming effect was detected. Thus after observing through a transparent barrier a person reach over an obstacle, the participant's subsequent reach was higher. This result is in contrast with previous work by Meegan and Tipper (1999) and Tipper et al. (2002). However, it should be noted that in these previous studies the transparent cover was placed over the target, so it did not influence much of the reach path, but affected the final adjustment of the hand as it depressed the target key. In contrast, in this experiment the obstacle block was placed midway between the hand and target and influenced the reach aspect of the prehension system. These different findings perhaps reveal a further contrast between reach and the final stages of action, such as grasps and key depressions. Certainly the results from Experiment 10 support the notion that the simulation of another person's obstacle avoidance reach path is determined by the metric distance of the obstacle from the observer's hand, and not the higher-level factor of potential for action.

Since the work for this part of the thesis was carried out a paper investigating action simulation and peripersonal space in monkeys has been published. Caggiano, Fogassi, Rizzolatti, Their, and Casile (2009) selected neurons in F5 that activated when the monkey carried out hand goal-directed movements. They then examined the mirror responses of these neurons within and beyond peripersonal space, that is, the responses to observing an experimenter executing goal-directed movements. To summarise: 26% of neurons examined only responded when the experimenter carried out the action in extrapersonal space, 27% only responded when the action was carried out within the peripersonal space of the monkey, and 47% of the neurons responded to observed actions independently of location. This is of course further strong evidence for the separate encoding of extra- and peripersonal space. Interestingly, however, they extended the experiment and investigated the nature of the space coding. These mirror neurons could have coded the metric distance to where the observed action was being carried out, or they could have coded the potential for action at that distance. Caggiano et al. sat the monkey in front of a clear barrier to observe actions carried out within metric peripersonal space that was now blocked from action. Of the 21 space-selective neurons that were tested a subset of 9 changed their tuning. Of these, the neurons that had previously responded only to actions carried out in extrapersonal space now responded and those which had been activated by actions in peripersonal space no longer responded. This demonstrates that, in monkeys at least, there exist two kinds of mirror cells: those that code for actions in terms of metric distance (unaffected by transparent barriers) and those that code in terms of the monkey's ability to act in a particular area of space. It should be noted that these mirror neurons respond to goal-directed hand actions. There is, as yet, no evidence that monkeys are able to encode kinematics of the observed reach movement to the goal object.

Humans are of course able to make judgments about how far away something is and whether or not an object can be acted upon, that is both metric and potential action decisions. Where in the brain this occurs and at what stage of processing this information is assembled are complex questions. A partial answer to these questions has come from the research by Quinlan and Culham (2007), who carried out an fMRI study to investigate the role of the SPOC (in the SPL) in coding near and far space. They found that this area shows a preference for objects in near space. They additionally investigated whether oculomotor cues alone were sufficient to activate this area.

The brain uses a number of different sources of information to judge depth and how distant an object is. These include optical information such as texture, shadows, and familiarity with an object. It also uses ocular information, information from the eyes themselves. There are two types of information that the eyes provide, accommodation and convergence. Convergence is inward movement of the eyes so that they see one object and not two. Accommodation is the change in the shape of the lens so that the viewed object is not blurred.

Quinlan and Culham (2007) removed all the optical cues to depth by conducting the experiment in total darkness. Participants viewed light emitting diodes (LEDs) at different distances. The luminance and the retinal size of the LEDs were controlled so that with monocular vision the LEDs appeared identical. The brain's activation indicated that, despite the reduced information, the SPOC was able to distinguish that these objects appeared at different distances. Further, they found that the pattern of activation was the same as with the object stimuli. Their finding demonstrates that SPOC encodes peripersonal space using oculomotor, eye movement, cues alone. This area is not encoding space in terms of how close an object is to a hand or whether that object is in space that can be acted upon, but rather as a fixed measure of peripersonal space in metric terms. Experiment 10 provides evidence that embodiment of an observed reach depends on such a judgment, that is, it occurs when an obstacle avoidance action takes place within a fixed distance, rather than depending on whether that obstacle is reachable by the observer's hand. The SPOC area may well make a key contribution to the embodiment of observed reach trajectories.

5.2 Introduction to Experiments 11a and 11b: outside of peripersonal space

The experiments presented so far have demonstrated that action priming of reach trajectory by observation is dependent on whether the observed deviations in reach path trajectory take place over obstacles within the viewer's peripersonal space. The results from Experiment 10 further suggest a system that uses quite low-level information to determine whether or not an action is embodied. However, given the widely held view that the human mirror system and embodiment contributes to a human's ability to understand the motor intentions, higher goals and state of mind of others, and the role of motor gestures in communication, it would be surprising if action simulation was indifferent to higher concepts and goals (Rizzolatti & Arbib, 1998; Blackmore & Decety, 2001; Williams, Whiten, Suddendorf, & Perrett, 2001; Gallese, 2001; Rizzolatti & Craighero, 2004; Jackson & Decety, 2004; Gallese, Keysers, & Rizzolatti, 2004; Brass & Hayes, 2005).

There is certainly evidence that people's own motor acts are affected by higher-level concepts such as the intention of a simple motor act and the social setting, competitive or cooperative. For example Becchio, Sartori, Bulgheroni, and Castiello (2008) showed that the kinematics of the reach and grasp when lifting and placing a block was significantly affected by whether the block was lifted and placed in a non-social setting or if the block was placed in order to give it to another, a social setting. Interestingly both the reach-to-grasp and placing phase were affected (see also Sartori, Becchio, Bara, & Castiello, 2009). Not only has a social context been found to affect reaching but also the nature of that context (Georgiou, Becchio, Glover, & Castiello, 2007). Here participants were affected by whether the movement was in a competitive or cooperative setting.

These are examples of how intentional reach and grasp movements are affected by higher-level concepts. But research has also shown that unconscious movements can be affected by setting. Häberle, Schütz-Bosbach, Laboissiére, and Prinz (2008) investigated ideomotor behaviour in competitive and cooperative settings. Ideomotor acts are those movements an individual involuntarily exhibits whilst observing other events, especially actions of other individuals. Examples include watching motor racing and veering with the movement of the car, or as Häberle et al. mention, a passenger pressing an imaginary break pedal as the driver approaches a bend too quickly. In their experiment participants were asked to play a ball rolling game. They could either manipulate the ball or a target so that the ball hit the target and they gained a monetary reward for the number of hits. The participants were told they would be paired with another person, sat in another room, whose game they would see on their screen in between their own games. Half the participants were assigned to a cooperative game, where hits from each participant would add to the monetary reward of both participants. In contrast, the other half of the participants were assigned to a competitive game, where a successful hit would add to that person's reward and at the same time be deducted from the other's monies. The participant's hand remained on the controller whilst they viewed the other's game. They found that in the cooperative setting the participants unconscious ideomotor movements of the controller were towards achieving the goal, in the competitive setting the movements reflected their desire that the other player not succeed as non-conscious movements were away from the target.

These studies demonstrate that our own actions are strongly affected by the context in which that action is performed. In simulating the actions of others we utilise part of the system that we use for our own actions. If our own actions are affected by higher-level concepts then it seems logical that the simulation of other's actions could also be affected by higher-level concepts.

Other such higher-level concepts include ownership. A sense of ownership of an item is a strong bond and can endow an item with greater value than it would inherently have by itself. For example a fathers' day cup purchased by a child is of great sentimental value. If someone broke the cup and offered an identical replacement, that replacement would clearly not have the same value. It is also unlikely that the recipient would be willing to part with that cup even when offered substantially more than it cost to purchase (Kahneman, Knetsch, & Thaler, 1990; see also Kogut & Kogut, 2010). Even a brief sense of ownership can have effects. Cunningham, Turk, Macdonald, and Macrae (2008; see also van den Bos, Cunningham, Conway, & Turk, 2010) found that a sense of ownership improved memorability. In their experiment participants sat with a confederate. Each was given a coloured basket and the participant was asked to sort picture cards, by coloured markers, into the appropriate basket. In a later memory test participants remember the items on the cards placed in their basket significantly better than the other cards.

The purpose of the last two experiments presented in this thesis was to investigate whether or not manipulation of higher-level concepts can be used to induce action priming outside peripersonal space, with Experiment 11a being the baseline experiment for comparison with Experiment11b. The concept of ownership was chosen as it has been demonstrated that it can have strong effects on memory and a possession's value. In Experiment 11b participants shared the same obstacle and target block. The idea behind this was that the viewing participant would have a sense that the other participant was using "their" blocks. In addition to sharing the blocks both participants shared a common workspace, a wooden tablet onto which the blocks, were placed and moved between participants. The participants would see “their” blocks being moved away and being used by the other.

5.3 Experiment 11a: Seated at 90º, no shared blocks or tablet, outside peripersonal space

This experiment was the baseline for Experiment 11b. A second purpose of this experiment was to replicate the findings from earlier experiments, and provide further confirmation that the action priming effect is mitigated by observation of obstacle avoidance in peripersonal space. This thesis has presented a number of experiments that demonstrate action priming in peripersonal space, at various perspectives. Only Experiments 4 and 5 demonstrated the absence of priming outside peripersonal space, and only when participants were seated opposite each other. In the current experiment participants viewed actions taking place outside of peripersonal space at 90°. It was expected that, as with Experiments 4 and 5, there would be no effect of action priming by observation.

5.3.1 Method

5.3.1.1 Participants

A total of 16 right-handed students (13 female), with a mean age of 20.7 years, participated in this study in return for course credits. All participants had normal or corrected-to-normal vision.

5.3.1.2 Procedure and design

Both participants used their right hands. They were seated at 90° to each other on two sides of a table. Each participant had their own obstacle and target block; one participant had a yellow obstacle and a yellow target, the other a blue set. Each participant also had a thin (12 mm) A3 sized (420 mm x 297 mm) wooden tablet work surface, one grey, the other dark green (see Figure 5.3). As with all the experiments, the table, at which the participants sat, was covered in black material to reduce reflection. Each participant's obstacle was 20 cm from their hand's resting position, and the target was 40 cm away. The participants' targets were 90 cm apart, and their obstacles 115 cm apart. Each participant's hand resting position was therefore 130 cm away from the other's obstacle, considerably outside peripersonal space.

Participants alternated between reaching and watching the other participant reach. In the previous two-person experiments participants were instructed to close their eyes at the end of the reach, without instruction from the experimenter. In the current experiment participants waited to hear the instruction before closing their eyes, viewing the scene for an extra few seconds after the reach. The reason for this was to match the length of exposure to the blocks and the scene with the following Experiment 11b, which will be described shortly. In that experiment participants viewed the experimenter move the tablet between participants, and in doing so viewed the scene and the blocks for additional time. In the previous two-person experiments participants were not given explicit instructions to watch the reach of the other, only to note when the action ended and then close their eyes. Because participants in this experiment have to wait to hear the experimenter give the instruction to close their eyes rather than observing the other participant there could be no guarantee that participants would observe the other's movements. Therefore in Experiments 11a and 11b participants are given an explicit instruction to observe the reach.

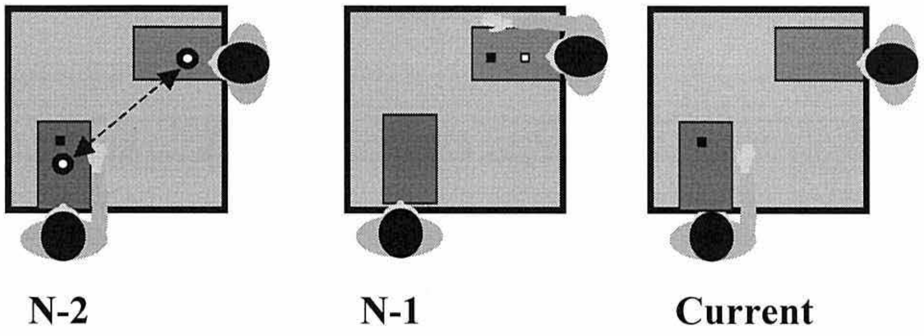


Figure 5.3. Experiment 11a: Seated at 90°, outside of peripersonal space. The black square is the target, the white square the obstacle. The circles in the first frame show the position of the participants' obstacles, which are 115 cm apart.

5.3.2 Results

A number of trials were removed due to collisions, recording failure and where participants had failed to open their eyes on the previous observation trial (1.18%).

The results are shown in Figure 5.4. As predicted there was no effect of observing the other participant reach over an obstacle outside peripersonal space [n-1: $F(1,15)=0.00$, $p=.993$]. The participants were affected by their own previous reaches over obstacles [n-2: $F(1,15)=4.80$, $p=.045$]. There was no interaction [$F(1,15)=0.25$, $p=.627$]. Further planned contrast *t* tests (two-tailed) between the baseline No-No-No and an obstacle at n-2 (O-No-No) revealed a significant difference [$t(15)=3.02$, $p=.004$]. No significant difference was found between No-No-No and those trials where an obstacle appeared at n-1 (No-O-No) [$t(15)=0.33$, $p=.371$].

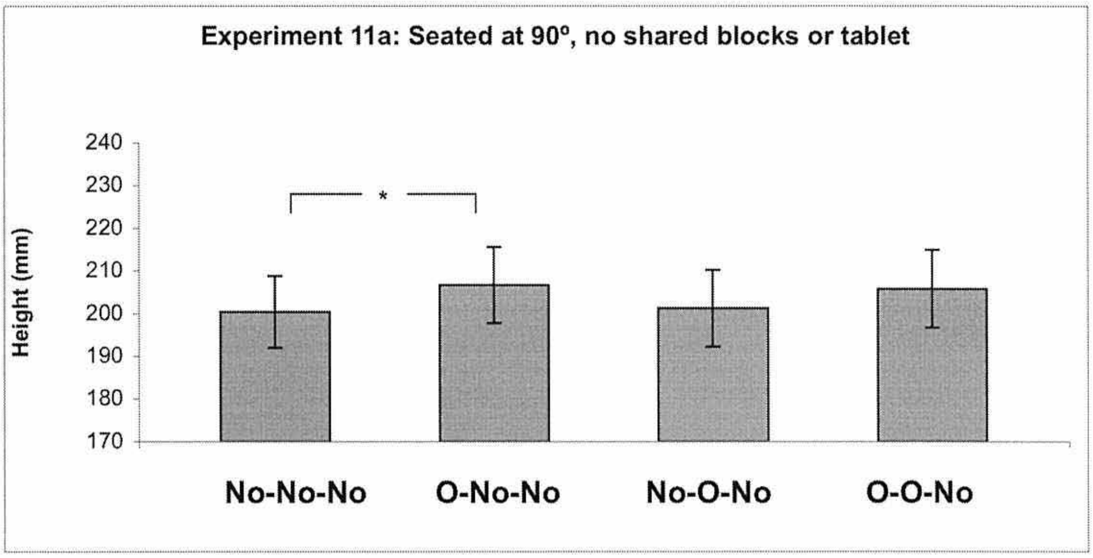


Figure 5.4. Experiment 11a: Seated at 90°, no shared blocks or tablet, outside peripersonal space. Means of the maximum height reached for non-obstacle trials, with their standard errors. The bar indicated by * show a significant t test results at *p*<.01. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

5.3.3 Discussion

The results from this experiment are as predicted; there is no effect of action priming from observation of obstacle avoidance outside peripersonal space. These results replicate and extend those from Experiments 4 and 5, demonstrating that even at other viewing perspectives action simulation requires the observed action to take place in peripersonal space. It should be noted that due to the 90° position each participant had a very clear view of the action of the other. One significant change in this experiment, compared to Experiments 4 and

5 is that participants are specifically instructed to observe the movement of the other. Despite this instruction there was no effect of action observation. However, unlike Experiments 4 and 5, this experiment produced significant n-2 effects, that is, participants were affected by their previous reaches. The effect of a participant's previous reaches on their current reach is usually a robust effect. Jax and Rosenbaum (2007) found that this effect persisted over at least four trials (during a within-person experiment). It is not unexpected that this effect was present in Experiment 11a but more puzzling that it was absent in Experiments 4 and 5. Speculation as to the possible reasons for the effect's absence were discussed after Experiment 9, Chapter 4, but it remains an open issue.

Nevertheless this experiment provides an excellent baseline for the following Experiment 11b, as it confirms that obstacle avoidance reaches outside peripersonal space do not prime an observer's subsequent reach path. Whether a sense of ownership can influence this action observation priming effect is the focus of the following Experiment 11b.

5.4 Experiment 11b: Seated at 90 °, shared bocks and tablet, outside peripersonal space

Experiment 11a confirmed the earlier results from Experiments 4 and 5, that observation of another's reach trajectory does not affect the observer's subsequent action if that reach took place over an obstacle outside of the viewer's peripersonal space. The seating arrangement in the present Experiment 11b was identical to that of Experiment 11a. Therefore the participants in this experiment will be viewing an action that is identical to the one that participants viewed in Experiment 11a. This experiment however, was designed to induce action simulation through the manipulation of higher-level concepts. It was hoped that instilling in the participants a sense of ownership over the blocks and transferring a workspace between them would produce action priming.

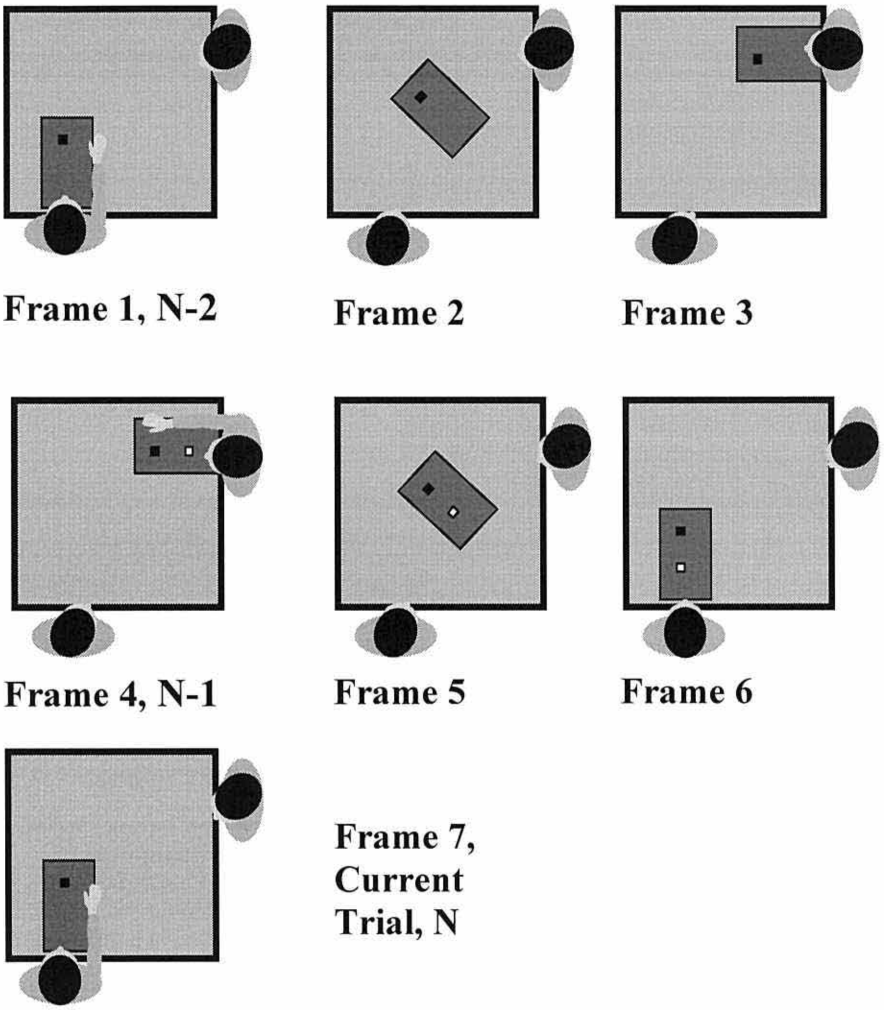
5.4.1 Method

5.4.1.1 Participants

A total of 16 right-handed students (14 female), with a mean age of 21.3 years, participated in this study in return for course credits. All participants had normal or corrected-to-normal vision.

5.4.1.2 Procedure and design

The seating position in this experiment was identical to that in Experiment 11a Participants shared an A3 sized work surface as described in Experiment 11b, and one set of blocks. The colour of the tablet and blocks was balanced across participant pairs. Participants alternated between reaching and observing a reach. They were given explicit instructions to observe the other's reach. They were explicitly told that there was only one set of blocks and one tablet and that they would be sharing it. Figure 5.5 shows the procedure of the experiment. Participants began with their eyes closed. On instruction both participants opened their eyes and the first participant made their reach. The experimenter then slid the tablet with the blocks on across to the second participant. They were then instructed to close their eyes and the experimenter removed or replaced the obstacle block as necessary. The participants were then given the instruction to open their eyes and the second person executed their reach.



Frame 1, N-2

Frame 2

Frame 3

Frame 4, N-1

Frame 5

Frame 6

Frame 7, Current Trial, N

Figure 5.5, Seated at 90°, shared tablet and blocks, outside peripersonal space.
The black square is the target, the white square the obstacle.
Frame 1: Both participants have their eyes open and the first participant reaches.
Frame 2: Both participants have their eyes open as the tablet and blocks are moved.
Frame 3: When the tablet is in place the participants are instructed to close their eyes and the blocks are set up.
Frame 4: The participants are instructed to open their eyes and the second participant makes their reach.
Frame 5: Both participants have their eyes open as the tablet and blocks are moved.
Frame 6: When the tablet is in place the participants are instructed to close their eyes and the blocks are set up.
Frame 7: The participants are instructed to open their eyes and the first participant makes their reach.

5.4.2 Results

A number of trials were removed due to collisions, recording failure and where participants had failed to open their eyes on the previous observation trial (1.36%).

Results are shown in Figure 5.6. As with Experiment 11a, there was a significant effect of a participant's previous reach on their current reach [n-2: $F(1,15)=22.49$, $p<.001$]. However, in stark contrast to the previous experiment, there was a significant effect of observing the other participant's reach over an obstacle [n-1: $F(1,15)=5.83$, $p=.029$]. There was no interaction between n-1 and n-2 [$F(1,15)=2.64$, $p=.125$]. Further planned (two-tailed) contrast *t* tests, comparing the baseline (No-No-No) to conditions with obstacles at n-2 and n-1, revealed significant effects in both cases [O-No-No: $t(15)=4.86$, $p<.001$; No-O-No: $t(15)=3.65$, $p=.001$].

In addition to the analysis above the results from Experiment 11b were compared to those from 11a in a mixed two-way ANOVA. This revealed a significant interaction between n-1 (obstacle priming by observation) and experiment [$F(1,15)=4.50$, $p=.042$], that is, the n-1 effects significantly differed between experiments. There was no significant interaction between n-2 and experiment [$F(1,15)=1.96$, $p=.172$], that is, no significant difference in the priming of participants by their previous reaches between experiments. There were no other significant interactions.

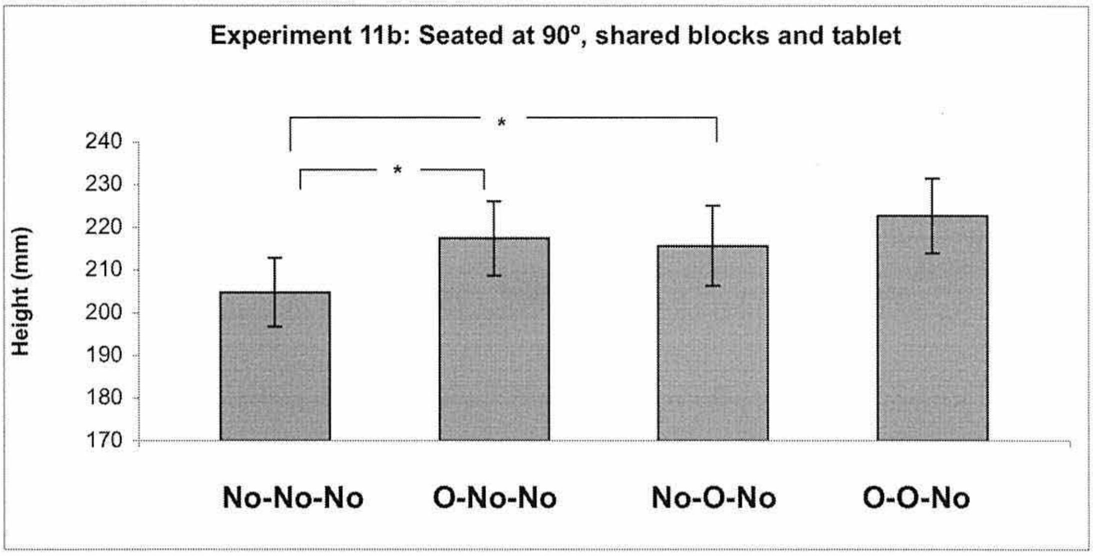


Figure 5.6. Experiment 11b: Seated at 90°, shared blocks and tablet, outside peripersonal space. Means of the maximum height reached for non-obstacle trials, with their standard errors. The bars indicated by * show a significant t test results at *p*<.01. The bars are labelled with the trial type (n-2, n-1, n), where "No" represents non-obstacle trials and "O" where an obstacle was present. The error bars represent the standard error of the mean (S.E.M.)

5.4.3 Discussion

The results from Experiments 11a and 11b are quite distinct. In Experiment 11a, when participants used a separate workspace and blocks, there was no priming effect from action observation. In contrast, in Experiment 11b, where participants share the blocks and the workspace, there is clear action priming from observation. This is a remarkable difference because both sets of participants view identical movements from an identical perspective and distance. Action simulation cannot therefore be dependent only on the visual properties of an observed action.

The design of this Experiment 11b manipulates several things. The participants were explicitly told they would share the blocks and that the workspace would be moved between them. Labelling either the blocks or the workspace in this way alone may have been sufficient to either induce a sense of ownership over the blocks or to induce a sense of them both working in the "same" workspace, either of which could have lead to action simulation. In addition to the verbal description the participants saw the other participant act upon the objects they had recently used and were about to use. This may have made the blocks more relevant. Finally participants also witnessed the tablet being moved across the table to the other person. Being able to follow this movement may have meant that the workspace remained coded as peripersonal space, either as an extension of their peripersonal space or a separate visualisation of it.

Attention would seem a strong contender to account for this effect. Bach et al. (2007) showed that attention can modulate embodiment. However in these experiments both sets of participants are specifically told to attend to the reach of the other. If greater attention were the cause of the results in Experiment 11b it would be expected to produce the same results in Experiment 11a. There is no reason to think that the participants in Experiment 11a paid less attention to the others' reaches and so it is less plausible that the difference in these two conditions is one of attention.

It is tempting to think that these results occurred as a result of peripersonal space being extended. There is a considerable body of literature investigating how peripersonal space can be extended, both in patients and healthy participants. For example, Berti and Frassinetti (2000) studied patient PP who suffered from neglect. One way in which this condition manifested was in line bisection tasks. When asked to mark the mid-way point in a line this patient consistently bisected towards the right. This effect only occurred in peripersonal space, and not when the patient bisected a distant line using a light pen. However when the patient was asked to bisect a distant line using a stick they showed the left neglect. Other patients with lesions in their right hemispheres show extinction. When patients are presented with stimuli in both left and right hemi-fields they do not detect the contralesional stimulus. Some patients can have cross-modal extinction, where a tactile stimulus is undetected when a visual stimulus is placed near the ipsilesional hand (Làdavas, 2002). This cross-modal extinction is less evident when the stimulus is placed far from the hand. However, when such patients hold a stick, stimuli placed close to the end of the stick will cause extinction (Farné & Làdavas, 2002). This use of tools temporarily remapped far space as near space.

Healthy participants also show a smaller version of neglect called pseudoneglect (Bowers & Heilman, 1980; for a review see Jewell & McCourt, 2000) when bisecting a line. They tend to make a leftward bias. This effect is seen only in peripersonal space shifting rightward when bisecting lines at a distance using a laser pointer. However when bisecting lines with a stick healthy participants show a leftward bias in far space (Longo & Lourence, 2006; Gamberini, Seraglia, & Priftis, 2008).

A study by Iriki, Tanaka, and Iwamura (1996) examining specific neuron activity of monkeys revealed that neurons which code for near space around the hand but do not fire for stimuli in far space change their activity after the monkey had been trained to use a rake to retrieve food. After training the neurons would respond to stimuli placed close to the end of the rake, even though this was far beyond normal peripersonal space for the animal. Interestingly this extension of peripersonal space did not take place when the monkey simply held the rake without using it.

It is impossible from the current study to know for certain whether the participants' perception of peripersonal space had been extended or whether simulation took place due to some other mechanism. However one important distinction between the previous literature described above and Experiment 11b is that all these previous experiments investigating tool use required active involvement with the tool where participants received visuomotor and tactile feedback. If no such learning was experienced, then peripersonal space was not extended. In sharp contrast, no such feedback occurred in Experiment 11b, where participants merely passively observed the tablet moved across the table and the other participant's subsequent reach.

As discussed earlier, studies have shown that a sense of ownership has been linked to stronger memory (Cunningham et al., 2008; see also van den Bos et al., 2010). Jax and Rosenbaum (2007) propose that action priming occurs because a memory of the action remains and is modified and reused. Perhaps observing an action outside peripersonal space does not create or modify such a memory. It is possible that the sense of ownership over the blocks used in Experiment 11b lead to a stronger memory trace, which remained while the blocks were used by the other participant. The observation of the other participant's interaction with "their" blocks may have caused that observed movement to be associated in memory with the original action plan and thus modified it. This is of course speculation and the results of this experiment do not establish exactly which aspects of the experimental design invoked action simulation and produced priming effects. Further experiments would be needed to tease apart which of these manipulations caused the action simulation.

Chapters 2 to 4 presented a number of experiments establishing that people do encode the kinematics of observed reaches, and that this can prime the subsequent reach of the observer. These experiments further demonstrated that the priming effect was mitigated by whether or not the observed obstacle avoidance took place within peripersonal space. The purpose of the experiments presented in Chapter 5 was to investigate the limits of this embodiment.

Experiment 10 explored more deeply the nature of the peripersonal space effect on action priming. The experiment tested two hypotheses, first that the hand-centred effects occurred when the obstacle could be acted upon, and second that the effects occurred when the obstacle was within a certain metric distance from the observer. Participants observed each other avoiding obstacles within peripersonal space but behind a transparent barrier, which removed the obstacle's potential to be acted upon.

It was hypothesised that not being able to act upon the obstacles would inhibit action simulation and no priming effects would be obtained. This was not the case and the effects of observing another person's reach on a participant's subsequent reach was clearly detected.

Such a finding suggests that the system undertakes a simple computation of metric distance between a participant's hand and an obstacle, and it does not take account of the potential for action. The work of Quinlan and Culham (2007) has shown similar computations in SPOC. This area uses oculomotor cues alone to determine whether or not an object is within peripersonal space.

However, although the results of Experiment 10 suggest that the action priming system is somewhat simple, only computing metric distance, the results of Experiment 11b suggest that the priming effects can be influenced by higher-level social factors, such as ownership. Compared to the baseline Experiment 11a, which confirmed no action priming when observed actions were beyond peripersonal space, subtle changes to the procedure in Experiment 11b completely changed the effects. As remarked upon earlier, the visual properties of the observed actions are identical in both Experiment 11a and 11b.

The results from the experiments in this chapter are somewhat paradoxical. On the one hand the priming effects seem to rely on the simplest of visual information, the metric distance of the obstacles avoided, rather than on more integrated information such as reachability. And yet two situations that present identical visual information produce very different results, suggesting that the effects are dependent on more than just the visual properties of the observed action and may in fact be influenced by higher-level abstract concepts such as ownership. At this time there is no clear conclusion, but these results are certainly motivation for future research into other mediating mechanisms.

CHAPTER 6:
GENERAL DISCUSSION

6.1 Discussion

This thesis has reported a series of experiments investigating priming of reach trajectory by action observation. The most important result from these experiments is that observing another person avoid an obstacle primes the viewer's subsequent reaches. Those subsequent reaches show significantly more deviation when following obstacle avoidance than when following reaches that had not involved obstacle avoidance. That is, when participants had observed another person reach over an obstacle their subsequent reach was higher. This is the first time that people have been shown to encode and simulate the specific kinematics, or the means, by which a goal is reached.

The priming effect is very robust and occurs under a number of different circumstances. The effect generalizes across a range of different interpersonal viewpoints. In Experiment 8 participants sat opposite each other (allocentric perspective), whereas in Experiment 6 they sat next to each other (egocentric perspective). Priming also takes place independently of whether or not participants jointly act on the same objects. In Experiment 6 participants shared no objects, whereas in Experiments 7a and 7b participants shared the obstacle and target object, respectively.

Numerous studies have demonstrated that goal-orientated actions, such as grasping, can be embodied (Castiello et al., 2002; Edwards et al., 2003; Dijkerman and Smit, 2007). This has lead to the assumption that, like mirror neurons in monkeys, the human mirror system is only concerned with encoding the goal of an action, rather than the low-level specific reach properties of that action. The results presented in this thesis are in contrast to the data collected from research on monkeys, which provide no evidence that the mechanics of movements are encoded. The goal-orientated nature of monkey mirror neurons has been shown in a number of excellent experiments, where in fact there was no kinematic detail available to the monkey. Umiltà et al. (2001), for example, showed that even when the last part of the action upon the goal object was hidden, monkeys were able deduce the goal of the action. Further, Kohler et al. (2002) demonstrated that monkey mirror neurons fire when the monkey hears the sounds of a goal-orientated action, such as cracking a peanut, in the total absence of any visual information.

It is perhaps not surprising that the human mirror system is capable of encoding much more than actions focused on the manipulation of a goal, in contrast with monkeys. Humans are capable of complex behaviours, such as imitation and gesture for communication, which rely on specific nuances of the mechanics of the movements to communicate. It is theorised that mirror neurons play a key role in imitation and that our ability to embody the actions of others may have, through gesture, allowed language to develop (Arbib, 2002). There is certainly evidence that poor performance in imitation of oral movements is correlated with deficits in language production in children (Alcock & Krawczyk, 2010).

The second important result from this thesis is that priming of reaches by observation does not take place under all circumstances. Experiments 4, 5 and 11a show that there are boundary conditions to the effect. Viewing obstacle avoidance outside of peripersonal space does not produce priming. This highlights an important difference between priming of goal-orientated actions, such as grasping, and the priming of reach kinematics. There is no literature reporting that goal-orientated actions are affected by the proximity of the object and action to the viewer. One explanation of why observed actions, such as grasping, are encoded from a distance but not specific reach kinematics may lie in the advantages of encoding grasp, but not of encoding reaches. The way in which an object can be manipulated is not dependent on distance. The information gained by encoding another's interaction with an object, even from a distance, is information that will be useful and relevant once that item is within reach. Conversely the reach kinematics of how someone has avoided an obstacle is only relevant if that obstacle comes within reach and is in a similar position. Therefore the information about an observed reach outside peripersonal space is far less useful. Further, there are usually a limited number of ways in which an object can be picked up or manipulated. In contrast, reaching towards a goal object, and negotiating a scene with obstacles, can be completed in very many ways. With relatively little encoding and thus effort, information about how to manipulate an object can be gained from watching a person interact with the object, which provides a useful advantage. In contrast encoding the many possible ways an object may be reached contains more detail, more encoding effort, and may in the end provide no advantage. Clearly there is utility in encoding object manipulations outside of peripersonal space but not reaches.

Such theoretical advantages, as discussed above, are speculation. However what is certainly the case is that there is strong evidence that the human brain processes peripersonal and far space differently. The idea of distinct cortical networks dealing with near and far space is supported by evidence from both monkey and imaging studies (Colby & Duhamel, 1991; Fogassi et al., 1992; Graziano et al., 1994; Colby & Goldberg, 1999; Weiss et al., 2000; Weiss 2003). Evidence from patients, in particular, has provided strong evidence of the dissociability between near and far space (Halligan & Marshall, 1999; Vuilleumier et al., 1998). There is also evidence for separate streams of processing for reaches and object manipulation (Binkofski et al., 1998; Tanné-Gariépy et al., 2002; Cavina-Pratesi et al., 2010). Areas dealing with reaching seem more closely linked to those areas involved with coding peripersonal space. As discussed after Experiment 8, this seems logical. Reaching can only take place in peripersonal space and information about the environment of peripersonal space is required for a successful reach. The results reported in this thesis are consistent and fit well with the data from these studies.

In addition to providing support for the idea that peripersonal and far space are dealt with differently, these experiments also provide some support for Jeannerod's (1981) theory that reach and grasp are processed separately. Further to the points mentioned above, there is another important difference between reaching and grasping. Edwards et al. (2003) reported that in addition to action observation priming participant's grasping actions, the mere presence of an object was enough to prime subsequent grasps. Experiment 9 was carried out to establish that reach trajectory priming occurs as a consequence of observing action and not just the presence of the obstacle and target. In Experiment 9 participants alternated between acting on the blocks and viewing the scene set out for the second participant in Experiment 8 (which produced action priming) but viewed no action in relation to those blocks. Viewing the objects produced no priming. This result is in contrast to Edwards et al.'s (2003) results. It bolstered the conclusion from the earlier experiments that priming occurs because the actions viewed are embodied. The results reported by Edwards et al. seem robust and raise the question of why mere exposure to blocks in Experiment 9 did not produce priming of reach trajectory. If the mere presentation of blocks can prime goal-orientated actions, such as grasp, why do they not also prime higher reaches associated with obstacle avoidance? It is not possible to give a definitive explanation but the answer may be similar to that discussed above in that reach path priming is only activated when relevant to ongoing action. In Experiment 9 reaches are never made in well-specified situations.

An object can usually be grasped in a limited number of ways. We are likely to interact with it in the same way next time. There is, therefore, utility in remembering how we have interacted with an object, and storing that memory long-term. Recalling the action plan associated with that object as soon as it is seen again provides an advantage. Tucker and Ellis (1998, 2004; see also Ellis & Tucker, 2000) showed that the objects elicit strong action affordances, even when that action is not required, and when their experimental participants did not interact with the objects viewed. These effects depend on the stored knowledge about the object, rather than occurring as a consequence of very recent interaction with the object.

In contrast to the constrained and limited range of hand-object interactions, there are very many ways in which a hand may negotiate avoiding an obstacle. There is little advantage in remembering long-term the specific kinematics of how an obstacle was avoided. In all likelihood, the next time we encounter it we will not be negotiating our hand around it in the same way. Of course the experiments presented in this thesis do show that, at least for a short time, how participants have negotiated obstacles remains in memory and allows subsequent priming. These motor plans are likely to be quite temporary and different to the long-term action memories that seem to be laid down after handling goal objects. It is, though, an intriguing result that viewing another participant negotiate over the obstacle in Experiment 8 does affect subsequent action, but viewing the obstacles presented in that same position but with no action does not elicit priming. It might be expected that some priming by the obstacle alone should occur. It may be that actions upon objects are encoded quite differently to reach trajectories. With goal-orientated actions it seems likely that the action plan may be encoded in memory with a representation of the object that was manipulated. When the object is seen again information stored about the object is also accessed, including appropriate action plans. When obstacles are avoided perhaps only the trajectory itself is encoded in the memory, with no representation of the actual object avoided. Thus when the obstacle is seen again there is no association in memory with this object and an action plan. Note that in Experiment 6 changing the action and object had no effect on the reach path priming effect within a participant. Hence the idea that reach path is not associated with object identity or form of grasp is well supported in this thesis.

The experiments in Chapter 5 were designed to explore further the role of peripersonal space in action embodiment. Experiment 10 was designed to test whether priming in peripersonal space was related to the ability of participants to act on the obstacle they observed being avoided, or whether it was the simple metric distance of the object from the hand that was calculated. This experiment was identical in design to Experiment 6, where participants sat next to each other and did not share any blocks, except that participants were separated by a Perspex® screen. The screen allowed each participant to clearly see the blocks and the action of the other participant, but now placed those blocks out of the reach of the viewing participant. The presence of the screen did not prevent the viewed obstacle avoidance from being embodied and produced action priming. These results suggest that embodiment of an observed reach depends on whether or not that reach takes place within a fixed distance rather than on whether or not the obstacle can be acted upon. The results from the experiment were unexpected, however, they are consistent with fMRI experiments such as Quinlan and Culham (2007). Their study of the superior parieto-occipital cortex suggests that this area, which is involved in encoding space within reach, measures that distance in fixed terms.

The results from Experiment 10 suggest a system that uses relatively low-level visual information to determine whether or not an observed reach is encoded. The purpose of Experiments 11a and 11b was to examine whether higher-level concepts, such as ownership and a shared workspace, could induce action priming outside of peripersonal space. In Experiment 11b participants were explicitly told that they would be sharing the target and obstacle blocks, and that they would use a common work surface that would be moved between them. Despite the fact that the observed obstacle avoidance took place well beyond peripersonal space, participants showed the priming effect. In Experiment 11a participants did not share the work surface or obstacles and sat in identical positions to the participants in Experiment 11b. The participants in Experiment 11a showed no action priming. The difference between these two results is remarkable because in both experiments participants viewed identical actions from identical angles at identical distances. Action simulation cannot therefore be dependent on the low-level visual properties of the reach alone. As discussed at the end of Chapter 5, there are a number of aspects of Experiment 11b that may have induced action priming. The transfer of the work surface between participants is one candidate. Having seen the work surface transfer between each other may have lead to the surface being visualised as part of peripersonal space. Alternatively the concept of ownership of the blocks may have lead participants to create stronger memory traces and associations of the observed obstacle with their own action plan. Further research is needed to examine the possible factors that caused priming. These results certainly provide an intriguing counterpoint to the results of Experiment 10. On the one hand the results from Experiment 10 suggest that embodiment may depend on fairly simple factors such as metric distance, whereas the results from Experiments 11a and 11b suggest that embodiment might be influenced by higher-level concepts such as ownership.

6.2 Future research

Whilst the studies in this thesis have provided some interesting insights into action embodiment and the functioning of the mirror system they have also raised a number of interesting questions, Experiments 11a and 11b in particular.

These experiments have demonstrated that action priming of reach trajectories can depend on more than just visual information. Although the actions seen in these experiments are identical, there are a number of differences between the two experiments, and it is not clear from these initial studies, which factor(s) contributed to the action being embodied. Further experiments are required to elucidate on what factor(s) contributed to the embodiment. For example, they should restrict the participants to sharing either the blocks or the workspace. This could be followed up by experiments, the designs of which, manipulate whether or not verbal information is given that specifically mentions that the objects or work surface will be shared.

Further studies could also investigate whether recent experience of reaching in a certain part of space can induce embodiment. If participants spend half of the experiment reaching (outside each other's personal space) and then swap places, would the experience of sitting in the other chair and reaching in that space produce priming. That is, in the second part of the experiment participants would be observing actions in the space they previously interacted with. Naturally of course this would have to be compared to a control experiment where participants change seat half way through but to another seat where the other participant had not been sitting.

A very small number of reaches in each of the experiments reported were removed due to collisions. The following reach of the observer and the person who knocked the block over were also removed. There is evidence that errors by others are encoded. Schuch and Tipper (2007) found that in a stop signal task participants were slower and more accurate after observing another person's error. Due to so few errors in these studies it was not possible to investigate if participants had been affected by viewing errors. It is hypothesised that reaches following observation of a collision are likely to be much higher. This scenario could quite easily be investigated using a confederate. There is however an alternative possibility, that a person is less likely to embody the unsuccessful actions of others. Failure may inhibit simulation. Our perception of someone may be enough to mitigate whether or not a person's actions are embodied, rather than direct experience of their success. For example are we more likely to embody the actions of an individual labelled as an expert, rather than someone labelled as a novice? Bach and Tipper (2006) have shown that viewing famous athletes does affect the motor system, specifically effectors that are associated with the sportsmen, feet with footballers and hands with tennis players.

The two-person experiments in this thesis all involved participants making reaches over obstacles, as well as viewing those reaches. An interesting question to consider is whether it is necessary for participants to experience reaching over obstacles in order to embody the actions of another reaching over an obstacle. It may be that participants will only encode the reach of another if it is a relevant action, that is, if they themselves are going to reach over an obstacle on some occasions. However viewing obstacles alone, as in Experiment 9, did not produce any priming. It was speculated in the earlier discussion in this chapter that whilst the kinematics of the obstacle avoidance leaves a trace in memory (which prime subsequent reaches) the obstacle itself may not have been encoded. It is therefore possible that the actual obstacle is irrelevant for action embodiment and that priming will occur even if the viewing participant does not reach over an obstacle. It may also be possible that viewing artificially high reaches, without any obstacle avoidance, will also produce action priming.

The results presented in this thesis have indicated that there are differences between the encoding of goal-orientated actions, such as grasping, and movement of the hand through space during reaching, with reaching being mitigated by peripersonal space. Being able to encode observed reaching in terms of reference to hand position likely plays an essential role. Encoding of other's grasps though, as mentioned earlier, can take place even when the action is presented on a 2-d monitor. The experiments in this thesis were designed to be as ecologically valid as possible, using real objects. The results from reach priming suggest that viewing obstacle avoidance actions presented on a 2-d screen may not lead to encoding due to the lack of 3-d spatial reference points. The author is not aware of any studies that have directly compared viewing real actions on real objects with those presented on a screen. This is a particularly important point since many studies investigating action and action embodiment, especially those involving fMRI scanning, routinely use images and videos presented to participants on screen, and this may dramatically affect the areas in the brain in which activation is seen.

The experiments in this thesis have only considered one particular behaviour, reaching to lift. Whilst the situations presented have necessarily been limited, in order to control various factors, the experiments do have ecological validity. One naturalist example would include being seated at a table to eat, reaching for various things on the table. In a typical eating scenario when required items are out of reach we do not typically stand up or lean across the table; those items are passed to us. We are unconcerned about negotiating around items out of reach. However, that encoding does not generally occur outside of peripersonal space in a seated arrangement does not rule out the possibility that in other scenarios we might encode the hand paths of others. For example, in a more dynamic situation, such as with sports like bowls, we might encode the hand trajectories of others even though they occur outside peripersonal space. Likewise only the movements of hands through space have been considered. Foot and leg movements, for example, may show different patterns of action priming, and movements of the feet or legs may be primed by the observation of actions outside peripersonal space. There is evidence that during walking, for example, a person will adjust their stride length to avoid an obstacle several steps before avoiding it (Moraes, Lewis, & Patla, 2004). It is therefore quite possible that viewing another person some distance away stepping over an obstacle might well be encoded and affect subsequent movements.

6.3 Summary

This thesis has presented strong evidence that the human mirror system is concerned with more than just goals, such as grasping objects. Under certain circumstances the specific means to achieve that goal, the reach kinematics, is also encoded. The encoding of reach trajectory seems quite separate and unaffected by the encoding of goals. Chapters 3 and 4 and Experiment 11a presented consistent evidence that reaches are encoded when obstacle avoidance takes place, but critically this is only the case within peripersonal space. No such limitation of observed action distance seems to apply to the encoding of goal-directed actions such as grasp. Although only speculation at this time, one reason for this difference may lie in the fact that the information from reaches is less constrained than goal-orientated grasps and that the utility of embodying reach kinematics is limited.

The final experimental chapter in this thesis explored the limits of action embodiment and how it can be manipulated. It appears that encoding can be influenced by very simple visual aspects of a given scene, and yet two scenes where identical information from reaches is seen, produced two completely different results, suggesting that embodiment is dependent on more than just visual information. Given that the mirror neuron system is believed to be involved in understanding the intentions of others and their state of mind it would be surprising if embodiment was unaffected by higher-level concepts. Chapter 5 has raised a number of interesting questions and motivates a number of future avenues of research.

Primate studies have been very informative and provided valuable research that has directed investigations in human motor research. The results presented in this thesis, however, highlight important differences between primates and ourselves. The ability to encode the means by which an action is achieved may partly account for our ability to imitate the actions of others, a skill which to date has not been found in our closest primate relatives (Rizzolatti, 2005).

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APPENDICES

Table 1a. *Mean Heights* ** (mm) for Trials Type Without an Obstacle*

Experiment	Condition	No-No-No	O-No-No	No-O-No	O-O-No
1	Single-person, reaching horizontally*	47.02	50.39	55.11	57.43
2	Single-person, reaching vertically	196.72	202.12	209.49	221.52
3	Single-person, two different targets	195.76	198.67	201.94	205.97
4	Seated opposite, shared target, same hands	193.81	195.54	194.82	197.21
5	Seated opposite, shared target, mirrored hands	217.23	218.49	214.07	216.45
6	Seated adjacent	188.51	195.37	193.07	198.95
7a	90° near, shared obstacle	186.21	194.85	192.65	196.42
7b	90° near, shared target	210.32	224.41	217.51	229.30
8	Seated opposite, shared obstacle	189.95	196.93	196.54	208.53
9	Single-person, control	202.39	210.23	202.94	209.27
10	Seated adjacent, transparent barrier	240.86	251.86	250.94	253.82
11a	90° far, nothing shared	200.40	206.58	201.21	205.73
11b	90° far, shared blocks & tablet	204.73	217.37	215.64	222.67

Note. The columns are labelled with the trial type (n-2, n-1, n), where “No” represents non-obstacle trials and “O” represents obstacle trials.
*Width

Table 1b. *Mean Heights* ** (mm) for Trials Type With an Obstacle*

Experiment	Condition	No-No-O	O-No-O	No-O-O	O-O-O
1	Single-person, reaching horizontally*	117.91	119.36	119.47	120.92
2	Single-person, reaching vertically	307.59	308.82	309.20	312.15
3	Single-person, two different targets	329.83	331.51	332.03	334.31
4	Seated opposite, shared target, same hands	318.11	325.79	322.59	323.65
5	Seated opposite, shared target, mirrored hands	325.51	326.60	323.37	325.93
6	Seated adjacent	317.38	317.22	316.66	319.82
7a	90° near, shared obstacle	312.74	318.56	313.73	317.03
7b	90° near, shared target	320.52	325.03	322.11	328.07
8	Seated opposite, shared obstacle	314.58	315.77	312.64	315.93
9	Single-person, control	309.76	306.28	304.51	305.17
10	Seated adjacent, transparent barrier	336.16	336.82	337.48	338.72
11a	90° far, nothing shared	304.81	307.31	305.65	306.18
11b	90° far, shared blocks & tablet	309.24	305.10	305.62	308.70

Note. The columns are labelled with the trial type (n-2, n-1, n), where “No” represents non-obstacle trials and “O” represents obstacle trials.
*Width

Each of the graphs in Figure 4.5 compares two trial types. For example, Panel A compares No-No-No trials with O-No-No trials, that is, trials where the preceding two trials were not obstacle trials with trials where only the participants previous (n-2) trial was an obstacle. Each participant carried out each of these trial types ten times.

During each trial the tracking system recorded X, Y, and Z coordinates at a sample rate of 200Hz. To produce these graphs a program written by the author extracted the data from each trial showing the heights at intervals of 4mm (from the start position to the goal object), giving 100 height data points for each trial. The average at each of these 100 data points was calculated for each group of ten trials for each participant. A final average combining the results from the twenty-four participants was calculated and these final 100 data points per trial type were then shown on the graphs in Figure 4.5.