What spatial reference frame is used for priming in visual search?

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Abstract

The perception-action model proposes that vision for perception and vision for action are subserved by two separate cortical systems, the ventral and dorsal streams respectively (Milner & Goodale, 1995, 2006). It is argued that the dorsal stream codes spatial information egocentrically, that is, relative to the observer, and that these representations are highly transient. The purpose of this thesis was to investigate whether short-term spatial memory can use egocentric information. This was achieved by using spatial priming in visual search. Spatial priming manifests itself in speeded detection times for a target when that target appears in the same location that it previously appeared in (Shore & Klein, 2001). Target locations can be defined in either egocentric (i.e. relative to the body or a specific part of the body) or allocentric (i.e. relative to other items in the display) frames of reference. However, it is unclear which of these are used in spatial priming.

It was found that both allocentric and egocentric cues were used, and that egocentric cues were the most effective for short-term priming (Study A). In exploring the nature of the egocentric frame of reference further, it was found that target location was not coded using an eye-centred frame of reference but rather it was coded relative to the observer's body (Study B). Moreover, when participants moved to a new location and the relationship with the target was maintained, priming effects were still observed (Study C). The availability of egocentric information was tested further, and the priming effects were still observed after a minimum delay of eight seconds between the first and second presentations of a target location (Study D). Finally, it was found that the application of transcranial magnetic stimulation to the posterior parietal cortex did not modulate either allocentric or egocentric spatial priming effects (Study E).

While the perception-action model predicts that egocentric information is short lived, the findings from the experiments presented in this thesis suggest that egocentric information can persist for several seconds.

Chapter 1 - Introduction

A division in the visual system

On a daily basis humans process an infinite number of objects. In doing so they display the ability to recognise and identify objects, even novel objects, under multiple viewing conditions, including various orientations, distances, and illuminations (Bruce, Green, & Georgeson, 1996; Wallis & Bulthoff, 1999). Furthermore, they are able to interact with, and manipulate these objects; for example, having identified that the object located on the table, to the right of the stapler, is a pen, the individual is then able to reach forward the appropriate distance, scale their grip accurately, and pick up the pen. These abilities not only demonstrate the existence of dual functions within the visual system, namely, identification and localisation, but also the capability of using allocentric and egocentric spatial codes. Both of these distinctions are central to this thesis, and are discussed in turn.

Schneider (1969) was the first to formally suggest the existence of two visual systems, proposing that one visual system was dedicated to processing object identity, and the second visual system was dedicated to processing the location of the object. This distinction between processing object identity and location led to the introduction of studying “what” and “where” visual processes. Ungerleider and Mishkin (1982) further developed this initial distinction neuroanatomically in their two cortical visual systems model. Here they proposed the existence of two anatomically separate visual processing pathways in the human brain: a ventral stream and a dorsal stream. Figure 1 shows these two pathways. Ungerleider and Mishkin (1982) argued that the ventral stream, which encompasses visual areas V1 to V4 and extends to the posterior and anterior infero-temporal areas, is concerned with object identification, whereas, the dorsal stream, which is mediated by the posterior parietal cortex, processes the spatial information of objects, that is, their location in space (see also Carlson, 2001; Decety, 1999).

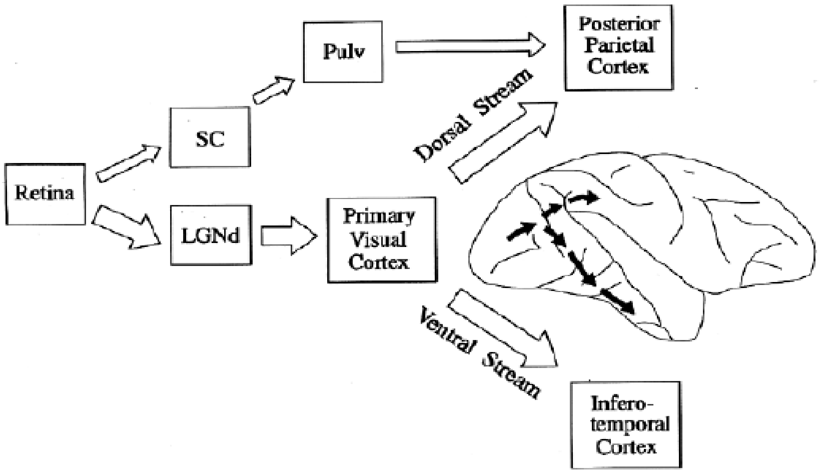

Figure 1. The anatomical location of the ventral and dorsal streams, taken from Milner and Goodale (2006). LGNd, lateral geniculate nucleus, SC, superior colliculus, Pulv, pulvinar nucleus.

Much of the evidence that Ungerleider and Mishkin (1982) based their two visual systems model on was provided by behavioural and physiological observations in primates (Kastner & Ungerleider, 2000). Specifically, it was found using single cell recordings, that cells in ventral and dorsal areas (the infero-temporal and posterior parietal areas respectively) have different response properties to visually presented stimuli: V4 neurons (ventral stream) were found to selectively respond to visual properties such as colour and shape, whilst middle temporal neurons (dorsal stream) responded to those features of an object that were involved in visuo-spatial processing, such as object motion and the direction of the motion (Desimone & Ungerleider, 1989; Goldberg & Colby, 1989).

Furthermore, non-human primate lesion studies have provided considerable strength to the notion of two separate visual pathways, with a double dissociation between lesion site and impaired function being revealed. Lesions to infero-temporal areas have been found to result in deficits in object discrimination; for example, in the form of reduced pattern recognition abilities, while performance on visuo-spatial tasks remains unaffected. Conversely, whilst those primates with posterior parietal lesions displayed impairments in completing visuo-spatial tasks, their performance on an object discrimination task was not affected (Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Haxby, 1994). These observations thus support the proposed distinction for different visual processing in the dorsal and ventral streams by Ungerleider and Mishkin (1982).

With the advent of cognitive neuroscientific methodologies, greater understanding of the organisation of the ventral and dorsal streams has been achieved. These methodologies are crucial in moving understanding of visual processing away from animal models into research involving human participants. Using *positron emission tomography* (PET) Haxby et al. (1994) compared regional cerebral blood flow (rCBF) in tasks which tapped into either stimulus identification or stimulus location processes. Haxby et al. (1994) observed that rCBF was greatest in occipito-temporal regions, namely, ventral stream areas, when participants completed the identification task compared to when they completed the location matching task, when activation was instead greatest in the occipito-parietal cortex (Haxby, et al., 1994; Ungerleider & Haxby, 1994). Similar dissociations have been observed using *functional magnetic resonance imaging* (fMRI); for example, Culham et al. (2003) found that the anterior intra-parietal region (AIP), in the dorsal stream, which has been implicated in grasping movements (Binkofski et al., 1998), was activated when participants had to grasp objects but not when participants passively viewed images of objects. Conversely, the lateral occipital complex, located in the ventral stream, which is believed to be central in object recognition processing (Grill-Spector & Malach, 2004; Kourtzi & Kanwisher, 2001), was less activated in the grasping condition relative to the object recognition condition (Culham, et al., 2003). Taken together, the findings from PET and fMRI research show that the brain areas involved in perceptual and visuomotor tasks map onto ventral and dorsal stream areas respectively, and thus support Mishkin and Ungerleider’s (1982) proposal of anatomically and functionally separate streams in the brain for object and spatial visual processing. Furthermore, the replication of dissociable patterns of activation using fMRI is highly advantageous in supporting the notion of separable processing streams, owning to its greater spatial resolution than that of PET (Carlson, 2001).

What, where, and how: The perception-action model

Although the two cortical visual systems model (Ungerleider & Mishkin, 1982) has been widely accepted, the properties of the pathways have been questioned. Specifically, Goodale and Milner (1992) argue that object information and spatial information is used by both visual streams, and therefore reasoned that the two systems should not be distinguished by the visual attributes that they process, namely identity and location. Instead Milner and Goodale (1993) proposed that it is the way in which the two systems use the object and spatial information, that is, for what function, that differentiates them, and not whether they process object and location information separately: “the fundamental differences in the required transformation of incoming visual information … has driven the evolution of separate streams of processing in the primate visual cortex” (Milner & Goodale, 2006, p.42). Consequently, the ventral stream was proposed as being responsible for perceptual functions and the dorsal stream with guiding motor actions, and thus Milner and Goodale proposed that “what” versus “how” was a more accurate description than “what” and “where” of the two visual pathway dissociation[1]. This is known as the perception-action model, and it has become the accepted model of visual processing (Goodale & Milner, 1992, 2004; Milner & Goodale, 1993, 1998, 2006).

Visual agnosia versus optic ataxia: Clinical presentation

The development of the perception-action model was influenced greatly by the study of patients with either ventral stream or dorsal stream damage, which initially began through independent research studies and where patients were typically studied in isolation. Damage to the ventral stream results in a disorder known as *visual agnosia*, which is characterised by a disturbance of visual perceptual functioning while motor abilities remain intact (Goodale & Milner, 2004). A frequently used paradigm to investigate perceptual and motor abilities is a slot posting task, whereby subjects have to either report the orientation of the slot (perceptual task) or post a card through the slot (visuomotor task). In testing visual agnosia patient D.F. on these tasks a clear dissociation in her abilities was revealed. When asked to use the orientation of the slot to complete a motor action, either to post her hand or a card through the slot, she showed no impairments; however, when asked to report the orientation of the slot her performance was significantly

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[1] Anecdotally, Blakeslee and Ramachandran (2005) comment that with regards to localising brain functions “… the question of “where” becomes less important than the question of “how” ” (p.11).

impaired. Thus, D.F. displayed impairments in her perceptual abilities of the slot but not in her actions towards the same slot (Goodale, Jakobson, & Keillor, 1994; Goodale & Milner, 2004; Milner, et al., 1991). See also Carey, Harvey, and Milner (1996), Goodale, Milner, Jakobson, and Carey (1991), and Humphrey, Goodale, Jakobson, and Servos (1994) for evaluation of D.F.'s performance on tasks other than slot posting.

The clinical presentation of damage to dorsal stream areas, usually unilateral damage to posterior parietal areas, is a disorder termed *optic ataxia*. Perenin and Vighetto (1988) state that optic ataxia represents a "disorder of coordination and accuracy of visually elicited hand movements not related to motor, somatosensory, visual acuity or visual field deficits" (p. 643). Optic ataxia patients demonstrate impairments in executing motor actions correctly; for example, they fail in pointing accurately to targets, scaling their grip appropriately to pick up an item, and orienting their hand correctly to post it through a slot (Jakobson, Archibald, Carey, & Goodale, 1991). Owing to the often unilateral nature of the damage, impairments are commonly observed when patients reach for or point to items placed in the contralateral hemifield to the side of their damage; therefore, it cannot be argued that optic ataxia reflects a generalised motor disorder (Milner & Goodale, 2006). Conversely, the shape discrimination abilities, and thus the perceptual functioning, of these patients are intact: they can report the orientation of the slot, as well as map the size of objects using their index finger and thumb (Ellis & Young, 1996; Perenin & Vighetto, 1988).

While the seminal papers of optic ataxia (Jakobson, et al., 1991) and visual agnosia (Milner et al., 1991) were conducted independently with differing tasks, the two types of patient have been evaluated within the same study. For example, Goodale, Meenan, et al. (1994) employed a perceptual task which required patients to compare asymmetric shapes with one another, and a visuomotor task which involved patients picking up these shapes between their index fingers and thumbs. As expected, although D.F. failed in judging whether the shapes were the same or not, she was able to successfully pick up the shapes. Conversely, while R.V., an optic ataxic patient, was able to discriminate between shapes, she was not able to pick them up (Goodale et al., 1994). Therefore, optic ataxia and visual agnosia patients display the reverse pattern of impairments to each other[2]. It is argued by the perception-action model that object agnosia and optic ataxia reflect a double dissociation in terms of the functions they affect: perception is impaired in object agnosia, and action in optic ataxia (Milner & Goodale, 1995, 2006).

The effect of temporal delays in task completion in healthy subjects

Another difference between the visuomotor and perceptual streams of the perception-action model is their temporal characteristics. By introducing a delay, or a number of different delays, into a task it is possible to evaluate how long motor and perceptual information can persist for. It has been found that movements that are made after a delay are typically less accurate than their non-delay counterparts. For example, Elliott and Madalena (1987) found a significant reduction in participants' pointing accuracy when a two second delay was introduced between the offset of a stimulus and when participants were instructed to make their movement, compared to when there was no delay. Additionally, Bradshaw and Watt (2002) found that

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[2] This is the same pattern reported in the monkey lesion literature (for example, Mishkin, et al., 1983).

both of the components[3] of a pointing movement were affected by the introduction of a delay. The transport component, in this case the wrist velocity, reduced as the length of the delay increased, while the grasp component of the same movement, evaluated by measuring grip aperture, increased as a function of delay. Likewise, in a series of experiments Hesse and Franz (2009) found that the *maximum grip aperture* (MGA)[4] when grasping disks after a delay was similar to the MGA for larger objects when the grasping was completed in full vision. This suggests that with a delay participants increase their safety margin for grasping by increasing the distance between their thumb and index finger.

Westwood, Heath, and Roy (2001) sought to evaluate how long movement representations can persist for and, using delays ranging from 500 ms to 2000 ms, found that even after the shortest delay, the degree of error was greater compared to when the reaching movement was completed in real time. These findings thus extend those of Elliott and Madalena (1987) who were only able to conclude that the movement representations decayed to some extent after less than two seconds. Westwood, Heath, and Roy (2003) went on to find that pointing errors were greater in a condition where the target was occluded at the same time as the pointing movement was cued compared to when the target was occluded at the point at which the participant initiated their movement. Taken together these findings suggest that visuomotor representations have a very limited duration.

Conversely, perceptual representations are believed to have an unlimited duration. In addition to evaluating the grasp and transport components of pointing

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[3] The two components of a pointing movement are the transport component, which is the moving of the hand to the location of the object, and the grasp component, which deals with how the object is picked up and grip parameters (Bradshaw & Watt, 2002).

[4] The MGA refers to when grasping an object the finger grip opens wider than the actual size of the object, and that this over widening is proportional to the size of the object (Jeannerod, 2006).

after a delay, Bradshaw and Watt (2002) compared performance on a perceptual task, whereby participants were required to match the locations of targets, over delay periods of up to four seconds. They found that perceptual performance was not affected by the introduction of a delay. Relative to real-world settings, it is frequently observed that individuals are able to recognise objects that they have been exposed moments before just as well as objects that they first encountered many years previously. Furthermore, this ability is not restricted to the distance and angle of viewing that the object was first perceived (Bruce, et al., 1996; Wallis & Bulthoff, 1999).

In the laboratory, it has been found that experience with a particular stimulus can influence encounters with that same stimulus at a later point in time. More specifically, it has been demonstrated that repetition of a specific feature can facilitate processing of that same feature in a future encounter. This phenomena has been termed between-trial priming (Shore & Klein, 2001; Tulving & Schacter, 1990). It is believed that between-trial priming results from the representation of the first trial being stored in memory, with that representation being retrieved when that same trial is presented at a later point in time, and that this leads to more efficient processing of that stimulus (Huang, Holcombe, & Pashler, 2004). Furthermore, Körner and Gilchrist (2007) found that when participants had to re-search an array for a second target, they were faster at locating this second target than they were at locating the first target. Körner and Gilchrist (2007) argue that the prior exposure to the search array facilitated the detection of the second target as some representation of the search array and the items that it contained had been held in short term memory. These effects were still observed when a delay of 800 ms was introduced between the initial presentation and the second presentation of the search array (Körner, Höfler, & Gilchrist, 2008).

In summary, while research has shown that visuomotor performance degrades with the introduction of a delay, thus suggesting limited availability of the representations used for motor tasks, the existence of priming effects indicates that perceptual representations can be stored, and that they have a longer influence on subsequent tasks than visuomotor representations. Therefore, it can be argued that the temporal characteristics of the representations used for visuomotor and perceptual tasks, and thus the representations used by the dorsal and ventral streams respectively, are fundamentally different. Further evidence of this temporal dissociation between visuomotor and perceptual representations from the study of patients will now be considered.

The effect of temporal delays on visuomotor performance: Agnosia versus ataxia

Research using patients with damage to either their ventral stream or dorsal stream has been particularly informative about these two processing streams and their temporal characteristics, particularly as the performance of these patients is differentially affected by the introduction of a time delay into the task. While optic ataxia patients typically show poorer visuomotor abilities than healthy subjects on tasks such as reaching for and grasping a block located in front of them or posting a card through a slot (for example, Jakobson, et al., 1991; Perenin & Vighetto, 1988), it has been found that their visuomotor deficits are reduced with the onset of a temporal delay, that is, their performance gets better. For example, Goodale, Jakobson, et al. (1994) observed that the accuracy of patient A.T.'s pointing increased when there was a delay between the offset of the light and her pointing response. Furthermore, Milner et al. (2001) observed that another optic ataxia patient (I.G.) showed the same pattern for immediate grasping and delayed grasping: whilst I.G. could not scale her grip accurately in the immediate condition, she was able to in the delayed version of the same task. In a second experiment, during half of the delayed grasping trials the block to be grasped was covertly replaced by the experimenter with one of a different width during the delay period. Whilst Milner et al. (2001) found that control subjects adjusted their grasp aperture according to the width of the block to be picked up after the delay, regardless of whether they saw one of a different width in the initial presentation, patient I.G. did not. Her grip was wide if she had seen the wide block in the initial presentation but was actually asked to pick up a smaller one after the delay. To account for this, Milner et al. (2001) suggest that I.G. was relying on stored visual information to scale her grip aperture. Converging findings of this observation are also reported by Milner, Dijkerman, McIntosh, Rossetti, and Pisella (2003) and Himmelbach and Karnath (2005). This improvement in patient performance is surprising as it has been well reported that the visuomotor performance of healthy individuals worsens when a delay is introduced (Bradshaw & Watt, 2002; Elliott & Madalena, 1987; Westwood, et al., 2001).

To explain the improvement in the visuomotor performance of patients with optic ataxia, it has been argued that when there is a delay these patients have to rely on the intact visual-perceptual abilities of their ventral streams to remember the location of the light or the size of the block, and not their impaired visuomotor system of dorsal streams, as is required when the task is completed in real time (Goodale, et al., 1994; Milner, et al., 2001). Therefore, it is suggested that when a delay is introduced into a visuomotor task, there is a shift from using dorsal stream representations to using ventral stream representations.

Unlike the improvements of delayed reaching and grasping that have been reported in optic ataxia patients, when a delay was introduced between presenting an object and reaching for it unseen, the visuomotor ability of visual agnosia patient D.F. deteriorated (Goodale et al., 1994). Furthermore, after delays as short as two seconds, D.F. no longer showed the anticipatory shaping of her hand that she showed when she was required to complete a real-time grasping movement. Goodale, Jakobson, et al. (1994) also found that D.F. was impaired at making pantomime reaching movements[5] next to the real object. It is believed that introducing a delay, or making the task a pantomime movement, meant that perceptual representations of the object have to be used instead of the visuomotor representations that are used when the movement is completed without a delay (Goodale et al., 1994). Thus, it is believed that this transforms a task from one requiring dorsal processing to one requiring ventral processing, and in D.F.'s case, her ventral stream damage would explain why she is severely disabled at pointing to targets after a delay. When there is no delay, the motor abilities of D.F. are the same as those of healthy individuals, supporting the contribution of the dorsal stream here, which is undamaged in D.F. (Goodale & Milner, 2004; Goodale, et al., 1991; Milner & Goodale, 2006).

In summary, patient research has demonstrated that the introduction of a temporal delay into a task has differential effects. Delay leads to an improvement in the visuomotor performance of optic ataxia patients and a reduction in the performance of visual agnosia patients. In light of this dissociation it is thought that

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[5] Pantomime reaching refers to picking up an object that is either no longer present or making the movement in space adjacent to where the object is located (Goodale, et al., 1994).

introducing a delay into a motor task transforms it from requiring dorsal stream processing to one that requires ventral stream processing (Milner & Goodale, 2006).

A discrepancy in patient D.F.'s abilities?

As had been discussed earlier, key supporting evidence for Milner and Goodale's (1993) perception-action model has been their observations of the visual agnosia patient, D.F., who suffered bilateral damage to her ventral stream. Milner and colleagues observed that, although D.F. showed the inability to complete visual-perceptual tasks; for example, she failed in copying objects, shape perception, and object identification tasks, she demonstrated the capability to use visual information to carry out motor actions (Goodale & Milner, 2004; Goodale et al., 1991; Milner et al., 1991). It has been widely accepted that the observations of D.F. illustrated an perception-action dissociation, and indeed they formed the cornerstone of Milner and Goodale's (1993) dual stream processing model.

However, this account of D.F.'s performance, that is, intact visual motor abilities and impaired visual perception, has recently been challenged by Schenk (2006) on re-evaluation of patient D. F. Like Milner and colleagues, Schenk (2006) compared the perceptual and visuomotor abilities of D.F. with those of ten healthy age matched controls, but unlike the previous research, he approached this assessment considering D.F.'s impairments within a framework of allocentric and egocentric coding for each task. Allocentric coding refers to making judgements about an object with regards to how it relates to other objects in a visual scene, whereas in egocentric coding the judgements of an object's location are made relative to the observer's body, or a specific part of their body (Burgess, 2006). The perceptual task that Schenk (2006) used involved judging which of two circles, placed either side of a pre-defined reference point, was nearest to this reference point. In the allocentric version of this perceptual task, the reference point was a cross and in the egocentric version it was the index finger of the subject's dominant hand. The motor task was a pointing task. In the allocentric motor task subjects were required to move their finger from a specified starting point so that it matched the relative location of a dot from a cross; and in the egocentric version of the motor task, subjects had to move their finger from the start position to the position of a dot (Schenk, 2006). All tasks were performed with free vision and central fixation, and subjects were not able to see their hands during trials. Figure 2 shows examples of the four experimental conditions.

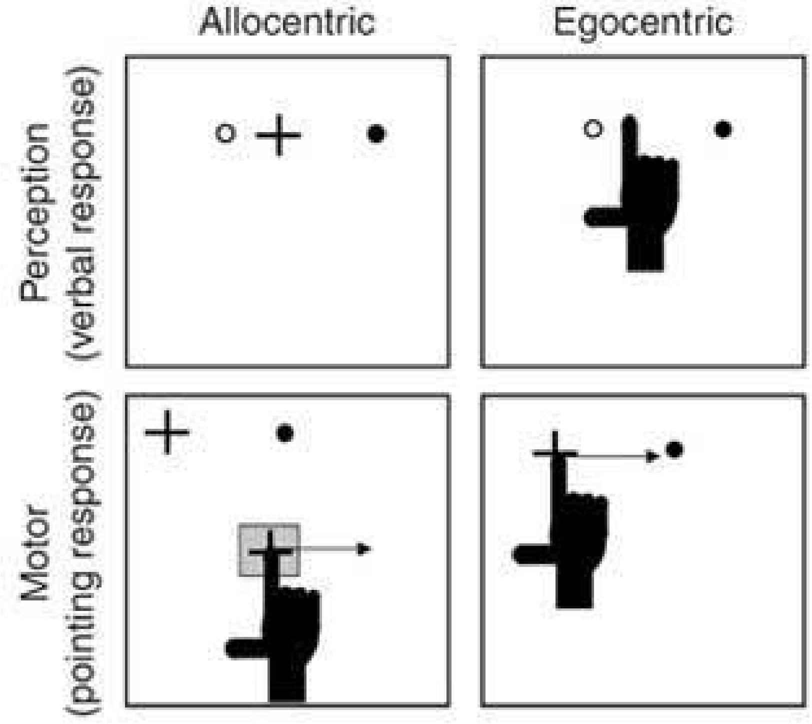

Figure 2. The four tasks used by Schenk (2006) to evaluate allocentric and egocentric coding in perceptual and visuomotor tasks.

Milner and Goodale's (1995, 2006) perception-action model predicts that while D.F. should not exhibit any problems with completing the two motor tasks, she would be impaired in the perceptual tasks. However, instead of observing global perceptual difficulties, Schenk (2006) found that, independent of whether the task was perceptual or motor, D.F.'s performance on the two allocentric tasks was impaired relative to that of the healthy controls. Schenk (2006) also found that D.F. was able to complete both the egocentric motor task and the egocentric perceptual task. Clearly, these observations are not in line with what would be predicted by the perception-action model (Milner & Goodale, 1993, 2006).

In finding impaired allocentric coding and preserved egocentric coding in patient D.F., Schenk (2006) concluded that the dissociation of D.F.'s abilities may better reflect a visual spatial coding dissociation, that is, the ventral stream, damaged in D.F., represents allocentric information and not perceptual information. This proposal by Schenk (2006) has raised numerous challenges to the perception-action model and the nature of the dissociation between the ventral and dorsal streams.

The findings of Schenk (2006) are supported by other research. For example, Dijkerman, Milner, and Carey (1998) evaluated the ability of D.F. to pick up disks when she had to insert either two or three digits into holes in the disks. Dijkerman et al. (1998) found that D.F. was unable to scale the opening between her thumb and forefinger(s), and thus was unable to pick up the disks. This task is thought to require allocentric spatial information as it was necessary to ascertain the location of the holes relative to the location of the other holes on the disk in order to know how to orient the hand and scale the grip distance accordingly. Therefore, Dijkerman et al. (1998) concluded that D.F. was not able to use allocentric information.

Furthermore, Murphy, Carey, and Goodale (1998) compared D.F.'s ability at pointing to a series of targets with her ability at copying the arrangement of a number of targets. It was argued that the pointing task relied on egocentric coding, while the copying task relied on allocentric coding. It was found that while D.F.'s performance on the pointing task was not different from that of healthy controls, thus she displayed intact egocentric processing, she performed poorly in the copying task, and thus her allocentric processing was impaired (Murphy, et al., 1998). However, the findings of Murphy et al. (1998) are not able to provide further evidence for the allocentric/egocentric dissociation in D.F. that Schenk (2006) reported as the two tasks are not equivalent. The task evaluating egocentric performance was a visuomotor task, while the task evaluating allocentric performance was perceptual task; therefore, it is not surprising that D.F. performed normally in the former and was impaired on the latter.

More recently, Carey, Dijkerman, Murphy, Goodale, and Milner (2006) followed the experiment of Murphy et al. (1998) up by comparing D.F.'s performance on allocentric and egocentric coding within the same task. They evaluated her performance on three tasks: a sequential pointing task (egocentric), a pantomime sequential pointing task, whereby D.F. was required to point to the locations of targets on a blank piece of paper that matched the locations of real targets in an adjacent work space (allocentric), and a copying task (allocentric). Carey et al. (2006) found that D.F. was impaired on the copying task and the pantomime pointing task, both of which required allocentric coding. Of interest is the direct comparison between her performances on the pointing tasks: she was impaired at the allocentric version of the task but not the egocentric version of the same task. These findings are thus in line with the motor task findings of Schenk

(2006). More recently, Carey, Dijkerman, and Milner (2009) found that D.F. was impaired on a bimanual pointing task when allocentric information was required.

Thus, there is evidence that suggests that visual agnosia patient D.F. displays a deficit with allocentric processing for both perceptual and visuomotor tasks, and not the selective perceptual deficits predicted by the perception-action model (Milner & Goodale, 1993, 2006). Allocentric and egocentric frames of reference will now be discussed in detail, with particular focus on any mappings between the ventral and dorsal streams and perception and action.

Frames of reference

The locations of objects in a visual environment can be defined using different frames of reference. Mou, Xiao, and McNamara (2008) state that two components are used to define an object's location: a reference direction (e.g. in front of, to the East of) and a reference object (e.g. the viewer, the post box). If the reference object is the viewer, it is an egocentric frame of reference, and if the reference object is a landmark, it is an allocentric frame of reference (Rains, 2002; Witt, Ashe, & Willingham, 2008)[6].

Egocentric frames of reference, which are also termed observer based metrics, define spatial positions using the body, or a specific part of the body, for instance, the trunk, or the head, as a constant point of reference. For example, the cup is on my left. Therefore, they represent subject-to-object relationships (Zaehle et al., 2007). Egocentric representations are highly precise, and as such their use is believed to be of great importance and evolutional significance. Having accurate

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[6] There is argued to be an additional frame of reference. Body space, which refers to stimuli in contact with the body and how the body parts are positioned in relation to one another (Rains, 2002). This frame of reference will not be further discussed in this thesis.

spatial representations of food items and predators is essential for an animal’s survival; for example, knowing how the location of a predator corresponds with your own location enables appropriate fleeing or hiding behaviour (Galati et al., 2000; Nadel & Hardt, 2004).

Conversely, allocentric frames of reference define spatial relations between objects. Allocentric frames of reference, also known as geocentric frames of reference or object-based metrics, rely on the external environment to define space, that is, by using landmarks; for example, the pen is to the right of the stapler. Therefore, they represent object-to-object relationships (Burgess, 2006; Zaehle, et al., 2007). Allocentric strategies are not restricted to using a single cue, but can define space on account of how multiple environmental cues relate to each other; for example, the pen is between the stapler and the ruler (Kolb & Whishaw, 2003; Nardini, Burgess, Breckenridge, & Atkinson, 2006). Tolman (1948) proposed that animals create maps of their environments which are based on allocentric representations, maps which he termed cognitive maps (Nadel & Hardt, 2004). Furthermore, O’Keefe and Nadel (1978) argued that using cognitive maps was central to spatial navigation tasks. For instance, in a Morris water maze task rodents are able to locate a submerged, and thus invisible, escape platform regardless of their point of entry into the maze. According to cognitive mapping theory, in order to locate the submerged platform the rodents create a map of the room based on the cues of the room, and the existence of this map can explain their ability to locate the submerged platform from variable starting positions (Blokland, Rutten, & Prickaerts, 2006; D'Hooge & De Deyn, 2001; Moghaddam & Bures, 1996).

Whilst distinctions can be made between allocentric and egocentric frames of reference, the two do interact: “the brain represents spatial information in multiple reference frames, with the reference frame dominating performance being dependent on task demands" (Keulen, Adam, Fischer, Kuipers, & Jolles, 2002, p. 525). Burgess (2006) argues that allocentric and egocentric frames of reference work in parallel and that integrating the two sources of information leads to greater navigational abilities; for example, after extensive self motion allocentric representations will be used in reconfiguring egocentric representations. Allocentric frames of reference are less accurate than their egocentric counterparts as they rely on relative coordinates, whereas egocentric frames of reference use absolute coordinates (Eysenck & Keane, 2000; Kolb & Whishaw, 2003); therefore, being able to use both frames of reference can facilitate behaviour. For instance, allocentric coordinates will enable an individual to get close enough a target object from where more precise egocentric frames of reference can take over to locate that object (Burgess, 2006). It is also believed that egocentric coordinates can be used when allocentric ones are not highly dependable: Mou, McNamara, Rump, and Xiao (2006) made participants stand amongst the selection of objects that they were required to learn the layout of, thus making it difficult for participants to get a clear map of how the objects were spatially arranged relative to one another; therefore, participants had to rely on egocentric representations.

Furthermore, it has also been reported that individuals can switch between frames of reference. Waller and Hodgson (2006) observed that whilst absolute pointing direction in healthy participants became more erroneous with disorientation, estimating the relative direction between objects became more accurate. They suggested that this was the result of switching between egocentric representations which are more transient and susceptible to motion, to allocentric based representations which are more enduring (Waller & Hodgson, 2006).

In summary, this thesis is interested in allocentric and egocentric frames of reference. Allocentric reference points can take many forms and be on a number of scales; for example, when giving directions, allocentric frames of reference are particularly relevant, and the more familiar the landmarks, the greater the success: the post office is next door to the police station and opposite the church. On a smaller scale, and more relevant to this thesis, when searching for a target on a computer screen, associations between the designated target and some other item in the search array can develop and subsequently enhance performance (Chun, 2000; Chun & Jiang, 1998). Egocentric frames of reference can again operate on different scales: the post office is 100 metres in front of me, compared to, the pen that I want to pick up in on my left. As with allocentric representations, learning an association between the target object and the body can lead to more fluent processing of where something is (Iachini, Ruotolo, & Ruggiero, 2009; Roskos-Ewoldsen, McNamara, Shelton, & Carr, 1998).

Frames of reference in action and perception

As discussed earlier in understanding the functions of the ventral and dorsal streams of visual processing, Milner and Goodale (1995, 2006) argue for dissociable visual streams, one for perception and one for action. In contrast to this, Schenk (2006) argues that a dissociation between allocentric and egocentric frames of reference is more accurate. Assuming that Schenk (2006) is correct in his proposal, it is important to establish whether these two frames of reference map onto the functions of the ventral and dorsal streams.

Wang and Spelke (2000) comment that, “objects tend to be the goals of our action, and so egocentric representations of their positions may facilitate the guidance of action" (p.247). According to Goodale and Milner's (1992) model, the output of the dorsal stream is a motor action; therefore, the individual will be directly interacting with a target object. This suggests that the frame of reference required is egocentric. To execute the appropriate and correctly scaled motor action the individual needs to know where the object is in relation to them self and the effectors that will carry out the action, and an egocentric frame of reference permits this accuracy (Milner & Goodale, 1995, 2006). Further support for the notion that the visuomotor stream utilises an egocentric frame of reference has been provided by studies probing the neural correlates of egocentric processing; for example, by Zaehle et al. (2007) using functional magnetic resonance imaging, and Gramann, Müller, Schönebeck, and Debus (2006) using electroencephalography. Specifically, Zaehle et al. (2007) reported that the fronto-parietal areas were selectively activated when egocentric judgements (e.g. is the yellow square to your right?) were made but not when allocentric ones were (e.g. is the blue triangle above the red circle?). Committeri et al. (2004), also using fMRI, concluded that regions in the posterior parietal cortex are responsible for mediating egocentric based judgements, and these areas correlate with the location of the dorsal stream.

Moreover, and as has been discussed previously, the symptoms of patients with damage to dorsal stream areas of their brains manifest as degraded visuomotor coordination abilities, known as optic ataxia (Jakobson, et al., 1991). Optic ataxia patients display impairments in reaching towards targets, in terms of reaching in the correct direction, turning their hand to the right angle, and changing the position of their fingers to reflect the shape of the target object (Ellis & Young, 1996). Therefore, the visuomotor deficits of these patients suggest impairments in their ability to utilise egocentric frames of reference. Taken together, the patient and neuroimaging findings support the notion that visuomotor performance relies on egocentric representations and that dorsal stream areas are responsible for egocentric processing.

When processing the identity or a certain property of an object, an egocentric frame of reference would be unnecessary because it is the content of that object which is important rather than the information about its exact location relative to the viewer. Object identification and perception involves retrieving stored representations of objects and their features; for example, their size, shape, and colour (Troje & Giurfa, 2001). Judgements of object attributes are made in relation to other objects in the visual scene; therefore, it is argued that vision for perception uses an allocentric frame of reference (Milner & Goodale, 1995, 2006). Whilst object processing relies on drawing upon stored object representations, it also contributes to the amassing of object information. For example, consider learning the layout of tables and chairs in a new college canteen. This not only involves constructing a new scene-based representation of that canteen environment, but it also reinforces existing object representations: chairs are traditionally placed next to tables (Eysenck & Keane, 2000; Mou, et al., 2006). Furthermore, as objects can generally be perceived and identified regardless of their orientation, vision for perception is not concerned with the angle of presentation (Eysenck & Keane, 2000). However, the representations of motor actions are viewpoint dependent: when reaching for a cup, the direction of approach is factored in so the individual grasps the side on which the handle is (Bruce, et al., 1996; Goodale & Haffenden, 1998).

Converse to the dorsal stream involvement in egocentric representations, ventral stream areas, namely the ventro-lateral occipito-temporal areas, have been found to be selectively activated for tasks with an allocentric component (Zaehle, et al., 2007). Interestingly, a further difference between the activation during egocentric and allocentric processing is the presence of hippocampal activation when allocentric judgements are being made, and notably its absence in egocentric processing (Bohbot, Iaria, & Petrides, 2004; Galati, et al., 2000; Neggers, Van der Lubbe, Ramsey, & Postma, 2006; Parslow et al., 2004). It has also been found that the areas activated when making egocentric judgements, namely the posterior parietal areas, are not activated when allocentric judgements are made (Connolly, Andersen, & Goodale, 2003; Neggers, et al., 2006). In summary of the neural underpinnings of allocentric and egocentric representations, Committeri et al. (2004) comment that, “viewer-centred (egocentric) coding is restricted to the dorsal stream and connected frontal regions, whereas a coding centred on external references requires both dorsal and ventral regions” (p.1517).

Frames of reference and visual illusions

The influence of visual illusions on perceptual and visuomotor performance has also contributed further to our understanding of the frames of reference that the two processes rely on. The Titchener circle illusion, also known as the Ebbinghaus illusion, whereby the perceived size of a circle is influenced by the size of the circles that surround it[7], has been frequently been used to investigate the representations used by the dorsal and ventral streams (for example, Aglioti, DeSouza, & Goodale, 1995; Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Haffenden & Goodale, 1998; Hu & Goodale, 2000). For example, Aglioti et al. (1995) observed that in order for participants to perceive the central circles of two Titchener displays as the same size

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[7] Circles surrounded by bigger circles appear smaller than their true size, and circles surrounded by smaller circles appear larger than they actually are (Milner & Goodale, 2006).

there needed to be a physical difference of at least 2 mm between them, thereby suggesting that perceptual judgements are susceptible to this visual illusion. Conversely, when participants were required to pick up the central disk, the scaling of their grip was not affected by the perceived size of the disk. Haffenden and Goodale (1998) found that when participants were required to estimate the size of the central disk they were influenced by the illusion, whereas when they were required to reach for it, their grip aperture matched the physical size of the central disk. Likewise, using the horizontal-vertical illusion, where a vertical line is placed centrally along a horizontal line, Vishton, Rea, Cutting, and Nunez (1999) found that while perceptual judgements were affected by the illusion, in that observers reported that the vertical line was longer than the horizontal line when in actual fact they were the same length; the grip scaling of same participants was not affected by the illusion. Taken together, these findings suggest that action and perception are differentially affected by visual illusions, and it is argued that this can be explained by the different representations used by the two functions.

Interestingly, Vishton et al. (1999) modified the presentation of the horizontal-vertical illusion so that participants were first required to make a perceptual size judgement when only one of the two lines was present, and then subsequently estimate the length of one of the lines when they appeared together. In this version of the task, there was no difference between the effect of the illusion on perceptual report and grip scaling. Vishton et al. (1999) argued that the perceptual effects of visual illusions are the result of comparisons being made between items in the display; for example, in the line illusion, the length of one line is compared with the length of a second line, and in the Titchener illusion the size of the inner circle is judged relative to the size of the circles that surround it. Therefore, it is again argued that perceptual tasks rely on relative judgements. Conversely, in reaching and grip scaling tasks the size of other items is irrelevant and “grip aperture is calibrated to the true size of an object” (Haffenden & Goodale, 1998, p. 122); therefore, it is argued to rely on the absolute metrics of the object. These findings indicate again that the ventral stream uses relative metrics and the dorsal stream uses absolute metrics (Haffenden & Goodale, 1998; Hu & Goodale, 2000; Milner & Goodale, 2006).

In summary, the evidence presented here suggests that owing to the different nature of the outputs of the dorsal and ventral streams, they rely on different frames of reference. The dorsal stream, which is concerned with motor control and action, relies on egocentric frames of reference, whilst the ventral stream, responsible for perception, utilises an allocentric frame of reference (Milner & Goodale, 1995, 2006). Furthermore, and of key interest, is the apparent mapping of egocentric and allocentric representations onto the dorsal and ventral streams respectively. Additionally, the research into the effects of visual illusions on perception and action suggests that perceptual tasks rely on relative metrics, thus allocentric frames of reference, whist visuomotor tasks use the absolute metrics of an item and are said to work in egocentric frames of reference.

Allocentric and egocentric representations: Temporal characteristics

Owing to the differential effects of temporal delays on action and perception, in both healthy subjects and patients, it is believed that the information utilised by the two streams operates within different temporal parameters. Milner and Goodale (1998) state that the “dorsal stream is designed to guide actions purely in the here and now, and its products are consequently useless for later reference… it is only through knowledge gained via the ventral stream that we can exercise insight, hindsight and foresight about the visual world" (p.12). Therefore, it follows that the representations guiding vision for action and vision for perception operate on different time scales. In considering a mapping between egocentric and allocentric processing onto dorsal and ventral stream functioning, it is necessary to now consider the temporal properties of egocentric and allocentric representations.

It is thought that egocentric coding is the "transient representations of one's immediate environment" (Finlay, Motes, & Kozhevnikov, 2007, p. 266), thus suggesting that egocentric representations are short term. Of the relationship between vision and action, Berkeley (1709/1950) simply states that, "vision guides movement and movement alters vision" (Sekuler & Blake, 1994, p.259). Indeed, there is a body of research advocating the updating process of egocentric representations, specifying that it needs to be a continuous process in order to take account of object and/or individual motion (Mou, McNamara, Valiquette, & Rump, 2004; Wang & Simons, 1999; Wang & Spelke, 2000). There would be no advantage to storing egocentric representations after they have either been used to execute a particular movement or they are no longer relevant to the particular motor action. Similarly, owing to the precise nature of egocentric representations and their sensitivity to changes in observer and object locations, Westwood and Goodale (2003) propose that a movement to a visible target is not programmed until immediately before the commencement of that movement, thus minimising potential errors; for example, errors in the direction of reaching. Milner and Goodale (1993) also argue that owing to the fact that we constantly change the position of our head, body, and eyes relative to external objects, the representations used in motor control must be highly transient. These observations therefore validate the premise that egocentric representations have a short time span and should be thought of as being dynamic (Finlay, et al., 2007; Wang & Spelke, 2000).

This is not the case for allocentric representations: object recognition abilities often last a life time (Gazzaniga, Ivry, & Mangun, 1998; Nardini, et al., 2006). The argument for the long term storage of object representations is believed to be circular. Object processing relies on drawing upon stored object representations, object processing must therefore contribute to the amassing of object information, and the information has to be stored in the first place to be able to be drawn upon at a later point in time. Therefore, both components to object processing indicate that these representations are stored over long time periods. Burgess (2006) illustrates the validity of the long term storage of allocentric representations, but not egocentric ones, by stating that, "a simple forward movement requires different individual changes to the egocentric locations of every object in the environment but changes only self-location within an allocentric environmental representation" (p.554). Thus, there is great validity for the long term storage of allocentric representations as, even though the individual moves, the relations between the environmental features, providing they are static, remain the same.

Taken together these findings support the idea that allocentric representations are involved in spatial memory, particularly, long term spatial memory. This has been further supported by the cache-retrieving behaviour in birds. It has been demonstrated that not only are these animals able to store a high number of caches in a variety of locations, possibly up to a thousand, but that they also have an accurate spatial memory for these locations after an extensive period of time; for example, returning to them throughout the winter months having stored them in the summer months, thus demonstrating a very high level of spatial memory (Balda & Kamil, 1992; Clayton & Dickinson, 1998; Jeffery & O'Keefe, 1998; Shettleworth & Krebs, 1982).

The differential neural underpinnings of allocentric and egocentric frames of reference discussed earlier further support the differences in the temporal characteristics of the two types of representations. Activation of the hippocampus has been repeatedly observed when tasks requiring allocentric representations are completed but not when egocentric tasks are employed (Bohbot, et al., 2004; Galati, et al., 2000; Parslow, et al., 2004; Zaehle, et al., 2007). The hippocampus has long been thought to play a central role in spatial memory (O'Keefe & Nadel, 1978), and specifically in the transfer of information from short term to long term memory. Therefore, its selective role in allocentric processing indicates a difference in the temporal characteristics of egocentric and allocentric representations (Gazzaniga, et al., 1998; Nadel & Hardt, 2004; Zaehle, et al., 2007).

Patients who have undergone the removal of unilateral hippocampal areas show impairments at completing tasks requiring spatial processing abilities, such as the Morris water maze (Astur, Taylor, Mamelak, Philpott, & Sutherland, 2002). Additionally, the hippocampal structures of taxi drivers have been found to be larger than those of individuals who are not experts in spatial navigation (Maguire et al., 2000). Likewise, the hippocampal complex in species of birds that exhibit food storing and retrieving behaviours has been found to be bigger compared to those species that do not engage in such behaviours (Clayton, 1998; Krebs, Sherry, Healy, Perry, & Vaccarino, 1989). Indeed, there is a vast body of research into the role of the hippocampus in spatial memory (see Suzuki & Clayton, 2000, for a review). In summary, the selective involvement of the hippocampus in allocentric spatial memory, as well as the disruption that object and observer movement causes to egocentric representations, suggests different temporal characteristics of allocentric and egocentric memory representations.

Topographical memory

There has also been research which has directly manipulated allocentric and egocentric frames of reference and evaluated their temporal characteristics; however, the findings have not been conclusive about whether egocentric representations can be stored or not. The paradigm frequently used in studies of topographical memory involves participants learning the spatial relations of a table of different objects relative to themselves (egocentric coding) or relative to the other objects on the table (allocentric coding). After the initial presentation of the object array, either the observer would move to occupy a new viewing location or the table on which the objects were placed would be rotated. The observers would then be required to answer questions about the visual array (Finlay, et al., 2007; Simons & Wang, 1998; Wang & Simons, 1999).

Some such studies have shown that changing the egocentric information between the learning phase and the testing phase causes less disruption than changing the allocentric information; for example Burgess, Spiers, and Paleologou (2004), Simons and Wang (1998), and Wang and Simons (1999). This suggests that whilst the stored allocentric information causes a conflict when new allocentric information is presented, resulting in a decrease in accuracy at recalling the relative positions of objects, owing to their short term nature, the egocentric representations formed in the learning phase are not able to cause conflict when new egocentric information was presented. However, a number of other studies found that egocentric changes, that is, changes in viewpoint, do affect recognition performance of the spatial location of objects (1999; Diwadkar & McNamara, 1997; Finlay, et al., 2007; Shelton & McNamara, 2004) suggesting some memory for egocentric information.

It is believed that two points about the methodology of the studies of topographical memory should be discussed. First, the tasks used in these studies often required the participants to make whole body movements between the learning phase and the testing phase, and as a result it can be argued that the egocentric information amassed by the participant may lose any informative value, thus determining the need for a new egocentric representation to be formed. Supporting this, Finlay, et al. (2007) found a linear relationship between accuracy of recall and the distance that the egocentric representation shifted between the learning phase and the recall phase. As distance from the starting point increased, participant responses became more erroneous; therefore, suggesting that the greater the movement, the greater the disruption. This may mean that the egocentric representations were discarded as they were no longer useful, and thus does not provide information about their time course.

Second, with regards to the time course, in these experiments participants were required to hold the spatial information for between 7 seconds (Burgess, 2006; Simons & Wang, 1998; Wang & Simons, 1999) and 13 seconds (Burgess, et al., 2004). At these time points the egocentric information may have already been lost so it is not possible to gain understanding of the duration of egocentric representations. Finlay et al. (2007) go some way to answering this question by testing recall of egocentric and allocentric locations with a series of temporal delays between the first presentation and the second presentation (0, 6, and 12 seconds).

Whilst there was no difference in recall performance between the three delay conditions, it could be argued that in the no delay condition (0 seconds) there is in actual fact a delay: the time taken for the participant to move from the learning position to the testing position. Westwood and Goodale (2003) comment on the very limited life span of egocentric representations, and how they are only available immediately prior to movement, so moving to the new location for the testing phase may have been a sufficiently long enough delay for the egocentric information to have decayed in. Therefore, it is believed that such spatial orientation tasks cannot be used to fully investigate the temporal characteristics of egocentric representations, and thus test the much stronger prediction that egocentric information cannot be stored at all, not even for a few seconds.

In summary, after considering research from a number of different fields, it can be said that allocentric and egocentric representations do appear to operate on different time scales. While it makes intuitive sense that egocentric representations are needed to be continually updated to take account of observer and object motion, there is some disagreement in the topographical literature as to whether egocentric representations can be (or are) stored or not.

Switching between streams

As has been discussed previously, Schenk (2006) found that the visual form agnosia patient D.F. was impaired at completing both a perceptual task and a visuomotor task when allocentric processing was required, whereas she was unimpaired at performing the same tasks when they required egocentric processing. Therefore, Schenk (2006) concluded that the deficits in patient D.F. reflect an allocentric-egocentric dissociation and not a perception-action dissociation as predicted by Milner and Goodale (2006) and Milner et al. (1991). Support for Schenk’s (2006) findings have been provided by the extensive research that indicates that egocentric information is used in the completion of visuomotor tasks, and that dorsal stream areas are involved in egocentric processing, and likewise, the findings that ventral stream areas are engaged in perceptual tasks, and that perceptual tasks typically use allocentric representations (Milner & Goodale, 1993, 2006; Wang & Spelke, 2000). While the effects of temporal delays on the perceptual and visuomotor performances in visual agnosia and optic ataxia have been presented previously, these observations will now be considered from a frame of reference viewpoint.

It has been found that when a delay was introduced between presenting an object and allowing visual agnosia patient D.F. to reach for it, her performance deteriorated compared to when no delay was imposed (Goodale et al., 1994). The perception-action model argues that the introduction of a delay, on account of the short term nature of dorsal stream representations, transformed the visuomotor task to a perceptual task, and as D.F.’s ventral stream was damaged she was no longer able to complete the task (Milner & Goodale, 1995, 2006). However, it could instead be argued that the introduction of a delay does not transform a visuomotor task to a perceptual task, but shifts the task from requiring egocentric coding to a task requiring allocentric coding. Given that egocentric information has been associated with dorsal stream structures, one might therefore expect that egocentric information cannot be stored, and this being a task which relies on visual memory, D.F. has to use allocentric representations, which Schenk (2006) found her to be impaired at doing in tasks where there is no delay. Mou et al. (2004) also support this by concluding that individuals switch to using environmental representations to compensate for the decay of egocentric representations with the passage of time.

Conversely, the pointing and reaching accuracy of patients with optic ataxia has been found to increase after a delay. It has been suggested that when a delay is introduced into a visuomotor task, there is a shift from using dorsal stream representations to using ventral stream representations (Goodale, et al., 1994; Himmelbach & Karnath, 2005; Milner, et al., 2001). However, owing to the match between their neural underpinnings and the two visual streams, it could be the case that these patients are required to switch from using egocentric representations to using allocentric representations. Neuroimaging research indicates that allocentric representations derive from the ventral stream (Parslow, et al., 2004; Zaehle, et al., 2007) which is intact in this group of patients, thus explaining the observed improvement in their performance. Underpinning the explanations of the effects of delay in patients is that after a delay a switch is made to a different method of processing and/or representation being used.

There has been a great deal of research looking at switching between dorsal stream and ventral stream representations with the onset of a temporal delay; however, there appears to be some disagreement over the nature of this switch. Westwood et al. (2001) believe that upon occlusion of the item to be grasped, the switch from using dorsal stream representations to ventral stream representations happens fairly immediately. Furthermore, Westwood and Goodale (2003), in the strongest version of the limits of dorsal stream representations, argue that “real-time visuomotor mechanisms are engaged for the control of action only after the response is cued, and only if the target is visible” (p. 243), thus suggesting no memory for visuomotor representations. This again would advocate that the switch between dorsal and ventral stream processing when there is a delay is very swift (Westwood & Goodale, 2003; Westwood, et al., 2003). Conversely, Himmelbach and Karnath (2005) found that there was a linear relationship between the degree of the pointing error and the length of the delay between viewing the target and being signalled to initiate a pointing movement to the target location, finding that the pointing performance of an optic ataxia patient increased as a function of delay length. Thus, Himmelbach and Karnath (2005) proposed that the introduction of a delay to a motor tasks results in a "gradual change between dorsal and ventral control of reaching behaviour, rather than a sudden switch between two separated cortical pathways" (p. 635). Likewise, Hesse and Franz (2009) found evidence to suggest the visuomotor information that is used in movements completed after a delay decays exponentially.

The research into the effects of visual illusions on perception and action has been particularly informative in looking at switching between the dorsal and ventral processing streams after a delay. It has been generally found that while visual illusions have very little effect on visuomotor actions performed in real time, that is, when there is no delay, under the same timing conditions they have strong effects on perceptual tasks (Aglioti, et al., 1995; Haffenden & Goodale, 1998; Vishton, et al., 1999). However, visual illusions do have an effect on visuomotor performance when a delay is introduced; for example, Westwood and Goodale (2003), using a size-contrast illusion, observed a significant effect on visuomotor performance after a delay of a couple of seconds. It is thought that after a delay it is the ventral stream, rather than the dorsal stream, which provides the visual information for the control of the movements, and the perceptual information is susceptible to visual illusions, again suggesting a switch between the two with the onset of a delay (see also Hu & Goodale, 2000).

However, in investigating the effects of visual illusions on grasping in delay and no delay conditions, Franz, Hesse, and Kollath (2008) observed that in the no delay condition visual feedback is available throughout, whereas in the delay condition this is not the case. As a result, Franz et al. (2008) went onto systematically vary the amount of visual feedback that participants received when grasping Müller-Lyer stimuli[8]. In doing so they observed that the effects of the illusion were reduced when greater amounts of visual feedback were available. Therefore, Franz et al. (2008) concluded that it is the presence of visual feedback, which allow on-line corrections to be made, that reduces the apparent effects of the illusion. Thus, when the movement is being undertaken, it is the availability of visual feedback that causes the differential effects of visual illusions in delay and no delay conditions previously reported. Furthermore, when Franz et al. (2008) matched the amount of feedback in delay and no delay conditions there was no difference in the size of the effect of the illusion. Therefore, they argue that the research into the effects of visual illusions in delayed action does not provide conclusive evidence of a transfer from dorsal stream processing to ventral stream processing under such conditions.

There seems to be some dispute in understanding the change of information used in visuomotor control after a delay. Clearly, whether the switch from dorsal stream representations is made either very swiftly, that is as soon as visual information is removed and the action has to be performed “off-line”, or more

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[8] Müller-Lyer stimuli are doubled ended arrows with the ends either both pointing in or both pointing out. The direction of the arrows affects the perceived length of the line, such that arrows with ends pointing are perceived as being shorter (Franz, et al., 2008).

gradually, is heavily linked with the temporal characteristics of the representations involved.

Summary of the literature reviewed

A number of issues have been discussed relating to Milner and Goodale's (1993) perception-action model, with the main focus being on the frames of reference that are used in perceptual and motor tasks. There is extensive neuroimaging and behavioural evidence to support an anatomical connection between ventral and dorsal processing and allocentric and egocentric frames of reference, with ventral stream areas, that is, ventro-lateral occipito-temporal areas, being recruited in allocentric processing while dorsal stream areas, namely fronto-parietal areas, are selectively involved in egocentric processing. However, the functional nature of this connection is not clear. Whilst Milner and Goodale (1993) believe that perception and action form the basis of the ventral-dorsal dissociation and that allocentric and egocentric processing map onto them respectively, Schenk (2006) proposes that the two frames of reference form the basis of the dissociation. Clearly, further understanding of the temporal characteristics of egocentric representations in particular would aid in the discussion of the transformation between visual streams after a delay. The aim of the experiments presented in this thesis is to investigate the availability of egocentric information after a delay.

Finally, based on the belief that motor tasks use egocentric coding and perceptual tasks use allocentric coding (Milner & Goodale, 1995, 2006), it is likely that past experimental designs reflected this difference without explicit acknowledgement. This would result in the presence of a consistent, yet unmeasured, frame of reference difference between the visuomotor tasks and perceptual tasks. Indeed, when Schenk (2006) compared allocentric and egocentric versions of perceptual and visuomotor tasks he found results different to those that had been previously reported. Therefore, to formally investigate the properties of allocentric and egocentric representations it is necessary to directly compare the two using the same task parameters. This is possible using spatial priming in a visual search paradigm, which is the principal methodology used in this thesis.

Visual search and spatial memory

Searching our environments forms part of our daily behaviour; for example, finding a friend at a crowded train station or locating a misplaced book in the office. Furthermore, efficient searching behaviour is essential to the survival of any organism: being able to locate and identify food sources is crucial, as is detecting threatening stimuli amongst their non-threatening counterparts (Dijksterhuis & Aarts, 2003). Understanding search mechanisms, and specifically the characteristics of successful search methods, is of great validity, and indeed the visual search literature is vast (for a review see Wolfe, 1998a).

Successful searching behaviour has to be organised. It would be inefficient if the same location was repeatedly searched after an initial search in that location failed to yield the target. Therefore, attention should not perseverate on searched locations but should continue to move to sample new locations until the target is identified (Tipper, Jordan, & Weaver, 1999). Or likewise, if it is known that the target item occupies a certain location, maintaining memory for that location is important. Accordingly, it is believed that memory is critical to defining whether a search is organised or not (Desimone, 1996; Desimone & Duncan, 1995; Peterson, Kramer, Wang, Irwin, & McCarley, 2001).

Shore and Klein (2001) argue that there are three types of memory that are of particular relevance in visual search: perceptual learning, between-trial memory, and within-trial memory. Gibson (1969) states that as a result of experience with a certain environment or stimulus, individuals get better at being able to extract information from that stimulus; for example, individuals become faster at completing visual searches with practice. This process is termed perceptual learning. Of the three types of memory listed, the effects of perceptual learning last the longest, with effects carrying across experimental blocks and even testing sessions (Shore & Klein, 2001). For example, Sireteanu and Rettenbach (1995) found that with practice (two separate sessions on consecutive days) serial searches could became parallel (or switch from inefficient to efficient, according to the guided search model, Wolfe, Cave, & Franzel, 1989), in that the search times were no longer influenced by the number of items in the displays. Ahissar and Hochstein (1997) also reported that with continued experience with a specific visual search task performance improved, that is, the length of the presentation time needed to achieve a specified level of accuracy systematically decreased, and continued to do so for over 1500 experimental trials. Ellison and Walsh (1998) observed even longer effects of perceptual learning, finding that training led to improvements in visual search performance which lasted several days. Thus, perceptual learning can have long lasting benefits on visual search performance.

In contrast to the long lasting effects of perceptual learning, within-trial memories last in the region of milliseconds to seconds and are relevant only to the current search display (Shore & Klein, 2001). Klein (1988) proposed that within-trial memory prevents attention returning to items that have already been examined and discounted as being the target, and suggests that this is done by the attachment of an ‘inhibitory tag’ to them. In support of this inhibitory tagging account, Posner and Cohen (1984) found that when targets appeared in locations that had previously been cued (i.e. attention had previously been drawn to that location), response times were slower compared to when targets appeared in uncued locations (i.e. attention had not previously been deployed to that location). This slowing effect has been termed *inhibition of return* (Posner, Rafal, Choate, & Vaughan, 1985) and has been reported many times[9]. In visual search displays where the objects are stationary, inhibition of return (IOR) is believed to operate on the location that a non-target occupies, known as *location-based IOR* (Danziger, Kingstone, & Snyder, 1998; Tipper & Behrmann, 1996). It has also been found that IOR can be attached to object themselves, known as *object-based IOR*; therefore, should the object move to a new location, attention will not be expended on re-researching that object in its new location because the inhibition has moved with the object; for example, Abrams and Dobkin (1994); Gibson and Egeth (1994); Tipper, Driver, and Weaver (1991); and Tipper, Weaver, Jerreat, and Burak (1994).

The third type of memory argued to play a role in visual search is between-trial memory, known as trial-to-trial priming. The time scale of between-trial memory is longer than that of within-trial memory but shorter than perceptual learning. Between-trial memory lasts in the order of seconds to minutes (Shore & Klein, 2001). Between-trial priming refers to prior experience with a stimulus exerting an effect on subsequent encounters with that same stimulus; for example, the repetition of a stimulus in a search array can facilitate its processing when it is later re-presented, and this would be indexed by faster detection times to its presence. It is believed that this type of priming results from a memory

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[9] See Klein (2000) for a review.

representation of the first trial being stored which is subsequently retrieved when that same trial is presented at a later point in time, and that this leads to more efficient processing of that stimulus (Huang, et al., 2004). Whilst it is most effective in the short term, that is, for trials that directly follow the initial presentation, between-trial priming is capable of facilitating response times for between five and eight trials later (Kristjansson, Wang, & Nakayama, 2002). The priming effect is also cumulative: response times continue to decrease when the target appears repeatedly in the same location. This type of priming has been found for a number of target characteristics, including target identity (Kristjansson, et al., 2002); target colour (Hilstrom, 2000; Huang, et al., 2004; Maljkovic & Nakayama, 1994); and target location (Kristjansson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Kumada & Humphreys, 2002; Maljkovic & Nakayama, 1996). The current research is concerned with between-trial memory, and specifically the priming of target location.

What is primed in position priming?

While there have been a number of demonstrations of position priming, whereby, search times decrease when a current target occupies the same location as a previous target did, it is not clear what is actually being primed. In many of the position priming experiments stimulus configurations meant that the absolute positions and relative positions of objects are confounded with each other. For example, if the target and distractor items are arranged in a circle and the target is presented in the 2 o’clock position, when the target appears in this location in a subsequent trial, it is not only the absolute position that is repeated but also its position relative to the other items in the display. Therefore, it is not clear whether it is the memory representation of the target position coded relative to the observer (i.e. the target’s egocentric position) or coded relative to other items in the search array (i.e. the target’s allocentric position) which underlies the priming effect. Alternatively, it is possible that both egocentric and allocentric information is being primed. If this is the case, the pertinent research issue is to evaluate their respective contributions to the priming effect.

Past studies have not typically dissociated allocentric and egocentric frames of reference as if the target position remained in the same location relative to other items on the screen across trials, it was also presented at the same position on the screen relative to the observer. Maljkovic and Nakayama (1996) attempted to separate allocentric and egocentric frames of reference by comparing an allocentric condition, where the target remained at the same location relative to the other items in the display, but occupied a different egocentric location, with a combined allocentric–egocentric condition, where both the allocentric location and the egocentric location of the target remained the same. However, their results were inconclusive. Although the priming effect appeared to be marginally larger when egocentric information was added, it remained unclear whether this effect would be statistically significant. Furthermore, and in order to add more weight to their conclusions, it is thought that priming an absolute position must be directly compared with priming a relative position that has no fixed absolute position within the same experiment. This third condition is critical to determining which of the two frames of reference drive the priming effect when both are available.

The suitability of priming in visual search

The experiments presented in this thesis investigated the use of egocentric and allocentric information in a visual search paradigm. It is believed that the use of a visual search paradigm is well suited to examining frames of reference and their temporal characteristics, and there are three main reasons for this. First, the nature of the task allows the evaluation of spatial memory over very short time spans, that is, in the range of 2 to 3 seconds. The existing research that has evaluated egocentric and allocentric memory, namely, topographical research, used long delays between the learning and testing phases; for example, often between 7 and 13 seconds Burgess, et a., 2004; Diwadkar & McNamara, 1997; Finlay, et al., 2007; Wang & Simons, 1999). A visual search paradigm allows greater control over the inter-trial intervals of search displays and much shorter time periods between displays can be investigated.

Second, it was thought necessary to use the same task for both the allocentric and egocentric task. According to the perception-action model, the two types of information are typically associated with different types of behaviour: allocentric information is associated with perceptual tasks, while egocentric information is associated with visuomotor tasks (Milner & Goodale, 1995, 2006). Under such circumstances, a direct comparison between the role and temporal properties of allocentric and egocentric representations is not possible. Instead it is critical that the same task is used in both conditions, and spatial priming in visual search allows this. Given the assumptions of the perception-action model, it is expected that regardless of whether a perceptual or a visuomotor task for both conditions is chosen, the task will be biased either towards allocentric information (in the case of a perceptual task) or towards egocentric information (in the case of a visuomotor task).

Since the aim of this thesis was to investigate whether there is any clear evidence that egocentric information might still be used after a delay, it was decided that a task that favours the use of allocentric information should be used, namely a perceptual task. Thereby, if it is found that egocentric information is used to a comparable extent as allocentric information under such circumstances, the finding cannot be easily be dismissed as due to the behavioural task favouring egocentric information and biasing against allocentric information.

A perceptual task is also favoured over a visuomotor task because it allows only visual information to be carried over from one trial to the next. In using a motor task, reports of motor priming (Dixon & Glover, 2009; Jax & Rosenbaum, 2007, 2009) are limited by the fact that the priming effects could be the result either the visual representation being repeated across trials or the motor representation being repeated. Additionally, using a perceptual task allows the claim of the perception-action model that egocentric information is not typically used for perceptual tasks to be tested.

Finally, a task that permits allocentric and egocentric information to be used in an implicit manner was sought. In such a task, participants would use the specific information because it facilitates their performance, possibly without even knowing that they did use the information. If they use this information without being instructed to use it, it can be argued that their performance reflects a naturally and automatic tendency to exploit that information. In contrast, if an explicit spatial memory task was used and instructions were given about the specific type of spatial information they are required to use, their use of this information (be it allocentric or egocentric) might therefore simply reflect the explicit instructions and not correspond to a natural trend to use this type of information. In most of the topographical studies the participant was required to report whether the location of an object had changed within the scene (e.g. Diwadkar & McNamara, 1997; Finlay, et al., 2007), thus the nature of the instructions dictated which frame of reference participants used to complete the task (i.e. allocentric). Therefore, in the visual search experiments reported here, no specific instructions about how the target should be coded were provided.

Overview of Experiments

The aim of the experiments presented in this thesis was to investigate the temporal properties of egocentric and allocentric frames of reference by using a spatial priming paradigm presented within a visual search task. The following chapters present the details of the methods employed, along with the rationale and findings, of each experiment. Table 1 lists the experiments presented in this thesis, along with a brief description of the purpose of each experiment.

Table 1. Outline of the studies presented in this thesis.

	Study/Experiment number	Purpose of Experiment
Chapter 2	Study A - Experiment 1	Allocentric and Egocentric priming in a feature search.
	Study A - Experiment 2	The effect of the allocentric anchor and spatial restrictions on search performance.
	Study A - Experiment 3	Allocentric and Egocentric priming in a feature search controlling for the allocentric anchor.
	Study A - Experiment 4	Letter reporting accuracy when eye movements are allowed and not allowed.
	Study A - Experiment 5	Allocentric, Egocentric, and Combined Allocentric-Egocentric spatial priming in feature search.
Chapter 3	Study B - Experiment 1	The effect of set size on feature and conjunction searches.
	Study B - Experiment 2	The specific egocentric reference frame that drives spatial priming in conjunction search.
Chapter 4	Study C	Body-centred coding in a conjunction search.
Chapter 5	Study D	Plotting the time course of spatial priming in a conjunction search.
Chapter 6	Study E	The role of the posterior parietal cortex in spatial priming in conjunction search.

Chapter 2 – Study A: Frames of reference in feature visual search

General Methods

The general methods used in Study A are presented here. The specific details of the stimuli and their presentation timings varied for each experiment, and are described in the appropriate sections.

Participants

Ethical approval was obtained from the Psychology Research Ethics Committee at Durham University prior to experimentation. Participants were students and academics from the University of Durham and received either monetary payment or course credit in exchange for taking part. Participants were required to have normal, or corrected-to-normal, visual acuity in both eyes. All participants were naïve to the purpose of the experiment and gave informed consent to take part (see Appendix A for a copy of the general consent form and Appendix B for an example information sheet that participants were given prior to taking part).

Apparatus

The experiment was programmed using E-prime, version 1.1 (W. Schneider, Eschman, & Zuccolotto, 2002), which presented the stimuli, controlled the presentation timing of the stimuli, and recorded participant’s responses and reaction times. The program was run on an IBM compatible personal computer with a 15-inch monitor (1280 by 1024 resolution, refresh rate 60 Hz). A projector was used to present the stimuli onto a blank wall. This setup was used to ensure that no other stable visual cues, such as the edge of a computer monitor, were available. The presence of additional visual information could have had two potential effects. First, in the egocentric priming condition, where the target location was repeated relative to the observer, participants could have instead used the allocentric landmarks of the room to locate the target. Likewise, in the allocentric priming condition, any additional allocentric information could be used by the participants instead of the allocentric information presented within the search array. Furthermore, the experiments were completed in semi-darkness, and thus, apart from the search items no other visual information was available to participants. Participants sat 3 metres from the wall (unless otherwise stated). Participants made their responses to the stimuli using a button box. There were two possible response options (target present and target absent) and each response was assigned a button. Participants were instructed to hold the button box so that they were responded with the index finger of each hand.

Stimuli

Two sets of stimuli were presented in each trial. First a letter was presented and participants were instructed to report the identity of this letter. The font size of the letter was such that participants could only recognize its identity if they foveated the letter. The purpose of this part of the trial was to ensure accuracy in identifying where participants were fixating at the beginning of each trial, and thus ensure that their gaze was not lingering at the location of the previous target. Furthermore, controlling the location of fixation at the start of each trial was central to the rationale for later experiments.

Second, a search array was presented. All visual search stimuli were created using Matlab, version 7.1 (2005). The visual search arrays consisted of white lines on black backgrounds. The defining feature of the target was its orientation: distractors were oriented at 20˚ from vertical (a forward slash) and the target was oriented at -20˚ from vertical (a backslash). Each visual search array consisted of 12 lines. In target present searches there were 11 distractors and 1 target, and in target absent searches there were 12 distractors.

Stimuli placement

In all experiments the search arrays measured approximately 10˚ both horizontally and vertically. These were placed onto black backgrounds so that the whole stimuli arrays measured 35˚ horizontally and 27˚ vertically. This is shown in Figure 3. A figure depicting the search arrays and the different conditions used in each experiment is presented in the appropriate method sections. It should be noted that in these subsequent figures, with the exception of Figure 20A in Study C, the black background has been cropped so only the search arrays are included (i.e. the figures resemble the stimuli presented in the upper part of Figure 3, while the stimuli presented to participants actually resembled the lower part of Figure 3).

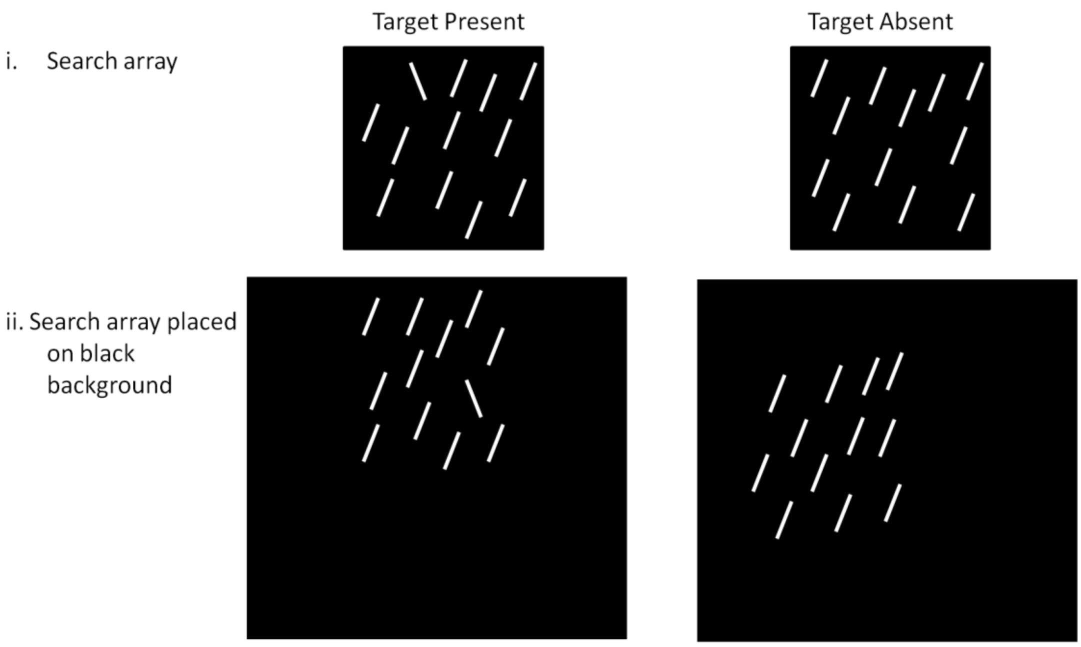


Figure 3. Illustration of search arrays and their placement on a black background.

i). Examples of target present and target absent search arrays (target is an oddly oriented line),

ii). Search arrays are placed onto black backgrounds so the boundary of the search array does not provide any additional spatial information.

Procedure and design

The timing of trial components and their presentation order were specific to each experiment so full details are provided when the experiment is presented. When a search array was presented, participants had to decide as quickly and as accurately as possible whether the specified target was present or absent, and make a corresponding key press response. Participants responded with the “3” button if the target was present and “5” if the target was absent. Search arrays remained presented until either participants made a response, or 5000ms had elapsed and no response had been made. The next trial was then initiated. In all experiments participants completed a series of practice trials to familiarise themselves with the task and the sequence of trials. The data from the practice trials were not analysed. All experiments were a repeated measures design with no between-groups factors.

Data Analysis

All analyses are concerned with participants' reaction times (in milliseconds), also referred to as search times, to decide whether the target line was present or absent in the search array. Reaction times were defined as the speed of response recorded from the point of stimulus onset. For each participant, incorrect answers were first removed from the data, followed by the removal of outlying responses (responses with reaction times more than two standard deviations above or below the mean). Trials where the participant did not correctly report the letter were also removed from the analysis, as this would indicate that they had failed to fixate correctly at the start of the trial.

All data were tested for normality using the Shapiro-Wilk statistic; the data were normal unless otherwise stated. Data violating this assumption was normalised using the log function. When this transformation could not be used to normalise the data (i.e. when values were negative) either a Wilcoxon Signed Ranks test (2 related samples) or Friedman's test (more than 2 related samples) was used. All data were also tested for sphericity, which assumes similarity between the relationship of experimental conditions, using Mauchly's test (Field, 2005); the assumption of sphericity was met unless reported. When data violated this assumption the Greenhouse-Geisser correction was applied. Unless otherwise stated, all post-hoc comparisons were paired samples t-tests, and where multiple comparisons were performed, a Bonferroni correction was applied. All inferential statistics used a significance level of $p < .05$.

Experiment preview

The experiments in Study A sought to establish what is actually primed in location priming, and to answer the following question: is a location primed in terms of its absolute position from the observer (egocentric coordinates) or its relative position with other items in the display (allocentric coordinates)? Furthermore, Experiment A5 compared priming for egocentric information and allocentric information with the priming effects when both co-ordinate systems define the target location. This enabled their respective contributions to the overall priming effect to be evaluated. If egocentric representations cannot be stored, as suggested by Milner and Goodale’s (1993, 1995, 2006) perception–action model, egocentric priming will not be observed; however, if egocentric representations can be stored, egocentric priming will be observed.

Study A - Experiment 1

The purpose of Experiment A1 was to compare the effect of spatial priming for targets defined using allocentric and egocentric coding.

Method

Participants

Twenty participants (10 female) took part in this experiment (age range 20 - 49 years, mean age 26.6).

Apparatus

The apparatus used was the same as described in the General Methods.

Stimuli

At the beginning of each trial, a letter (randomly chosen from a set of 7) to be reported was presented in the centre of the screen. This was followed by the presentation of a visual search display. In this experiment there were two priming conditions: allocentric and egocentric. In the allocentric priming condition the location of the target was positioned relative to a salient item in the display (two distractors positioned very close together, known as the *allocentric anchor*) but at different positions relative to the observer. In the egocentric priming condition, the target maintained the same absolute position relative to the observer but occupied different positions relative to the other items in the search array. The allocentric anchor was not included in the egocentric priming condition. Instead, the two distractors that the anchor comprised of were spaced out and behaved as the other distractors in the search array. Examples of allocentric and egocentric trials are shown in Figure 4A. Figure 4B provides an example of how the search arrays were placed onto the black backgrounds. It can be seen that while the absolute location of the target (egocentric condition) was the same across the two trials, it had no fixed location within the search array, and therefore it’s position within the search array could not provide any information about the location of the target.

Procedure

At the beginning of each trial a fixation cross was presented at the centre of the screen for 1000 ms. This was then replaced by a 1000 ms presentation of a letter before the fixation cross was re-presented in the same location for 500 ms. The white fixation cross and the letter were all positioned in the centre of the screen and were of visual angle 0.9° vertically and 0.6 horizontally° (font size 20, courier new, bold). The search display was then presented and remained on screen until participants made their response using the button box, or until 5000ms had elapsed and participants had not made a response. Once participants had responded, a blank screen was presented for 1000 ms and the next trial was then initiated. There was a minimum delay period of 3500 ms between two consecutive search displays. The sequence of a trial is shown in Figure 4C.

The target stimulus was present in 73% of trials. To induce position-priming sequences of trials were presented where a given target position was used 9 times within a given sequence. Interspersed within a sequence there were also 4 target absent trials, and 2 control trials, thus each sequence consisted of 15 trials. In control trials the target stimulus was present but at a new position (see Figure 4A for examples of control trials and how they compared to the other trials). For each priming condition 16 different sequences were used, thus a total of 240 trials were presented for each priming condition (144 present, 64 absent, and 32 control).

The experimental trials were divided into 8 blocks (4 allocentric blocks and 4 egocentric blocks). The presentation of these blocks alternated between allocentric and egocentric, and the first block (egocentric or allocentric) was counterbalanced between participants. Within each block, there were four search sequences, the order of which was randomised. The experiment took approximately 45 minutes to complete.

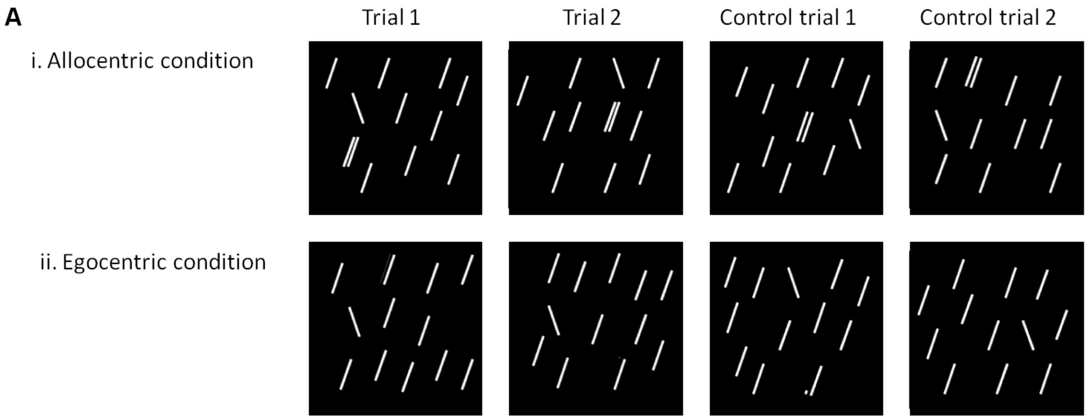
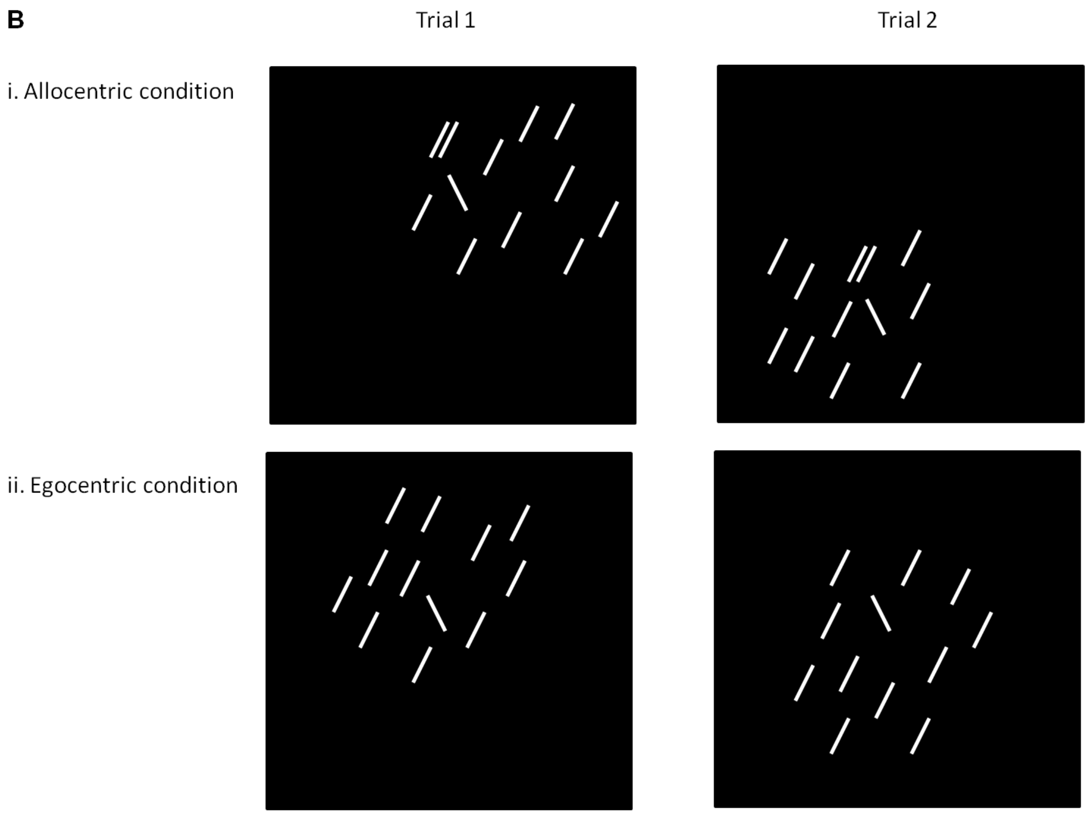


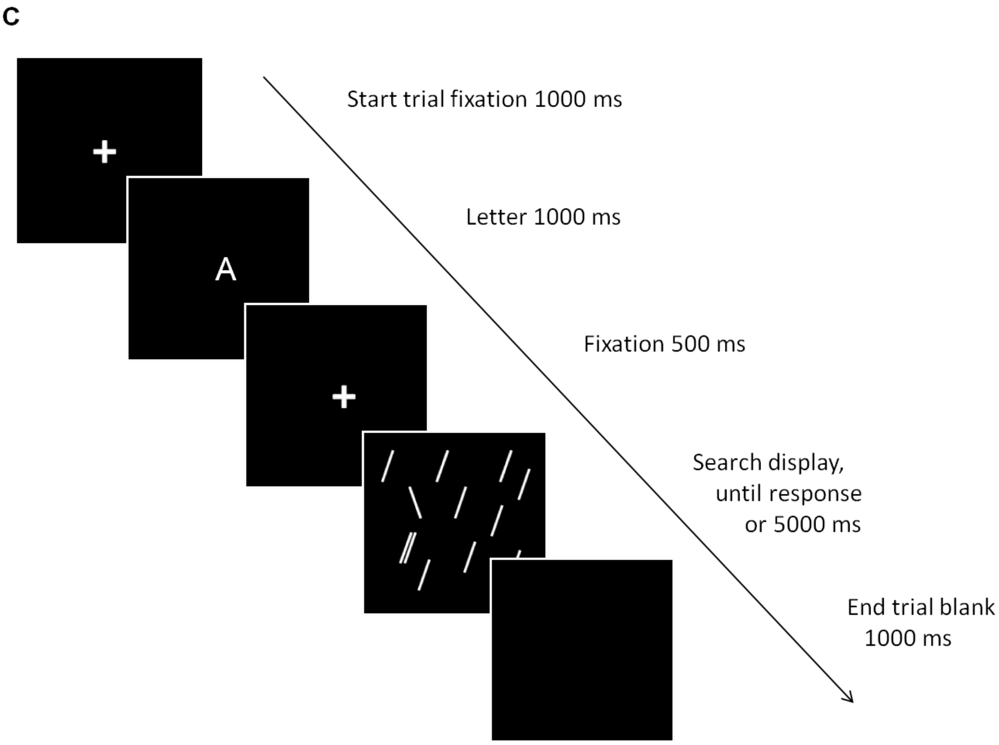
Figure 4. Priming conditions and trial sequence in Experiment A1.

(A). Schematic of stimuli for the two priming conditions.

(i) Allocentric priming condition. In trial 1 and trial 2 the target is above the anchor but it occupies different positions relative to the observer. In the allocentric control trials the anchor is present but it has no constant relationship with the target.

(ii) Egocentric priming condition. When the egocentric position is repeated, the target occupies the same absolute position on the screen. In the egocentric control trials the target occupies different positions on the screen.





(B). Schematic of the placement of allocentric and egocentric search arrays on the black backgrounds.

(C). Sequence and timing of each trial in Experiment A1.

Results

Accuracy

Participants were highly accurate in their responses to the visual search stimuli (the accuracy to target absent trials was 96%, control trials 98%, and target present trials 98%). Accuracy was the same across the two priming conditions (97%, *p* = .419, Wilcoxon signed Ranks Tests as data could not be normalised using a log transformation).

Present, absent, and control trials

Search times to target absent trials (*M* = 583.67, *SD* = 102.9) were significantly slower than those to target present trials (*M* = 519.96, *SD* = 109.6), *t*(19) = 7.20; *p* < .05. In order to compare search times to non-primed trials (control trials, where the target was present but not at the given position for that sequence) with those to primed trials (where the target was presented at the same position as in a previous trial in the trial sequence), the first target present trial of a sequence was classed as a control trial[10]. Search times to primed trials (*M* = 516.39, *SD* = 108.7) were faster than those to control trials (*M* = 549.18, *SD* = 123.8), *t*(19) = 6.80; *p* < .05. This difference in search times between present and control trials represents an indirect measure of priming, which was observed for both priming conditions (see Table 2).

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[10] This is the only analysis where the first present trial of a sequence is classed as a control trial.

Table 2. Mean Search Times (ms) to Present, Absent, and Control Searches in Experiment A1.

	Allocentric	Egocentric
Present	535.6 (114.8)	497.1 (105.1)
Absent	602.1 (116.3)	565.3 (93.7)
Control	576.5 (149.5)	521.8 (102.2)

Note. Standard deviations are shown in parentheses. For this data the first present trials of sequences were regarded as control trials.

Cumulative Priming

Within each sequence of trials, the target stimulus was at a given position 9 times (interspersed with target absent and control trials). Figure 5 shows search times to each of the 9 presentations of a target position for the two priming conditions. This data were subjected to a 9 x 2 repeated measures analysis of variance (ANOVA) with the factors Presentation Number (1 - 9) and Priming Condition (Allocentric, Egocentric). The ANOVA revealed a statistically significant main effect of Presentation Number, $F(4.45, 84.46) = 9.22$; $p < .05$ (Greenhouse-Geisser statistic); and a significant main effect of Priming Condition, $F(1,19) = 23.35$; $p < .05$. The Presentation Number by Priming Condition interaction was not significant ($p = .676$).

Figure 5 shows that search times decreased between the first target present trial and the ninth target present trial of a sequence in both the allocentric and the egocentric conditions. Indeed, post-hoc tests, in the form of repeated measures ANOVAs, revealed that the main effect of sequence was significant for allocentric searches, $F(4.50, 85.52) = 4.76$; $p < .025$ (Greenhouse-Geisser statistic), and for egocentric searches, $F(8,152) = 5.04$; $p < .025$. Thus, there were significant cumulative priming effects in both conditions.

In order to generate an index of the priming effects, the difference between search times to the first target present trial of a sequence and the ninth target present trial of a sequence was calculated (i.e. RT to the first target present trial minus RT to the ninth target present trial). In the allocentric condition there was an average reduction in search times of 47.91 ms (*SD* = 63.6), *t*(19) = 3.37; *p* < .025; and in the egocentric condition this reduction was 32.75 ms (*SD* = 32.6), *t*(19) = 4.50; *p* < .025. There was no difference between the priming effects in the two conditions (*p* = .235).

Following up the main effect of priming condition, post-hoc tests, in the form of two tailed t-tests, revealed that participants were faster in responding to searches in the egocentric priming condition (*M* = 500.56, *SD* = 104.7) compared to those in the allocentric priming condition (*M* = 539.37, *SD* = 117.0), *t*(19) = 4.83; *p* < .05.

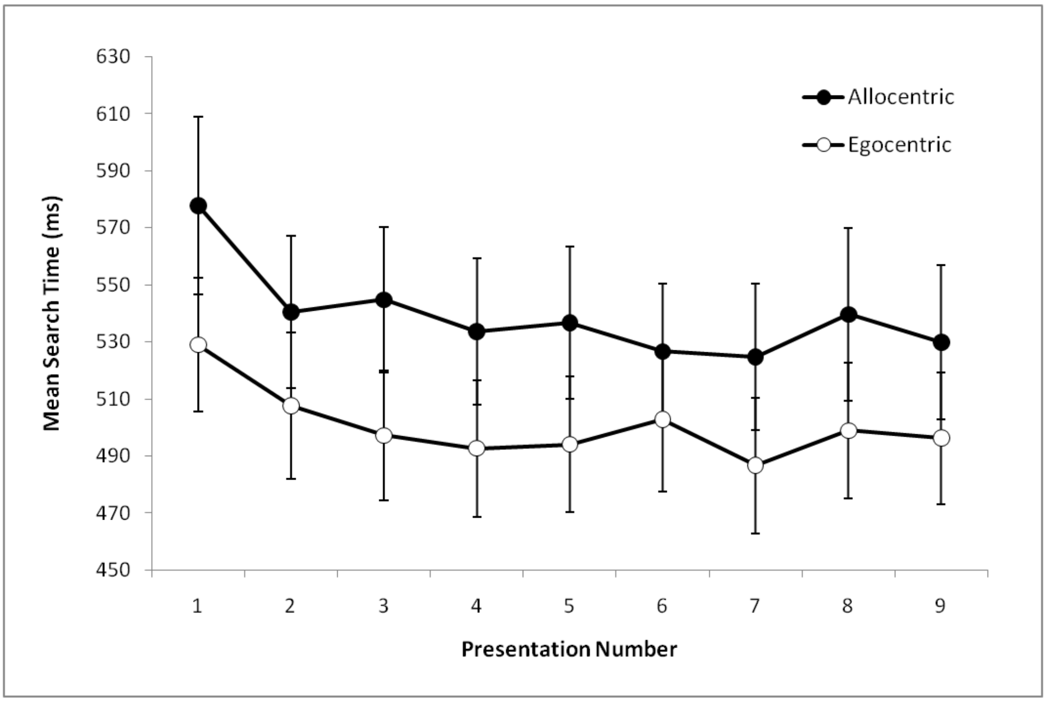


Figure 5. Mean search times (ms) to target present trials as a function presentation number in Experiment A1. Error bars represent the standard error (+ / - 1SE).

As this was the first priming experiment it was necessary to explore the priming effects fully, and therefore, it was decided that there should be 9 repetitions of each target presentation. On visual inspection of Figure 5 it can be seen that the greatest priming effects are observed in the first 5 or 6 trials of a sequence, and that after this point search times stabilise to some degree. It is thought that in future experiments the number of repetitions of a target location should be reduced, allowing a greater number of target positions to be explored. Therefore, in view of these proposed future changes, the following analysis will evaluate the priming effects for the first six target present trials of a sequence only, and compare these effects to when all 9 target presentations of a sequence are analysed to evaluate whether reducing the number of repetitions of a target location is justified.

Six present trials of a sequence

The effect of Presentation Number for the first six trials of a sequence is now considered. Again the data was subjected to a repeated measures ANOVA with the factors Presentation Number (1 - 6) and Priming Condition (Allocentric, Egocentric). The ANOVA revealed a significant main effect of Presentation Number, $F(3.44, 62.26) = 13.04$; $p < .05$ (Greenhouse-Geisser statistic), and a significant main effect of Priming Condition, $F(1,19) = 21.39$; $p < .05$. The Presentation Number by Priming Condition interaction was not significant ($p = .375$). The results of this analysis are consistent with those reported when all 9 presentations of a target position were analysed.

In the allocentric priming condition there was a mean reduction of 51.21 ms ($SD = 63.2$) between the first target present trial and the sixth target present trial of a sequence, and this difference was statistically significant, $t(19) = 3.62$; $p < .025$. In the egocentric condition the difference was 26.23 ms (*SD* = 38.3), again statistically significant, *t*(19) = 3.06; *p* < .025. The differences between the change in search times between the first and sixth presentations of a target location in the allocentric and egocentric conditions were not statistically significantly different from one another (*p* = .332, Wilcoxon Signed Ranks test used as the data violated the assumption of normality and a log transformation could not be used as some of the values were negative).

First target present trials of sequences and blocks

On inspection of Figure 5 it can be seen that search times to the first present trial of a sequence in the allocentric condition (*M* = 577.82, *SD* = 139.1) were slower than those in the egocentric condition (*M* = 528.98, *SD* = 104.6); a statistically significant difference of 48.84 ms, *t*(19) = 3.66; *p* < .05. This therefore makes any direct comparison between the amount of allocentric and egocentric priming more complicated. However, to assess whether this initial difference in search times is the result of a real difference between the searches or not, it is necessary to consider those trials that are truly free from any frame of reference information, that is, the first target present trial of the first sequence of a block of trials. When considering the data from only these trials, search times in the allocentric condition (*M* = 640.90, *SD* = 176.5) are still slower than those in the egocentric condition (*M* = 568.33, *SD* = 124.2), a difference of 72.57 ms, *t*(19) = 3.13; *p* < .05.

Experiment A1 Summary

In this first experiment, the location of the target was either defined using an egocentric frame of reference, in that the target occupied the same location on the screen relative to the observer, or an allocentric frame of reference, whereby the target had the same location relative to a landmark in the search array. Statistically significant cumulative priming effects, in that search times became faster when the location of a target was repeated across trials, were observed for targets defined in both frames of reference. These priming effects were significant when the analysis was included either the nine target present trials of a sequence or only the first six target present trials of a sequence.

There was a trend for greater cumulative priming in the allocentric priming condition relative to the egocentric priming condition; however, this difference was not statistically significant. Furthermore, a direct comparison between these effects was complicated by an initial difference in search times between the two priming conditions, with search times being faster in the egocentric condition. This therefore suggests that the searches in the two priming conditions are not equal in some way.

On reflection of the stimuli used in the two priming conditions, it is thought that there are two potential explanations for this difference in initial search times. The first of these is regarding the presence of the anchor (two distractors placed close together) in the allocentric searches where it provides predictive information about the location of the target. This anchor was not present in the egocentric searches (see Figure 4A). Second, owing to the nature of the egocentric stimuli the location of the target was restricted to a smaller, and more central, area of the screen. In the egocentric searches, the target occupied the same location on the screen for all the nine present trials of a sequence and the distractor items appeared to move around the target; therefore, sufficient space around the target for the distractors to be placed was required. This was not the case in the allocentric searches, where instead having a constant relationship between the location of the target and the anchor was necessary. Both of these potential confounds are explored further in Experiment A2.

Study A - Experiment 2

Whilst significant priming effects were observed in the allocentric and egocentric priming conditions in Experiment A1, the comparison between the two frames of reference was complicated as search times to the egocentric searches were faster than those to allocentric searches. Accordingly, it is necessary to ascertain whether the differences between the egocentric and allocentric searches can be explained by the differing stimuli configurations used in the two types of searches. There were two principle differences between the searches which will now be discussed.

First, in the allocentric searches, two distractors were placed close together and acted as a landmark in this condition; however, this anchor was not present in the egocentric searches. The presence on the anchor in the allocentric searches may have acted as a second target and slowed participants' responses to decide whether the real target was present or absent in this condition, and this led to an overall slowing in search times in this condition.

Second, possible target locations in egocentric searches were constrained. In the egocentric searches the target was required to stay in a fixed absolute position on the screen in the display, and thus maintaining the same observer related position whilst the distractors moved around it. This restriction in the placement of the target was not present in the allocentric priming condition; therefore, the position of the target in the egocentric searches was confined to a smaller area within the whole display than in the allocentric searches. It is possible that the faster response times to egocentric searches observed in Experiment A1 were the result of either the participant not having to make as many, or as large, eye movements to locate the target.

Therefore, it is necessary to investigate the influences of both the presence of the allocentric anchor and spatially constraining the location of the target on search performance. The results of this second experiment will aid the interpretation of the effects observed in Experiment A1, as well as guide the design of future experiments.

Method

Participants

Twelve participants (9 female) took part in this experiment (age range 18 - 48 years, mean age 27.8).

Apparatus

The apparatus was the same as in Experiment A1.

Stimuli

The visual search displays were the same as those used in Experiment A1. In this current experiment there were two variables: Spatial Constraint and Anchor Presence. Spatial Constraint referred to the possible locations of the target and was either Restricted or Unrestricted. Unrestricted meant that there were no spatial constraints to the location of the target; the same as the allocentric searches in Experiment A1. In the Restricted condition, the target could only appear in a smaller and more central region of the screen, which allowed distractor items to move around its location. This was the same as the egocentric searches in Experiment A1. The two levels of Anchor Presence were Anchor Present and Anchor Absent. The anchor was the same as the anchor used in the allocentric searches in Experiment

A1: two distractors positioned close together. In this experiment the location of the anchor had no predictive value on the location of the target. Thus, there were four conditions: Unrestricted Anchor Present, Unrestricted Anchor Absent, Restricted Anchor Present, and Restricted Anchor Absent. The experiment was not concerned with location priming; therefore, the location of the target was not repeated across trials. The fixation cross and the letter were of visual angle 0.9˚ vertically and 0.6˚ horizontally (font size 20, courier new, bold).

Procedure

The trial procedure and timings of stimuli presentations were the same as in Experiment A1 (see Figure 4C, page 58). For each of the four conditions participants completed one block of 50 trials, consisting of 35 target present trials and 15 target absent trials, thus the target was present in 70% of trials. Participants completed the four blocks of trials in a randomised order; therefore, each participant completed a total of 200 trials (140 target present and 60 target absent). The experiment took approximately 20 minutes to complete.

Results

Accuracy

Participants were highly accurate in their responding to the visual search stimuli (present trials 98% correct, absent trials 95% correct).

Present and absent trials

In accordance with the visual search literature, search times to target present trials (*M* = 566.5, *SD* = 76.9) were significantly faster than those to target absent trials (*M* = 607.3, *SD* = 48.4), *t*(11) = 2.30; *p* < .05. A 2 x 2 repeated measures ANOVA with the factor Spatial Constraint (Restricted, Unrestricted) and Anchor Presence (Present, Absent) was performed on the data. The data for these four conditions is shown in Figure 6.

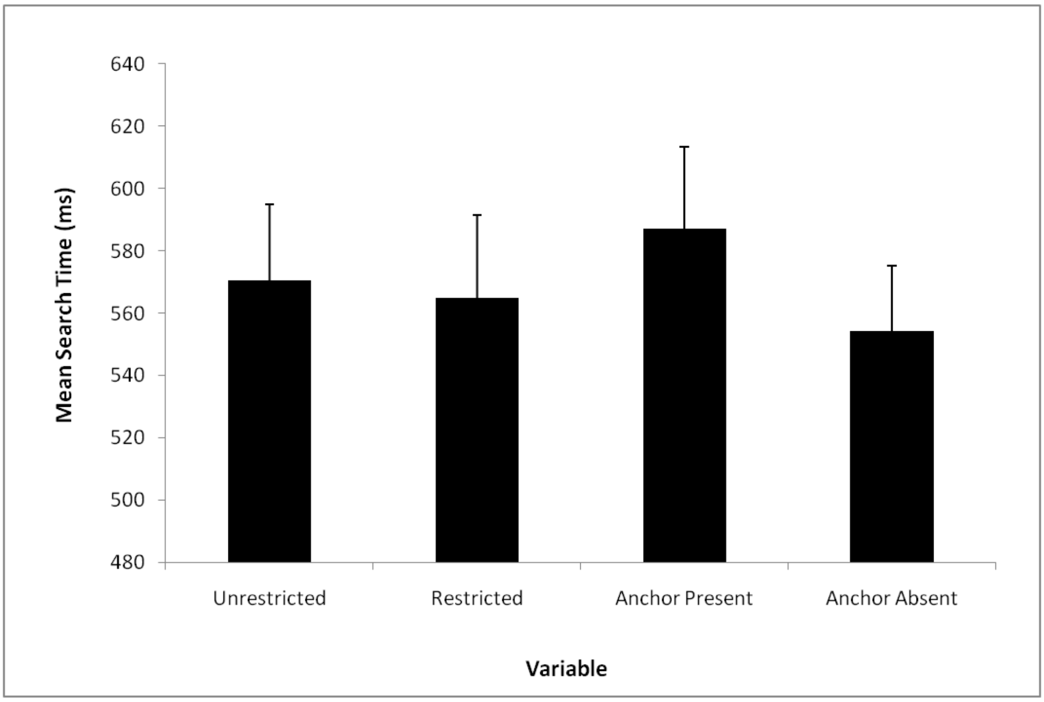


Figure 6. Mean search times (ms) to target present trials in the four conditions in Experiment A2. Error bars represent the standard error (+ 1SE).

Effect of Spatial Constraint

In order to compare the effect of spatial constraint of target location on search times, the data from the two conditions where the target location was unrestricted (Unrestricted Anchor Present and Unrestricted Anchor Absent) were averaged together and compared with the corresponding restricted conditions (Restricted Anchor Present and Restricted Anchor Absent). As can be seen from Figure 6 there is little difference between the average search times to unrestricted displays (M = 570.6, SD = 84.4) and restricted displays (M = 565.0, SD = 92.2). Indeed, the main effect of Spatial Constraint was not statistically significant (p = .748). This therefore suggests that participants took the same amount of time to locate the target irrespective of the distance from the fixation point that it was presented.

Effect of Anchor Presence

To get an overall measure of the effect of anchor presence on search times, the two conditions where the anchor was present (Unrestricted Anchor Present and Restricted Anchor Present) was averaged together, as were the two conditions where the anchor was not present (Unrestricted Anchor Absent and Restricted Anchor Absent). It was found that search times when the anchor was present (M = 587.0, SD = 90.9) were slower than search times in trials where the anchor was absent (M = 554.3, SD = 73.2). Furthermore, the man effect of Anchor Presence was statistically significant, $F(1,11) = 8.55$; $p < .05$.

The interaction between Spatial Constraint and Anchor Presence was not significant (p = .557).

Experiment A2 Summary

Experiment A2 found that search times were not affected by spatial constraints imposed on the location of the target, suggesting that participants took the same amount of time to locate targets irrespective of the distance from the fixation point that they were presented. Conversely, search times were affected by the presence of an anchor in the display, specifically; response times were slower when the anchor, in the form of two distractors positioned very close together, was included. This pattern of results mirrors the observation in Experiment A1 that the allocentric searches, which included an anchor, were slower than the egocentric searches where the anchor was not present.

The findings from Experiment A2 further the interpretation of the findings of Experiment A1 and can be used in two ways. Firstly, they offer an explanation of why search times to the egocentric searches were faster than those to allocentric searches. It is thought that this difference is explained by the omission of an anchor in the egocentric searches. It is possible that in the allocentric searches participants treated the anchor as a second target and that this slowed down search times for the real target. Secondly, the findings will be used to guide the construction of visual search stimuli in future experiments. It is clear that in order to directly compare allocentric searches, in which an anchor is required to define the frame of reference, with egocentric searches, where an anchor is not required, it is necessary to include the anchor in both searches in order to balance the visual characteristics of the two types of search.

Study A - Experiment 3

This experiment, like Experiment A1, compared the effect of repeating the location of a target defined in either an egocentric or an allocentric frame of reference; however, this experiment took into account the findings of Experiment A2. After observing speeded responses to egocentric searches in Experiment A1, Experiment A2 addressed reasons for this, and found that response times were significantly slower when the anchor was present in the search array. Therefore, in this current experiment the anchor that was required in the allocentric searches was also present in the egocentric search arrays. As before, in the allocentric searches the anchor provided predictive information over the target's location, while in the egocentric searches the anchor appeared at random positions relative to the target, and provided no predictive information over the location of the target. Furthermore, the possible target locations in both the allocentric and egocentric searches were constrained to an inner area within the whole array. Whilst this constraint was only necessary in the construction of the egocentric searches, to balance the stimuli as fully as possible, this restriction was also applied to the allocentric searches. Therefore, based on the findings of Experiment A2, in this third experiment both the presence of an anchor and spatial constraints of the position of the target are equivalent for the two priming conditions.

The aim of this current experiment was to determine the effect of repeating a target location defined in either allocentric or egocentric coordinates, with particular interest in whether there is a difference between the two.

Method

Participants

Twenty-two (16 female) participants took part in this experiment (age range 18 - 35 years, mean age 20.2).

Apparatus

The apparatus was the same as that used in Experiments A1 and A2.

Stimuli and procedure

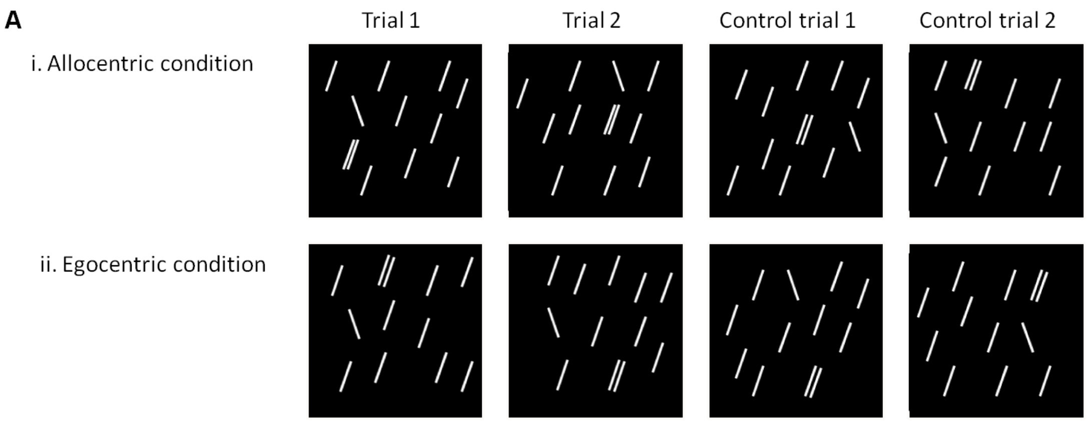
There were two priming conditions in this experiment: allocentric and egocentric. In the allocentric priming condition, as in Experiment A1, the location of the target was positioned relative to a salient item in the display (two distractors positioned very close together, known as the allocentric anchor) but at different positions relative to the observer. In the egocentric priming condition the target maintained the same absolute position relative to the observer but occupied different positions relative to the anchor. The stimuli configurations for the two priming conditions can be seen in Figure 7A (see also Figure 4B, page 58, for the placement of the search arrays onto the black backgrounds).

Procedure

The basic procedure is the same as that used in Experiment A1 with the following changes to the timing. After the initial presentation of the fixation cross for 1000 ms (font size 20, visual angle 0.9° vertically and 0.6 horizontally°, courier new, bold), a random letter was presented for 500 ms, followed by the re-presentation of the fixation cross for 200 ms. The blank screen at the end of each trial was presented for 500 ms. Therefore, there was a minimum of 2200 ms between two consecutive search displays. The trial sequences and timing can be seen in Figure 7B. The presentation timings of the fixation cross, letter, and end trial blank were shorter in this experiment compared to those used in Experiment A1 (see Figure 4C, page 58 for the timings used in Experiment A1). The presentation times were shortened in order to reduce the likelihood of participants making multiple fixations between the presentations of the letter and the fixation cross and the search array being presented. Reducing the overall time per trial also decreased probability of participants becoming fatigued.

To induce position-priming sequences of trials where a given target position was used 9 times within a given sequence were employed. Interspersed within a sequence there were also 2 control trials (the target stimulus was present but at a new position, examples of which can be seen in Figure 7B) and 4 target absent trials (the target stimulus was not present), thus each sequence consisted of 15 trials. For each priming condition 9 different sequences were used, thus a total of 135 trials were presented for each priming condition (81 present, 36 absent, and 18 control). The target stimulus was present in 73% of trials.

The experimental trials were divided into six blocks (three allocentric, three egocentric), with each block consisting of three sequences. The blocks alternated between allocentric and egocentric searches (half the participants started with an allocentric block). The experiment took approximately 30 minutes to complete.



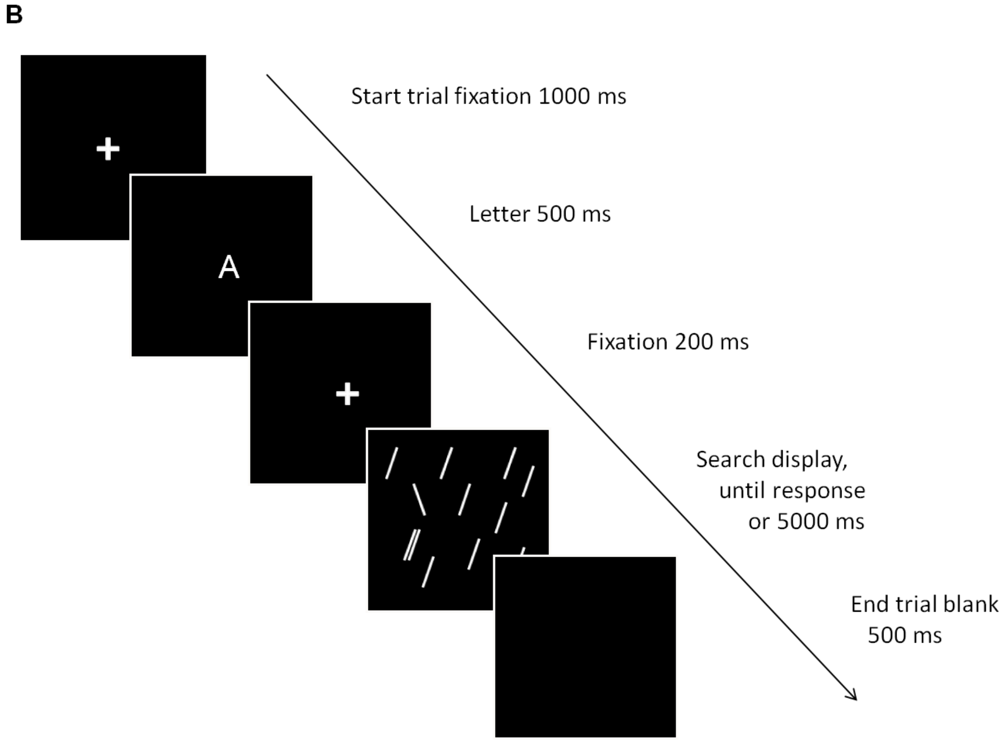


Figure 7. Priming conditions and trial sequence in Experiment A3.

(A). Schematic of the stimuli in the two priming conditions.

i) Allocentric priming condition. In trial 1 and trial 2 the target is above the anchor but it occupies different positions relative to the observer. In the allocentric control trials the anchor is present but it has no constant relationship with the target.

ii) Egocentric priming condition. When the egocentric position is repeated, the target occupies the same absolute position on the screen but it occupies a different location relative to the anchor. In the egocentric control trials the target occupies different absolute positions and has no fixed relationship with the anchor

(B). The sequence and timing of each trial.

Results

Accuracy

Participants were highly accurate in deciding whether the target was present or absent in the search array. Accuracy in absent trials was 96%, present trials 98%, and control trials 98%. The accuracy rates for the two priming conditions were the same (allocentric searches 98%, egocentric searches 97%, $p = .468$, Wilcoxon signed Ranks Tests as data could not be normalised using a log transformation).

Present, absent, and control trials

Search times to target absent trials ($M = 646.96$, $SD = 95.9$) were significantly slower than search times to target present trials ($M = 619.13$, $SD = 112.8$), $Z = -2.06$, $p < .05$, $r = -.440$ (Wilcoxon Signed Ranks Test). In order to compare search times to non-primed trials (control trials where the target was present but not at the given position for that sequence) with those to primed trials (where the target was at the same position as in a previous trials in the sequence), the first present trial of a sequence was categorised as a control trial[11]. It was found that search times to primed trials ($M = 616.65$, $SD = 114.0$), were significantly faster than those to non-primed trials ($M = 640.17$, $SD = 116.1$), $Z = -2.22$, $p < .05$, $r = .474$ (Wilcoxon Signed Ranks Test). This is an indirect measure of priming and was observed for both priming conditions (see Table 3).

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[11] Again, this is the only analysis of this experiment where the first present trial of a sequence is classified as a control trial.

Table 3. Mean Search Times (ms) to Present, Absent, and Control Trials in Experiment A3.

	Allocentric	Egocentric
Present	618.8 (103.4)	617.3 (131.7)
Absent	646.1 (95.1)	647.8 (102.7)
Control	633.6 (128.3)	646.7 (114.6)

Note. Standard deviations are shown in parentheses. For this data the first present trials of sequences were regarded as control trials.

Cumulative priming

Within each sequence of trials, the target was at a given position 9 times; this data is presented in Figure 8. The data, normalised using the log function, was subjected to a 9 x 2 repeated measures ANOVA with the factors Presentation Number (1 - 9) and Priming Condition (Allocentric, Egocentric). The ANOVA revealed a significant main effect of Presentation Number, $F(8,168) = 2.37$; $p < .05$; a non significant main effect of Priming Condition ($p = .944$); and a significant interaction between Presentation Number and Priming Condition, $F(8,168) = 2.09$; $p < .05$.

Figure 8 shows that overall search times decreased between the first presentation and the ninth presentation of a target position in a sequence. Post-hoc tests, in the form of a repeated measures ANOVA for each priming condition, revealed that the main effect of Presentation Number was significant in the egocentric priming condition, $F(8,168) = 2.64$; $p < .025$, but not in the allocentric priming condition ($p = .114$).

To generate an overall index of the priming effect, the absolute differences between search times to the first present trial of a sequence and the ninth present trial of a sequence was calculated for each priming condition. In the egocentric priming condition the mean reduction between the first and ninth presentation of a target location was 42.68 ms (*SD* = 107.75); however, this difference was marginally non significant (*p* = .057). In the allocentric condition there was an average reduction of 11.96 ms (*SD* = 60.34) between the first and last trial of a sequence, and this difference was not statistically significant (*p* = .473).

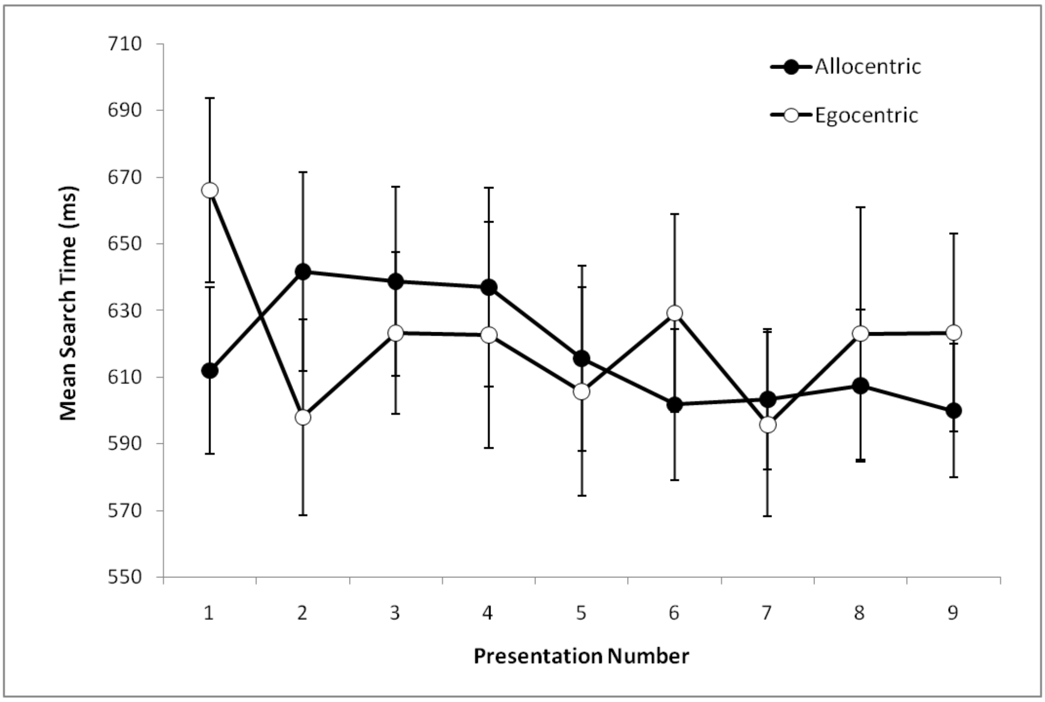

Figure 8. Mean search times (ms) to target present trials as a function of presentation number in Experiment A3. Error bars represent the standard error (+ / - 1 SE).

Six present trials of a sequence

As with the analysis of Experiment A1, the effect of Presentation Number for only the first six trials of a sequence will now be considered. This data can be observed in Figure 8. Again the data was subjected to a repeated measures ANOVA (normalised data), with the factors Presentation Number (1 - 6) and Priming Condition (Allocentric, Egocentric). The ANOVA revealed a non significant main effect of Presentation Number (*p* = .117); a non significant main effect of Priming

Condition (p = .848); and a significant Priming Condition by Presentation Number interaction, $F(5,105) = 3.22$; $p < .05$.

Post-hoc tests, in the form of a repeated measures ANOVA for each priming condition, revealed that the main effect of Presentation Number was significant in the egocentric priming condition, $F(5,105) = 3.11$; $p < .025$, but not in the allocentric priming condition (p = .112). In the egocentric condition the difference was 36.84 ms (SD = 108.9), again non significant (p = .096, paired samples t-tests). In the allocentric priming condition there was a mean reduction of 10.18 ms (SD = 74.7) between the first target present trial and the sixth target present trial of a sequence, and this difference was not statistically significant (p = .499).

First present trials of sequences and blocks

On inspection of Figure 8 it can be seen that the search times to the first target present trial in the egocentric condition (M = 666.04, SD = 129.2) are slower than those in the allocentric condition (M = 611.95, SD = 117.1), a difference of 54.09 ms, which is statistically significant, $t(21) = 2.20$; $p < .05$. This therefore makes any direct comparison between allocentric and egocentric conditions complicated. However, in order to assess whether this difference in search times is the result of a real difference between the searches, it is necessary to consider only those trials that are truly free from any frame of reference information, that is, the first present trial of the first sequence of a block. When looking at the data from only these trials, search times to egocentric searches (M = 707.0, SD = 148.8) are slower than those in the allocentric condition (M = 683.23, SD = 196.7), a difference of 23.77 ms which was not statistically significant, Z = .80; p = .426 (Wilcoxon Signed Ranks test).

Experiment A3 Summary

Unlike Experiment A1, the stimuli used in the two priming conditions in this experiment were equivalent in terms of the presence of the anchor and the restricted area in which the target could be located. As a result the main effect of priming condition was not significant in this experiment. Furthermore, when only the first target present trials of a block were compared for each frame of reference there was no difference between them. Therefore, as a result of the adjustments to the stimuli configurations that were made in accordance with the findings of Experiment A2, the stimuli for the two priming conditions have been balanced, both in terms of their visual characteristics and the speed at which participants require to process the search arrays.

This experiment observed a significant reduction in search times when the location of the target was repeated relative to the observer (egocentric priming condition); however, when the location of the target was repeated relative to the salient item in the display, namely, the allocentric anchor, priming was not observed. There was a minimum delay of 2200 ms between the presentation of two consecutive search displays; therefore, the observation that the priming effect for targets defined in an egocentric frame of reference built up over a number of trials, which were interspersed with target absent and control trials, suggests evidence of memory for egocentric representations being present in this experiment.

Each sequence of trials contained 15 trials (9 target present trials, 4 target absent trials, and 2 control trials). Owing to the high number of trials in each sequence, the number of different sequences that could be presented without making the experiment too long, and thus introduce fatigue effects, was limited. It is felt that in future spatial priming experiments the number of trials within a sequence should be reduced as this would allow more sequences to be presented. Reducing the number of repetitions of a target location is supported by the analysis performed in this experiment. The first analysis of cumulative priming effects assessed all 9 repetitions of a target location, while the second analysis only considered the first 6 repetitions. There was little difference in the priming effects between the two analyses; therefore, it is justified that in the experiments that follow the number of presentations of a target location will be reduced.

A final methodological point related to the number of trials in a sequence is that some of the priming effects were approaching significance; for example, while the main effect of presentation number was statistically significant in the egocentric priming condition for both the 9 and 6 target present trial analyses, the absolute difference between search times to the first and ninth/sixth present trials of a sequence were only approaching statistical significance. It is felt that a greater number of trials for each presentation number of a sequence would enable more valid statistical analysis.

The aim of Experiment A3 was to investigate the effect of repeating the location of a target in terms of either its position relative to the observer (egocentric condition) or its position relative to a landmark in the search array (allocentric condition). It was of particular interest whether priming for targets defined in egocentric coordinates would be observed. The finding of significant egocentric cumulative priming has implications for Milner and Goodale’s (1993, 1995, 2006) perception-action model which argues that egocentric representations are highly transient. Extensive discussion of how the findings from Experiment A3 fit with the perception-action model will follow; however, a further question will be addressed first.

While Experiment A3 evaluated allocentric and egocentric priming effects separately, it is of interest to investigate which of the two is responsible for driving spatial priming effects when both frames of reference are available at the same time. By assessing separate allocentric, separate egocentric, as well as the combined allocentric-egocentric priming effects, it will be possible to add to the conclusions of existing research. Maljkovic and Nakayama (1996) compared the effect of repeating the allocentric information of a target's location with the effect of repeating both the allocentric and egocentric information. They observed that although the priming effect appeared to be marginally larger when egocentric information was added, as they did not evaluate egocentric priming in isolation Maljkovic and Nakayama (1996) could only speculate about the relative contributions of allocentric and egocentric information to the overall priming effects. Therefore, the effect of repeating both the target's location relative to the observer and the target's location relative to the allocentric anchor are compared with the effect of repeating each one separately.

Study A - Experiment 4

In Experiments A1 - A3, participants were required to report the identity of a centrally presented letter prior to the presentation of the search array. This was to ensure that participants were always fixating at the centre of the screen, and not at some other location, before the search array was presented. Experiment A4 was a pilot study to evaluate the effectiveness of this part of the trial at ensuring participants had to foveate the letter in order to be able to accurately report its identity. If indeed it was necessary for participants to foveate the letters to be able to report them, it is possible to be confident that participants were not lingering at the location of the previous target at the start of each trial. If participants' gaze was lingering at the location the previous target was presented in this would impact search times and influence the true priming effects.

Method

Participants

Twelve participants (7 female) took part in this pilot study (age range 24 - 49 years, mean age 31.9).

Apparatus

The apparatus was the same as used in the previous experiments.

Stimuli and procedure

The stimuli used in this pilot experiment were different to those used in Experiments A1 - A3. First, a single green backslash was presented for 2000 ms.

This was presented at one of two locations: near the centre of the screen or far from the centre of the screen (see Figure 9 for examples of the two presentation locations).

There were two eye movement conditions: allowed and not allowed, and the trial procedure was slightly different for the two. In the eye movements allowed condition, after the presentation of the green backslash, a fixation cross was presented at the centre of the screen for 1000 ms (font size 12, visual angle 0.4˚ vertically and 0.3 horizontally˚). This was replaced with a random letter, which was presented for 500 ms (6 participants used font size 8, visual angle 0.2˚ vertically and 0.2˚ horizontally, and 6 participants used font size 10, visual angle 0.3˚ vertically and 0.2˚ horizontally). After the offset of the letter, a blank screen was presented for 500 ms before the next trial started. In this condition, participants were required to fixate on the green line only when it was presented and were free to make eye movements to the centre of the screen to read the letter. The trial procedure for this condition (eye movements allowed) is shown in Figure 9A.

Conversely, in the eye movements not allowed condition, the green line remained on the screen throughout the presentation of the cross and the letter. Participants were required to maintain fixation on the green line for the entirety of the trial and attempt to report the identity of the letter without making any eye movements. This condition is shown in Figure 9B.

Participants completed 40 trials: 20 trials where eye movements were allowed and 20 trials where eye movements were not allowed. Within each condition, in 10 trials the target line was presented near the centre of the screen and in 10 trials the target line was located far from the centre of the screen. The order of trials was counterbalanced across participants. The experiment took approximately 20 minutes to complete.

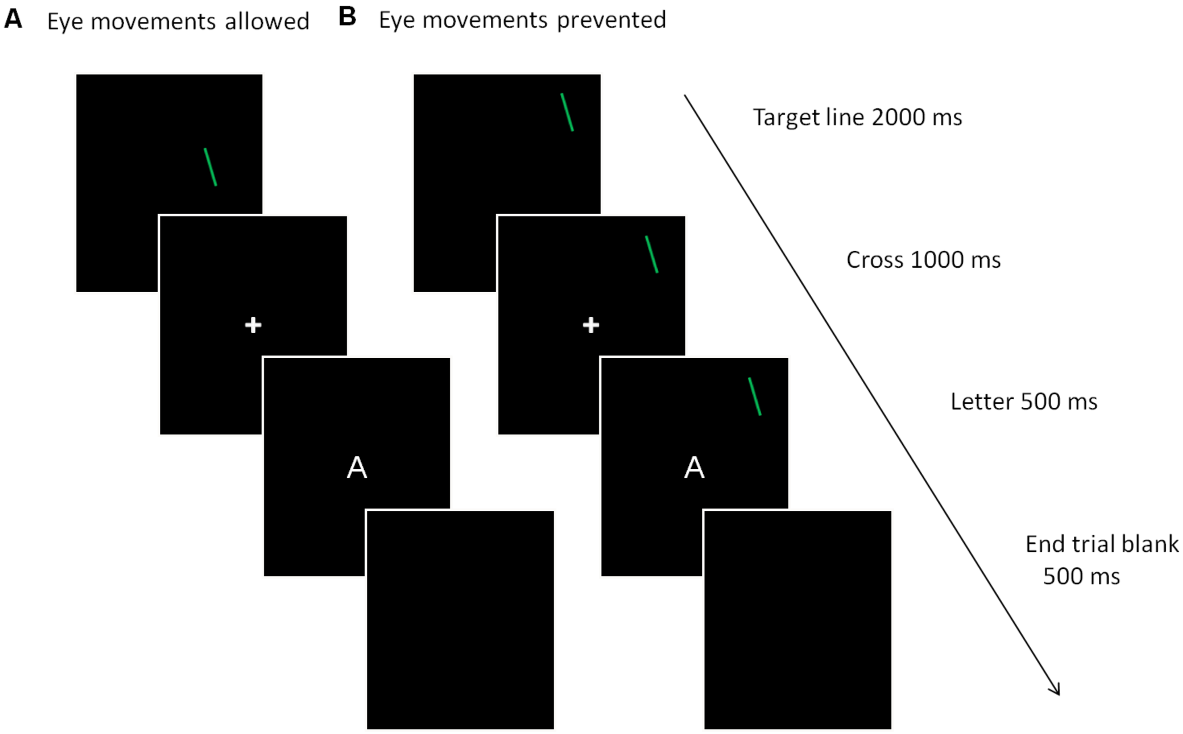

Figure 9. Trial sequence and timings in Experiment A4.

Results

The dependent measure in this pilot study was participant's accuracy at reporting the identity of the letters. Figure 10 shows the average percentage of letters correctly reported when eye movements were allowed and when eye movements were not allowed across the different conditions. The accuracy of reporting letters of font sizes 8 and 10 were very similar, so the data was combined[12].

It can be seen from Figure 10 that the accuracy of reporting the identity of central presented letters is affected by whether eye movements are allowed or not: letter accuracy decreased when eye movements to the letter were not allowed for both near and far lines. Using Wilcoxon Signed Ranks tests (data could not be normalised) a statistically significant difference between accuracy in the not allowed far condition (M = 20.83%, SD = 14.4) and allowed far condition (M = 91.67%, SD = 14.7) was found, $Z = -3.07$; $p < .05$, $r = -.627$. Furthermore, a statistical difference was also observed in the near condition: not allowed near (M = 66.67%, SD = 21.9) and allowed near (M = 100%, SD = 0.0), $Z = -3.08$; $p < .05$, $r = -.627$.

Overall, accuracy when eye movements were not allowed (M = 43.75%, SD = 15.4) was significantly lower than when eye movements were allowed (M = 95.83, SD = 7.3), $Z = -3.07$, $p < .05$, $r = -.626$. This can be seen in Figure 11.

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[12] The accuracy between the two font sizes was not statistically significant for any of the four conditions (Allowed Far $p = .256$; Not Allowed Far $p = .341$; Allowed Near = no variation; Not Allowed Near $p = .806$, Wilcoxon Signed Ranks tests).

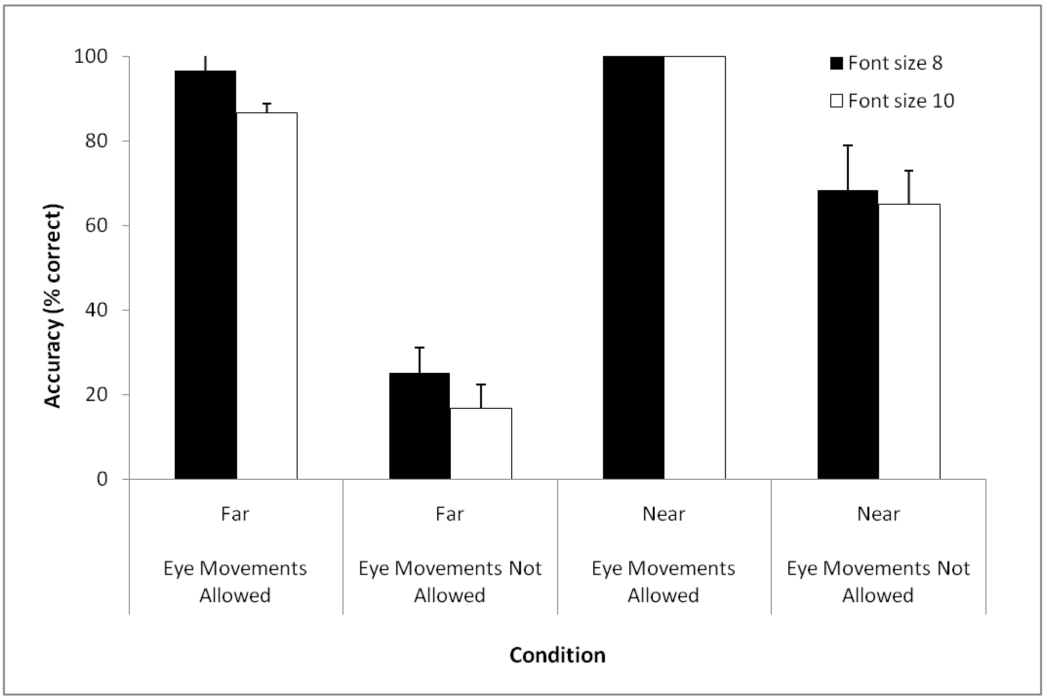

Figure 10. Average number of letters correctly identified (%) across the different conditions in Experiment A4. Error bars represent + 1 standard error.

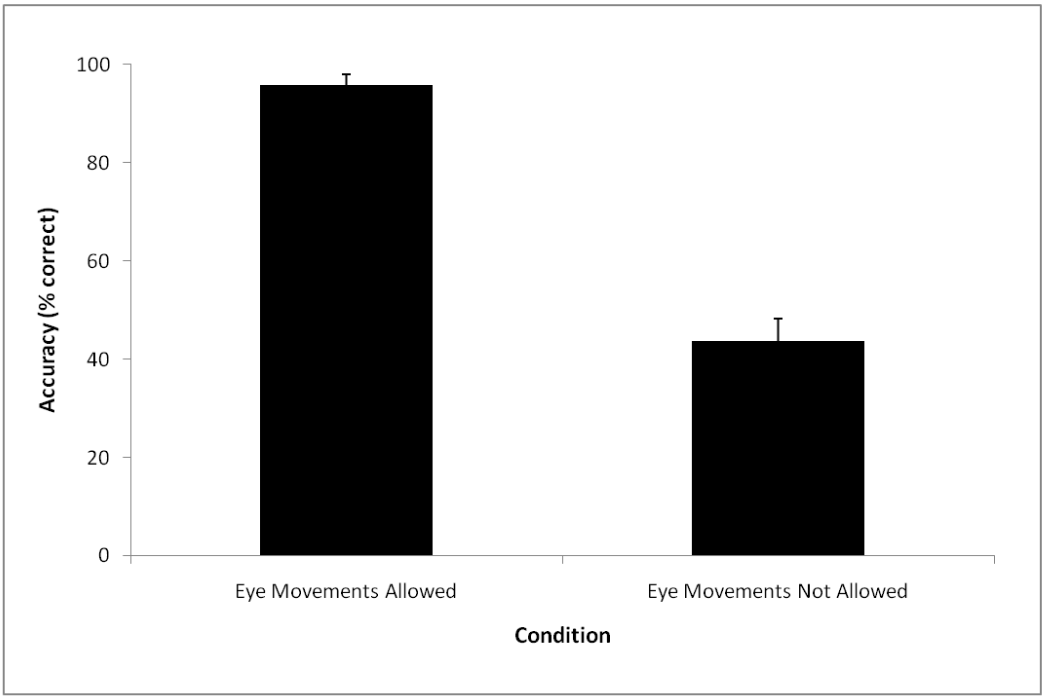

Figure 11. Average number of letters correctly identified (%) when eye movements were allowed and not allowed in Experiment A4. Error bars represent + 1 standard error.

Experiment A4 Summary

This pilot study sought to evaluate letter reading accuracy when participants foveated (allowed condition) and when they did not foveate (not allowed condition) the letter to be reported. It was found that letter reading accuracy fell below 50% when participants were not allowed to foveate the letter. In Experiments A1 - A3 the presentation of a letter was included, which participants had to report, before each visual search array was presented. This was a design consideration to ensure that participants would be required foveate the letter, and thus not be able to linger at the location of the previous trials, in order to be able to correctly report the letter. Experiment A4 has shown that this is indeed the case: accuracy of letter reading decreased significantly when participants were not allowed to foveate the letter.

A major limitation of this pilot experiment was that eye movements were not monitored throughout the trials. With the use of eye tracking equipment it would have been possible to ensure that participants did maintain fixation on the green line in the eye movements not allowed condition. However, it is thought that owing to the difference in accuracy of letter reporting in the two conditions, participants were not fixating on the letter in the not allowed condition, otherwise no difference between the two conditions would have been observed. In all future visual search experiments, trials where the participant fails to correctly report the identity of the letter will be removed from the subsequent analysis. As an additional control, participants will be required to select the smallest font size that they can read at the adopted observer distance.

Study A - Experiment 5

Experiment A5 was designed to investigate the spatial priming effects in the visual search paradigm when both allocentric and egocentric coordinates provide information about target location, and to compare these combined priming effects with purely allocentric and purely egocentric priming effects. This experiment aimed to extend the findings of Maljkovic and Nakayama (1996) who compared priming for targets defined in allocentric position with those defined in combined allocentric and egocentric coordinates. However, Maljkovic and Nakayama (1996) could only speculate as to the relative contribution of egocentric information as they did not formally test egocentric priming on its own.

Method

Participants

Thirty naïve participants (24 female) took part in this experiment (age range 18 – 49 years, mean age 21.4).

Apparatus

The apparatus was the same as that used in Experiments A1 - A3.

Stimuli

As in all the previous experiments (with the exception of pilot Experiment A4) each trial consisted of two sets of stimuli. First, a letter was presented at the centre of the screen. Participants had to foveate this letter and report its identity. In Experiment A4 it was established that for letters of a small font size, accuracy of letter identification dropped below 50% when participants had to fixate on a position other than the position at which the letter was presented. Furthermore, based on the findings of Experiment A4, participants selected the smallest font size that they could read at the adopted observer distance. The font sizes used varied between 8 and 14 (corresponding to visual angles 0.2˚ vertically and 0.2˚ horizontally, and 0.5˚ vertically and 0.4˚ horizontally, respectively). As an additional control, those trials where participants failed to correctly report the letter were removed from the data analysis.

During the second part of a trial the search array was presented, consisting of white lines on black backgrounds, as in previous experiments (A1 – A3). There were 3 types of priming conditions: Allocentric, Egocentric, and Combined (i.e. combining allocentric and egocentric information, see Figure 12).

In the allocentric priming condition the location of the target was positioned relative to the landmark (in both trial 1 and trial 2 the target stimulus is above the anchor) but the target has different positions relative to the observer (i.e. relative to the fixation point). In the egocentric priming condition, the target maintained the same position relative to the observer but occupied different positions relative to the landmark[13]. In the combined priming condition, the target occupied the same location relative to the observer and had the same relationship with the landmark. Finally, in the control condition neither the target position relative to the landmark nor the absolute target position, were repeated in trials 1 and 2.

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[13] See Figure 4B (page 59) for examples of search array placement onto the black backgrounds.

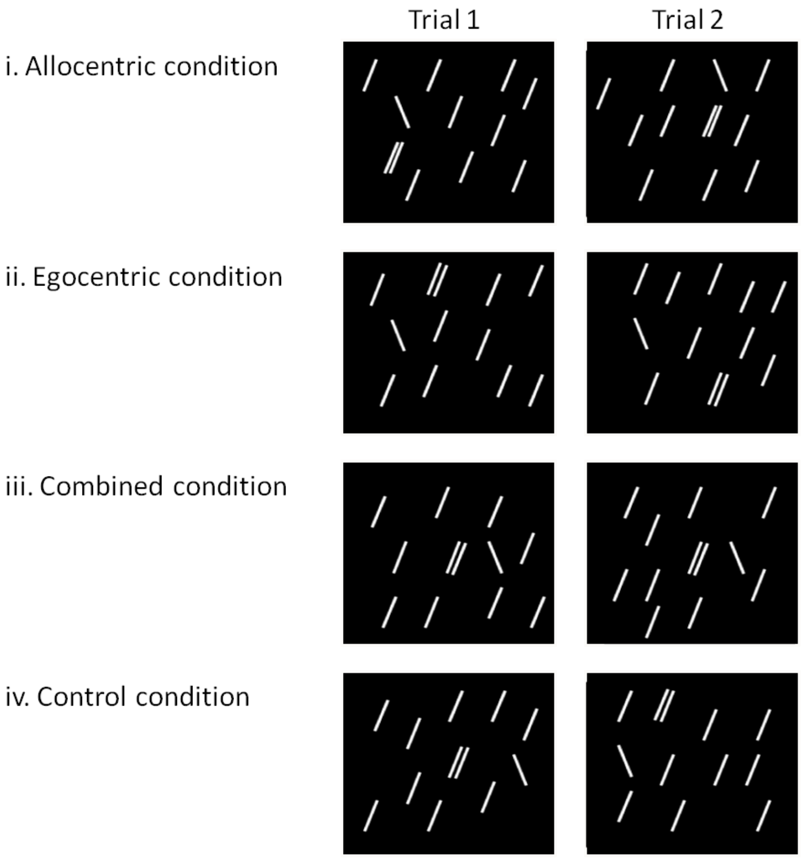

Figure 12. Priming conditions in Experiment A5.

i) Allocentric priming condition: in trial 1 and trial 2 the target stimulus is above the anchor but at different absolute positions.

ii) Egocentric priming condition: when the egocentric position is repeated, the target occupies the same absolute position on the screen, but has no constant relationship with the anchor.

iii). Combined allocentric-egocentric priming condition: when the combined position is repeated the target has the same relationship with the anchor and the same absolute position.

iv). Control condition: neither the relative target position or the absolute target position are repeated between trials 1 and 2.

Procedure

The trial sequence and timings used in this experiment are the same as those used in Experiment A3 (see Figure 7B, page 76), meaning that there was a minimum of 2200 ms between two consecutive search displays. To induce position-priming sequences of trials where a given target position was used 6 times within a given sequence were included. Interspersed within a sequence there were also 2 control trials (the target stimulus was present but at a new position, see Figure 12) and 2 target absent trials (the target stimulus was not present). Thus, each sequence consisted of 10 trials, and the target stimulus was present in 80% of trials. In previous experiments (A1 and A3) there was very little difference between the priming effects over the first six trials of a sequence and over nine trials of a sequence; therefore, it was decided that in this current experiment fewer repetitions of each target position within a sequence would be presented. This would allow a greater number of target positions to be presented which would increase the statistical power of the design.

For each priming condition, 20 different sequences were used, with a new priming position being used for each sequence, thus, a total of 200 trials were presented for each priming condition. These trials were divided into 4 blocks of 50 trials (each block contained 5 sequences). Three priming conditions were used; therefore, a total of 12 blocks, or 600 trials, were completed by each participant. Both the order of sequences within each block and the order of the blocks were randomised across participants; however, the same priming condition was never used twice in a row. The experiment took approximately 50 minutes to complete.

Results

Analyses

The first analysis of the data from this experiment is concerned with the immediate priming effects and involved performing a repeated measures ANOVA, with the variables Priming Condition (Allocentric, Egocentric, Combined) and Repetition (First present trial, Second present trial). This was followed by post-hoc t-tests evaluating the immediate priming effects for each frame of reference. The cumulative priming effects were then evaluated with a global ANOVA (Priming Condition: Allocentric, Egocentric, Combined; Presentation Number: 1 - 4). Simple effects analyses, in the form of an ANOVA for each priming condition, were then performed. Paired samples t-tests followed up the main effect of Priming Condition and the Presentation Number by Priming Condition interaction.

Letter reporting

For each participant the smallest font size they could read when fixating on it was established prior to the experimental trials (8 participants used font size 8; 17 used font size 10; 4 used font size 12; 1 used font size 14). The accuracy of letter reporting was recorded during the experimental trials and was 99.4% across all participants, indicating that subjects fixated correctly at the beginning of each trial. Trials where the letter was incorrectly reported were not included in the analyses (this resulted in the exclusion of 116 trials out of 18000 trials).

Accuracy

Participants were highly accurate in their responding to the visual search stimuli (present trials 99% correct, absent trials 94% correct, and control trials 98%

correct). Accuracy was the same across the three priming conditions: 97% correct ($p = .085$, Friedman's test was used as the data could not be normalised). Trials where participants responded incorrectly (369 out of 18000 trials) or were response time outliers (responses more than two standard deviations above or below the mean) were removed (1016 trials out of 17631 correct trials were classed as outliers).

Present, absent, and control trials

Search times to target absent trials ($M = 594.73$, $SD = 71.6$) were significantly slower than those to target present trials ($M = 502.44$, $SD = 56.4$), $t(29) = 5.14$; $p < .05$. Search times to primed trials (where the target was presented at the same position as in a previous trial in the sequence, $M = 496.89$, $SD = 55.9$) were faster than those to non-primed trials (where the target was present but not at the given position for that sequence[14], $M = 541.7$, $SD = 67.4$), $t(29) = 2.68$; $p < .05$. This speeding for primed trials relative to non-primed trials is an indirect measure of priming and was observed for all three priming conditions (Table 4).

Table 4. Mean Search Times (ms) to Present, Absent, and Control Searches in Experiment A5.

	Allocentric	Egocentric	Combined
Present	506.1 (59.4)	505.6 (62.2)	479.8 (52.8)
Absent	593.7 (74.5)	602.0 (78.0)	588.5 (69.0)
Control	545.8 (70.7)	547.8 (73.2)	531.5 (66.3)

Note. Standard deviations are shown in parentheses. For this data the first present trials of sequences were regarded as control trials.

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[14] For this analysis, and only for this analysis, the first present trial of each target sequence was classed as a control trial.

Immediate priming effects

Figure 13 compares the search times to the first two present trials of a sequence when they directly followed one another (i.e. when there were no intervening target absent or control trials). The first of these trials is the first presentation of a target position. A 2 x 3 repeated measures ANOVA with the factors Repetition (First present trial, Second present trial) and Priming Condition (Allocentric, Egocentric, Combined) revealed a main effect of Repetition, such that search times were faster on the second presentation of a target position, $F(1,29) = 80.42$; $p < .05$. There was also a significant main effect of Priming Condition, $F(2,58) = 7.41$; $p < .05$; and a significant Repetition by Priming Condition interaction, $F(2,58) = 9.66$; $p < .05$.

Post-hoc analysis, in the form of paired samples t-tests, revealed that the speeding in search times between the first and second present trials of a sequence when they directly followed one another was statistically significant in both the Egocentric priming condition, $t(29) = 6.78$; $p < .017$, with a mean reduction of 39.97 ms between the two trials, and the Combined priming condition, $t(29) = 6.64$; $p < .017$, with a reduction of 33.65 ms. The difference was not significant in the Allocentric priming condition ($p = .217$), reduction of 6.92 ms.

Further analysis (post-hoc t-tests) of the Repetition by Priming Condition interaction revealed that it was driven by significantly greater immediate priming for the Egocentric and Combined conditions compared to the Allocentric condition (Egocentric vs. Allocentric: $t(29) = 4.00$; $p < .017$; Combined vs. Allocentric $t(29) = 3.71$; $p < .017$). There was no difference between the Egocentric and Combined conditions ($p = .460$). Figure 13 illustrates this interaction.

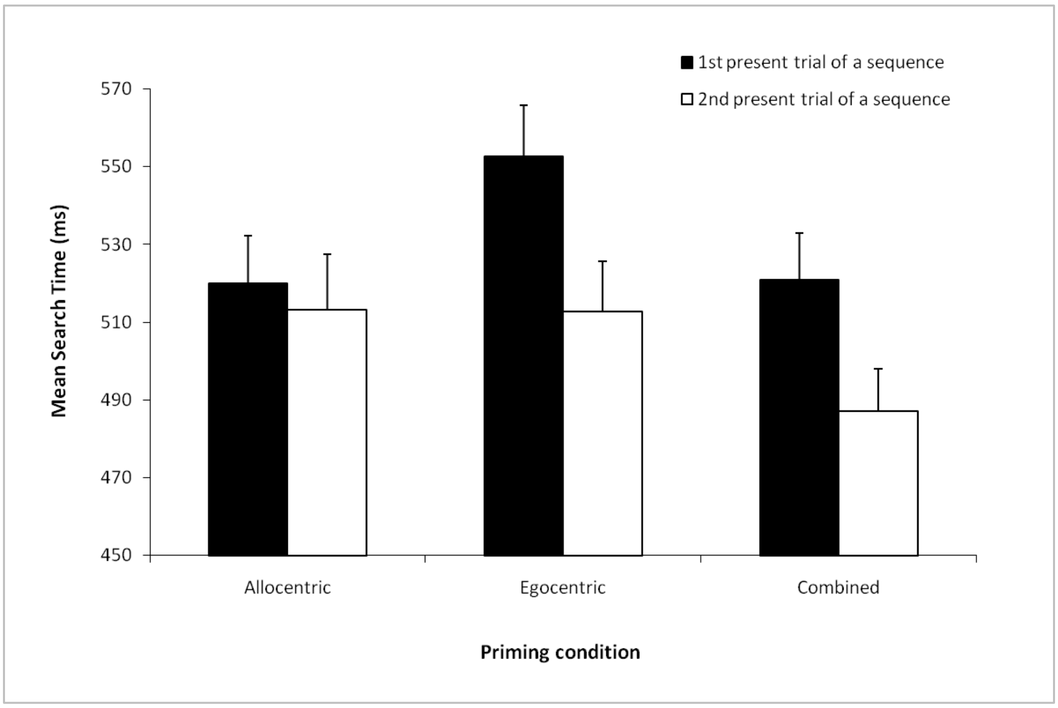


Figure 13. Mean search times (ms) to the first two target present trials of a sequence when they directly followed each other in Experiment A5. Error bars represent +1 standard error.

Cumulative priming effects

Within each sequence of trials, the target stimulus was at a given position 6 times. Figure 14 shows the search times to each of the 6 presentations of a target position for the three priming conditions. This data violated the assumption of normality and was normalised using the log function. Reaction time data were subjected to a 6 x 3 repeated measures ANOVA with the factors Presentation Number (1 - 6) and Priming Condition (Allocentric, Egocentric, Combined). The ANOVA revealed a statistically significant main effect of Presentation Number, $F(5,145) = 51.82$; $p < .05$; a main effect of Priming Condition, $F(2,58) = 20.88$; $p < .05$; and a Priming Condition by Presentation Number interaction, $F(10,290) = 4.07$; $p < .05$.

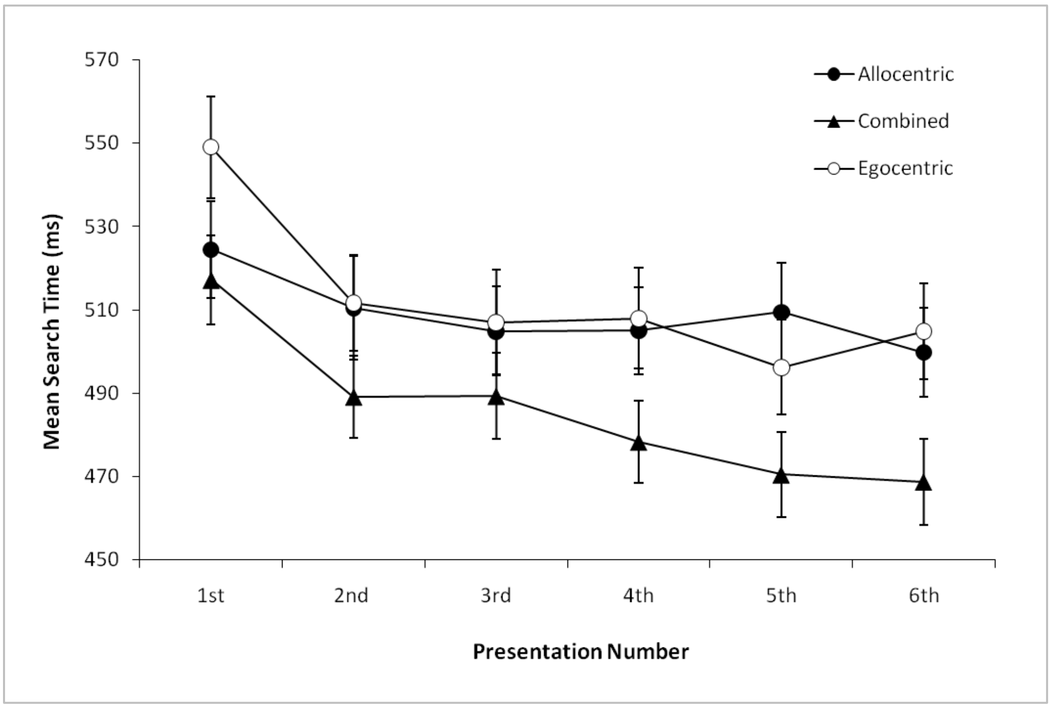


Figure 14. Mean search times (ms) to target present trials as a function of presentation number in Experiment A5. Error bars represent +/- 1 standard error.

Figure 14 shows that search times decreased between the first target present trial and the sixth target present trial of a sequence. Post-hoc tests, in the form of a repeated measures ANOVA for each priming condition, revealed the main effect of Presentation Number was statistically significant for the Allocentric condition, *F*(5,145) = 5.78; *p* < .017; the Egocentric condition, *F*(5,145) = 23.68; *p* < .017; and the Combined condition, *F*(5,145) = 25.62; *p* < .017. Thus, there was a significant cumulative priming effect for all three priming conditions.

On the significant main effect of priming condition, post-hoc t-tests found that participants were faster to respond in the Combined condition than in both the Allocentric condition, *t*(29) = 5.11; *p* < .017, and the Egocentric condition, *t*(29) = 5.95; *p* < .017. There was no difference between search times to the Allocentric and Egocentric conditions (*p* = .485).

Finally, the interaction between Priming Condition and Presentation Number. The effect of cumulative priming was greater in the Egocentric condition (44.2ms reduction between the first and sixth presentations of a target position) and the Combined condition (48.4 ms reduction) compared to the Allocentric condition (24.7 ms reduction), $t(29) = 2.63$; $p < .017$, $t(29) = 2.95$; $p < .017$, respectively. There was no significant difference between the magnitude of cumulative priming for the Egocentric condition and the Combined condition ($p = .616$).

Experiment A5 Summary

Significant priming effects, both immediate and cumulative, were found when the egocentric coordinates of the location of the target were repeated from one trial to the next. Significant cumulative priming effects were also observed when the allocentric coordinates of the location of the target was repeated across trials. Whilst the minimum delay between two trials was 2200 ms, it was also observed that the priming effects were cumulative and built up over the six target present trials which were interspersed with target absent trials. Therefore, this data suggests that egocentric information can be stored for more than one or two seconds. Furthermore, it was found that when both egocentric and allocentric information combined to define the target location, the priming effect was not statistically different from when egocentric information alone defined the target location. This latter result suggests that the egocentric information made a greater contribution to the combined priming effect than the allocentric information.

Discussion of Study A

The aim of this series of experiments was to investigate location priming for targets defined in allocentric or egocentric coordinates (Experiments A1 and A3), and compare this with targets defined in combined allocentric–egocentric coordinates (Experiment A5).

Stimuli balancing and letter identification: Experiments A2 and A4

Two important methodological issues were considered in Experiments A2 and A4. The first of these was the inclusion of the allocentric anchor. In the allocentric priming condition, it was necessary to include a specific landmark in the search arrays which the target could be defined relative to; for example, the target was to the left of the anchor for all the trials in a sequence. The inclusion of this anchor, while in keeping with the other stimuli in the search array (two distractors placed close together) was found to increase search times in Experiment A2. Therefore, to enable valid comparisons between priming conditions, the allocentric anchor was included in all search arrays, regardless of whether it provided any predictive information about the location of the target.

The second methodological issue concerned the location of participants' gaze at the start of each trial. To prevent participants lingering at the location of the previous target, as this would distort the spatial priming effects, a letter identification task was introduced before the presentation of each search array, as it was believed that this would require participants to foveate the letter in order to correctly identify it. Experiment A4 found that when participants were not allowed to foveate the letter, accuracy of report fell to below 50%. Therefore, in Experiment A5 when participants failed to correctly report the letter it was assumed that they had not correctly fixated at the start of that trial, and the data from that trial was excluded from the analysis. Furthermore, participants were required to select the font size that was the smallest they could read at the adopted observer distance. In all future experiments trials where the letter is not reported correctly will not be included in the analyses.

Priming effects

Table 5 shows the priming effects, that is the absolute difference in search times between the first present trial and the last present trial of a sequence, across all experiments in Study A. Experiment A1 found significant cumulative priming effects, both in terms of the main effect of presentation number, as well as in terms of the absolute reduction in search times between the first present trial of a sequence and the last present trial of the same sequence, when the target occupied the same observer related position across trials (egocentric priming condition), and also when the target has the same position relative to the allocentric anchor (allocentric priming condition). The minimum period of time between the presentation of two consecutive search arrays was 3500 ms; therefore, this experiment provided the first indication that the egocentric information presented a few seconds before is still available. However, the comparison between the egocentric priming effects and the allocentric priming effects was complicated by an overall speeding of search times to the egocentric displays. As a result of the findings of Experiment A2 it is believed that this is explained by the absence of the allocentric anchor in the egocentric search arrays.

Table 5. Cumulative Priming Effects in Study A.

			Priming Condition		
	Sequence	Minimum delay (ms)	Body + Eyes	Body + eyes + Allocentric	Allocentric
Exp A1	9	3500	32.8		47.9
Exp A1	6	3500	26.2		51.2
Exp A3	9	2200	42.7 (ns)*		12.0 (ns)
Exp A3	6	2200	36.8 (ns)**		10.2 (ns)
Exp A5	6	2200	44.2	48.4	24.7

* *p* = .057 ** *p* = .096

In Experiment A3 the stimuli were balanced in terms of their visual characteristics: the allocentric anchor was present in the egocentric searches, although it provided no predictive information about the location of the target. A statistically significant main effect of presentation number was found in the egocentric priming condition; therefore, replicating the findings of Experiment A1, and suggesting memory for egocentric representations over a couple of seconds. However, in contradiction to the findings of Experiment A1, when the magnitude of the priming effects were calculated (i.e. the absolute difference between the search times to the first present trial of a sequence with the last present trial of a sequence), the difference only approached statistical significance in the egocentric condition. It is thought that one reason for this is that different number of trial sequences were used in the two experiments: in Experiment A1, 16 different sequences of a target position were used, whereas in Experiment A3, only 9 sequences were presented. Therefore, it is thought that insufficient data for each presentation number can explain the differences in the egocentric priming effects between the two experiments. Moreover, Experiment A3 failed to find any evidence of allocentric priming, and as the nature of the allocentric displays had not changed between Experiment A1 and Experiment A3, it is thought that this is again related to the reduced number of sequences in Experiment A3. Furthermore, in inspecting the magnitude of the priming effects in the different experiments in the first study, the reduction in search times with repetition is actually greater in Experiment A3 in the egocentric condition; however, the difference only approached significance (see Table 5 for Egocentric and Allocentric priming effects across all experiments). Table 5 also shows the priming effects when all nine present trials of a sequence were considered and when only the first six were. As there was little difference between them, and search times appeared to stabilise after five or six target present trials, the number of repetitions of a target location was reduced in subsequent experiments, and thus a greater number of target positions could be investigated.

Experiment A5 investigated whether allocentric or egocentric information, if either, makes the greater contribution to spatial priming effects when both frames of reference define the location of the target. No difference between the magnitude of the priming effects in the egocentric condition and those when both allocentric and egocentric information defined the location of the target was observed. Therefore, it was concluded that egocentric information is responsible for driving the spatial priming effects in the visual search paradigm being used. Experiment A5 was heavily controlled: the effectiveness of the secondary letter identification task prior to the onset of the search arrays had been assessed in Experiment A4, the visual attributes of the stimuli used in the three priming conditions were matched, and the number of different sequences that were used (20) provided a sufficient number of trials for each presentation number of a target location for statistical analysis.

Therefore, the findings of this experiment provided the strongest evidence from the first series of experiments that egocentric information is still available some seconds after its initial presentation.

Contrary to the predictions made by the perception–action model (Milner & Goodale, 1993, 1995, 2006), in Experiment A5 cumulative priming was observed for all three conditions. Surprisingly, egocentric information not only makes a contribution to the combined priming effect but that it seems to be more effective than the allocentric information. This was evident with the cumulative priming in the combined allocentric–egocentric condition being greater than the cumulative priming in the allocentric only condition. It is clear from these findings that egocentric information does contribute towards the priming effects. Furthermore, given that a minimum delay of 2200 ms separated trials in these experiments, and that the cumulative priming effect built up over six present trials, which were randomly interspersed with target absent and control trials, this observation is sufficient to reject the notion that egocentric information cannot be stored for more than one or two seconds.

At first glance, the results from Experiment A5 appear to contradict those of Maljkovic and Nakayama (1996); however, on more detailed inspection, it is only the conclusions, and not the findings, that seem to contradict each other. Maljkovic and Nakayama (1996) emphasize that the majority of priming seems to be produced by allocentric information but they did not formally test the contribution of egocentric information. Thus, their data cannot be used to draw conclusions regarding the relative contribution of egocentric information to spatial priming effects. Experiment A5 did include an egocentric only priming condition, and therefore provides direct information about the role of egocentric priming.

One plausible explanation for the surprising superiority of egocentric priming is that in the egocentric condition participants did not learn a specific observer-relative position but they simply learned that a specific saccade from the fixation point would bring them to the correct target location. Eye movements were not monitored, and therefore this possibility can neither be confirmed nor rejected. However, it is important to note that while such a strategy might possibly explain the later priming effects, it is unlikely that it can explain the early priming effects, in particular the substantial priming that occurred with the first repetition of target location (see Figure 14, page 98). The stimuli displays measured 35˚ horizontally and 27˚ vertically, with the search arrays appearing at variable locations within this area. It has been found that the accuracy of saccades is reduced for targets presented eccentrically compared to those presented centrally, and consequently more saccades are required to locate eccentric targets (Scialfa & Joffe, 1998). While eccentricity effects on saccade patterns and saccade frequency are greater in conjunction searches, they have also been observed in single feature searches like the search task presented here (Carrasco, Evert, Chang, & Katz, 1995; Carrasco, McLean, Katz, & Frieder, 1998; Viviani & Swensson, 1982). Therefore, during the first trial of a sequence participants may have used a sequence of saccades to finally home-in on the target, particularly if the target was located eccentrically, whereas on the second present trial of a sequence they may have gone straight to the target. In this case, what participants used was not the same eye movements, but the same observer-related position. This would therefore suggest that at the very least, the priming effect observed during the first trial in the egocentric priming condition indicates an ability to store such egocentric information for several seconds.

It might be suspected that participants in the egocentric condition possibly could also have used allocentric landmarks. However, the experimental design went to great lengths to ensure that no allocentric landmarks were available during the egocentric condition. The experiment was performed in semi-darkness, the search display was projected onto a blank wall, and thus apart from the search items no other visual information was available. It might also be argued that the delay used in this experiment was relatively short. However, a short delay was deliberately selected to test the hypothesis that the inability to store egocentric information can explain the effects that such short delays have on the control of visually guided movements. It should also be noted that 2200 ms was the minimum delay; in some cases the delay between subsequent presentations may have been longer, and in this context it is also interesting that a cumulative priming effect was observed that occurred over a number of subsequent trials, thereby spanning a much longer time-interval. However, it would be interesting to conduct further experiments with varying delay-intervals to plot the time course of the use of allocentric and egocentric spatial information in visual priming tasks.

One final observation that needs to be discussed is the finding that the response times for the first present trial in the egocentric conditions were longer than those for the allocentric or combined condition. One might suspect that the more pronounced reduction of response times with repetition (i.e. greater priming effect) that was observed for the egocentric condition might simply be a consequence of the longer initial response times. In this experiment a longer response time also meant a longer presentation time of the search display. This might explain why the target location provided at the first presentation of the egocentric condition might have been more memorable. This cannot be ruled out, and thus while it cannot be claimed that egocentric priming is more effective than allocentric priming, the observation that egocentric priming is effective can be held true. This conclusion is also supported by the finding of superior priming in the combined condition as compared to allocentric priming alone. In this case both accuracy rates and response times, especially at the first present trial of a sequence (see Figure 14) are comparable for the two conditions and a significantly greater priming effect for the combined condition was observed, presumably reflecting the added benefit of egocentric spatial information.

While these findings suggest that egocentric information can be used for location priming, it is not known which particular egocentric frame of reference was used. In this experiment eye-centred, head-centred, or body-centred spatial information could have been used. McKyton and Zohray (2008) tried to dissociate the coordinate systems in their study of perceptual learning in pop-out search. They found that there was no difference in visual search performance when the head-based coordinates of a target location shifted between the learning phase and the testing phase, thus suggesting that learning is not based on head-centred coordinates. However, the effects of changing the retinotopic coordinates of target position between the two phases were more variable. There was a cost to performance when target positions were shifted horizontally, suggesting perceptual learning of retinotopic coordinates; however, there was no difference when they were translated vertically by the same amount (McKyton & Zohray, 2008). Therefore, dissociating the different egocentric coordinates is of interest to establish what specific frame of reference is primed. In future experiments this could be achieved by either varying the eye-position or the head- or body-position across trials while maintaining a constant relationship between repeated target locations and the current position of either the eyes, the head, or the rest of the body. Such experiments would help to establish which of the different potential egocentric reference frames is most effective in driving location priming during visual search.

In conclusion, these findings suggest that both egocentric and allocentric information are used in spatial priming during pop-out visual search tasks. Given that such priming effects are driven by information which has been provided more than two seconds before, the findings seem to suggest that egocentric information can persist for more than two seconds. This conclusion is at odds with the assumption of the perception-action model (Milner & Goodale, 1993, 1995, 2006) that egocentric representations are of a highly transient nature. These findings also suggest that, contrary to the assumption of the perception-action model, egocentric spatial cues are not only useful for the visual guidance of action but also play a role in perceptual tasks. The studies presented in the following chapter address some of the issues that have been raised in this discussion.

Chapter 3 – Study B: Frames of reference in conjunction visual search

In Study A the target that participants were required to locate in the search array was defined in terms of its orientation: the target was a backslash amongst forward slashes. It is thought that this type of search is characteristic of a simple feature search (Wolfe, 1998a), also known as a ‘pop-out’ search. By using this search paradigm to investigate frames of reference, it was found that defining the location of a target in either egocentric or allocentric terms led to significant cumulative priming effects, that is, when the location of a target was repeated across trials, search times became speeded. Moreover, in Experiment A5, it was found that the cumulative priming effects when both allocentric and egocentric information predicted the location of a target at the same time, were not different from those observed when egocentric information alone predicted target location. Therefore, two main conclusions were formulated from the experiments presented in the previous chapter. First, that egocentric information is more relevant to spatial priming than allocentric information; and second, that the observation of priming over six present trials indicates that egocentric information can be stored for at least a few seconds which is at odds with the assumptions of the perception-action model (Milner & Goodale, 1993, 2006).

Experiment preview

A number of additional questions have been raised by the first series of experiments and these will be addressed by the experiments presented in the coming chapters. Study B sought to investigate the nature of the egocentric frame of reference in greater detail. This was achieved by disentangling a body-centred frame of reference from an eye-centred frame of reference. It was also of interest whether the egocentric priming effects observed in Study A can be found in other forms of visual search. Therefore, to investigate this, the following experiments employed a conjunction search paradigm, whereby the target was defined by a combination of features, namely orientation and colour.

Study B - Experiment 1

It is felt that before a conjunction search task can be employed to evaluate allocentric and egocentric priming effects, it is first necessary to ensure that the two search paradigms used in this thesis are characteristic of simple feature searches and more laborious conjunction searches respectively. It is generally agreed that when targets are defined by a conjunction of features, search times increase as the number of distractors increases; for example, for each item added to the search array, the search times increase by between 20 and 30 ms (Horowitz & Wolfe, 1998; Kristjansson, et al., 2002; Wolfe, 1998b). Conversely, when a single feature distinguishes the target from the distractors, search times are unaffected by changes in set size (Bravo & Nakayama, 1992; Sireteanu & Rettenbach, 1995). Accordingly, the first experiment of this study sought to compare the effect of set size in searches where targets were defined by either one feature (orientation) or two features (orientation and colour), and thus ensure that the paradigms developed demonstrate the characteristic patterns of search times which are consistent with the existing literature (Wolfe, 1998b).

The purpose of Experiment B1 was to compare the effect of set size on the feature search used in Study A with the effects on a conjunction search task.

Method

Participants

Twelve participants (9 female) took part in this experiment (age range 19 - 33 years, mean age 25.9).

Apparatus

The apparatus used was the same as described in the General Methods.

Stimuli

In this experiment two classes of search stimuli were used: stimuli for a basic feature search and stimuli for a conjunction search. In the basic feature searches the target was defined by orientation only, as in the experiments presented in Study A. The target was oriented at -20˚ from vertical (a backslash) while distractors were oriented at 20˚ from vertical (forward slashes). The search arrays consisted of white lines on black backgrounds and the total number of items in the search arrays varied between 5, 9, 13, and 17 item displays (see Figure 15A). In the target absent searches the target was substituted with a distractor. In all searches, the allocentric anchor (two distractor lines were placed together) that was used in the previous study was included. Although this landmark was not used to define target location in this experiment, it would be required in subsequent experiments; therefore, in order to obtain a valid index of search performance it was necessary to include the allocentric anchor in the search arrays in this experiment as well, as it was found that in Experiment A2 the presence and/or absence of the anchor affected search performance.

In the conjunction searches the target was defined by both orientation and colour. The target was a green backslash (-20˚ from vertical) amongst two types of distractors: green forward slashes (20˚ from vertical) and red backslashes. Again these stimuli were presented on black backgrounds. As in the feature searches, the number of items in the search arrays varied (5, 9, 13, and 17 items). In all conjunction searches two green distractors were placed close to each other to ultimately act as the allocentric landmark (see Figure 15A). In target absent trials, an additional green distractor (forward slash) was added to the display so that the number of red and green items in target present and target absent searches was the same.

As before, the stimuli were projected onto a blank wall and observed from a distance of 3 metres. The search arrays measured approximately 10˚ both horizontally and vertically. These were placed onto a black background so that the whole stimulus array measured 35˚ horizontally and 27˚ vertically.

Procedure

The basic procedure was the same as that used in the previous study except for the timing of the displays. First, a fixation cross was presented for 1000 ms, followed by a randomly selected letter, presented for 1000 ms. The fixation cross was then re-presented for 500 ms. The fixation cross and the letter were all presented in the centre of the screen, and were of 0.5˚ visual angle both vertically and horizontally, (courier new, bold) A visual search display was then presented, and following the participant's button press response, a blank screen was presented for 1000 ms before the next trial was initiated. Figure 15B illustrates the sequence and timing of each trial.

For each search type a total of 80 trials were presented, 20 of each set size (15 present trials and 5 absent trials, thus the target was present in 75% of trials). Participants completed two blocks of trials. The first block contained the feature searches and the second block contained the conjunction searches. The order of the 80 trials within each block was randomised between participants. The experiment took approximately 30 minutes to complete.

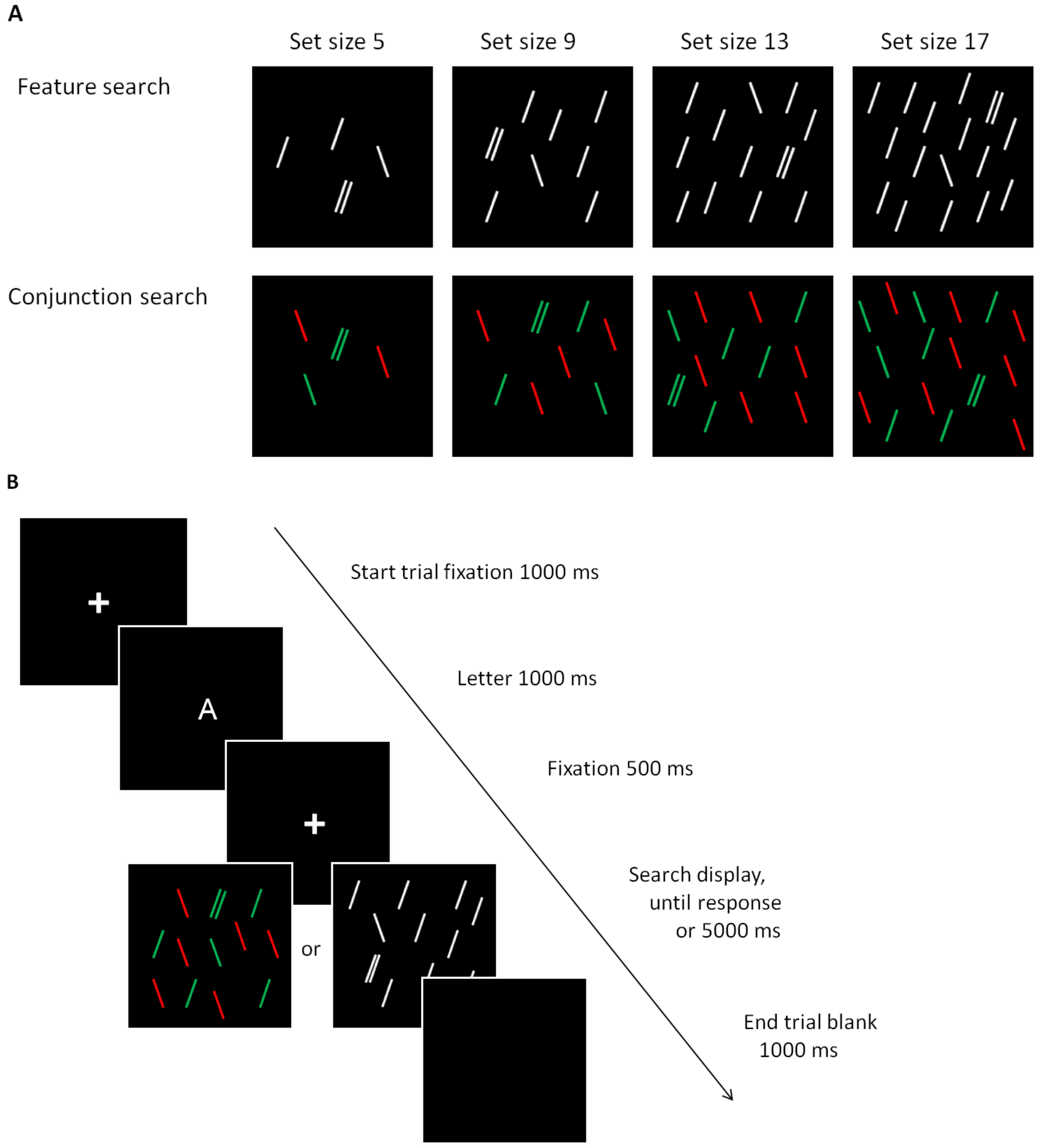


Figure 15. The two search types and trial sequence in Experiment B1.

(A). Schematic of stimuli for the search types and examples of the four set sizes.

(B). Sequence and timing of each trial.

Results

Analyses

A global ANOVA was performed on the data with the variables Search Type (Feature, Conjunction); Set Size (5, 9, 13, 17); and Target Presence (Target Absent, Target Present). Simple effects analyses, in the form of an ANOVA for each search type with the variable Set Size, were then performed.

Accuracy

Participants were highly accurate in their responses to the visual search stimuli (Feature searches: target present trials 97% correct, target absent trials 93% correct; Conjunction searches: target present trials 98% correct, target absent trials 84% correct). Overall, participants responded correctly on 96% of the Feature Searches and 93% of Conjunction searches. This difference was not significant (p = .088).

Present and absent trials

The data was subjected to a repeated measures ANOVA (normalised data) with the variables Search Type (Feature, Conjunction); Set Size (5, 9, 13, 17); and Target Presence (Target Absent, Target Present). This data is presented in Figure 16. The analysis revealed a statistically significant main effect of Search Type, $F(1,11) = 274.88$; $p < .05$, in that search times to Features Searches ($M = 560.86$, $SD = 160.8$) were faster than those to Conjunction Searches ($M = 1065.09$, $SD = 270.5$). The main effect of Target Presence was also statistically significant, $F(1,11) = 46.84$; $p < .05$, with search times to Target Absent searches ($M = 892.60$, $SD = 240.4$) being slower than those to Target Present searches ($M = 733.35$, $SD = 186.2$). Likewise, the main effect of Set Size was statistically significant, $F(3,33) = 77.30$; $p < .05$, such that search times increased as the set size increased (set size 5: *M* = 677.62, *SD* = 177.5; set size 9: *M* = 763.3, *SD* = 200.1; set size 13: *M* = 844.11, *SD* = 220.7; set size 17: *M* = 966.85, *SD* = 262.0). Of interest, the Search Type by Set Size interaction was statistically significant, *F*(3,33) = 38.09; *p* < .05.

Post-hoc comparisons were performed to further analyse this interaction. A repeated measures ANOVA, with the factor Set Size (5, 9, 13, and 17) when the target was defined by orientation only revealed that the main effect of set size was not significant (*p* = .256). It can be seen from Figure 16 that there was very little change in search times as the number of distractors in the search increased.

The same analysis was performed on the search times when the target was defined by both its orientation and its colour (the conjunction search condition). Unlike the orientation only searches, a main effect of Set Size for the conjunction searches was found, *F*(3,33) = 45.42; *p* < .025. It can be seen that search times increased as a function of set size for both target present and target absent searches.

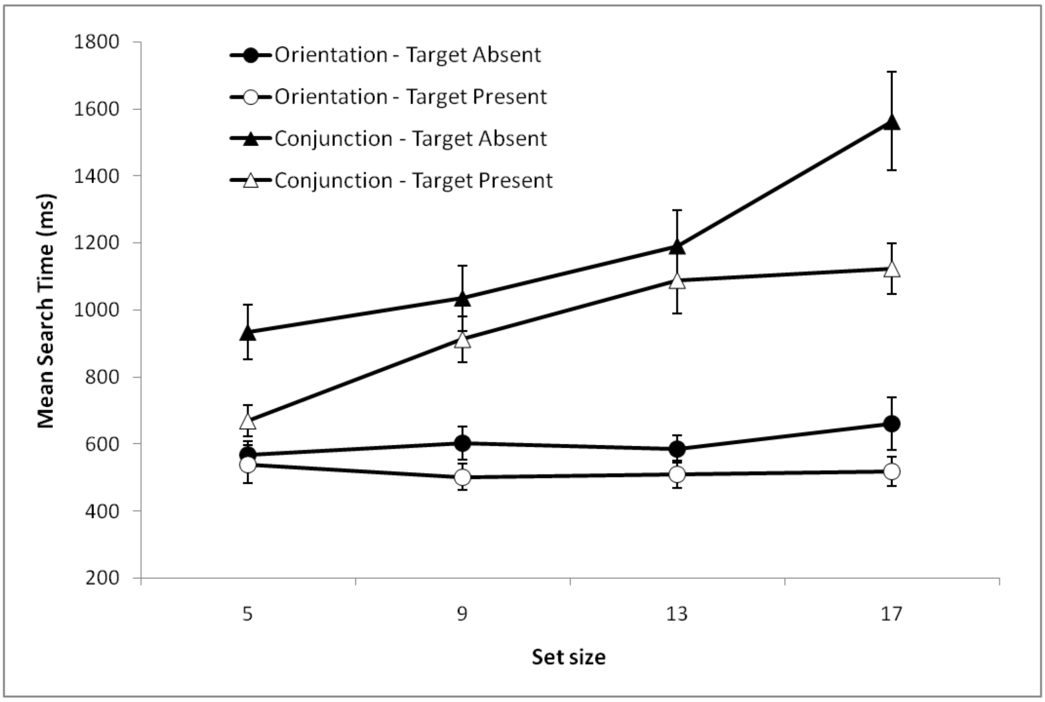


Figure 16. Mean search times (ms) for target present and target absent searches for feature and conjunction searches in Experiment B1. Error bars represent the standard error (+ / - 1 SD).

Experiment B1 Summary

This experiment found that the number of items in a search array differentially affected search times in the two types of visual search that participants were presented with. In the feature search condition, where the target was defined in terms of its orientation, search times were not affected by how many items were present in the search display (Bravo & Nakayama, 1992; Sireteanu & Rettenbach, 1995). Conversely, in the conjunction search condition, where the target was defined in terms of orientation and colour, the number of search items had a consistent effect on search times: search times increased as the number of items in as the number of distractors increased. This is in line with the existing literature (Horowitz & Wolfe, 1998; Kristjansson, et al., 2002; Wolfe, 1998b).

In summary, this experiment has found that the two search paradigms that have been developed are differentially affected by the number of items in the search array (i.e. the set size). This therefore suggests that different search mechanisms are likely to be involved in completing the search for the target (Duncan & Humphreys, 1989, 1992; Wolfe, et al., 1989). The findings from this experiment support the assumption that the paradigm where orientation alone defines the target is a simple feature search, and the paradigm where orientation and colour both define the target is a conjunction search. The following experiments use the conjunction visual search paradigm developed here.

Study B – Experiment 2

Experiment A5 evaluated whether egocentric information contributes to the spatial priming effect in a feature search task, allowing some information about whether egocentric information can be stored to be provided. It was observed that when the egocentric coordinates of the location of the target were repeated from one trial to the next, with a minimum delay of 2200 ms, there were significant priming effects. The priming effects were also found to be cumulative, building up over six present trials, interspersed with target absent trials, which is in line with the existing literature (for example, Huang, et al., 2004; Kristjansson, et al., 2002). Therefore, using the findings from Experiment A5, the notion that egocentric information cannot be stored for more than one or two seconds was rejected.

Experiment A5 however did not identify which specific egocentric reference frame was used for spatial priming. The two possibilities are that subjects used a retinotopic reference frame or a body-centred reference frame. Since the fixation position was always the same (i.e. centre of the screen), a repeated target’s location remained constant with respect to both the fixation position and the rest of the observer’s body. As a consequence, it was not possible to disentangle the effects of retino-centric and body-centric frames of reference. In Experiment B2 these two reference frames are examined separately and in combination. To achieve this, an allocentric priming condition and three different egocentric priming conditions were used: eye-centred, body-centred, and body- and eye-centred. In the eye-centred condition, the location of the fixation spot changed between trials, and the position of the repeated target changed accordingly to ensure that its position relative to the current fixation position remained constant. In the body-centred condition, the fixation position also varied between trials, but the position of the target was repeated. This meant that the target position was repeated relative to the body but changed relative to the position of the eye at the beginning of the trial. This condition also allowed another question which the previous experiment left unanswered to be addressed. During the egocentric condition in Experiment A5, participants might have used the same saccade to foveate targets in trials where the target location was repeated, and this might have accounted for their shorter response times during those trials. In this current experiment such a strategy would be possible in the eye-centred condition but not in the body-centred condition, since in the latter condition the position of the target relative to the fixation spot differs between trials, meaning that for each trial the amplitude and direction of the target-foveating saccade will have to be computed *de novo*. Thus, it is possible to compare the priming effect in the eye-centred condition with that in the body-centred condition, allowing evaluation of the extent to which the priming effect is determined by the occulomotor strategy described above. The final condition combined the body-centred and eye-centred reference frame. To achieve this, the fixation position remained constant across trials, meaning that if the position of the target remains the same relative to the body, it also remained the same relative to the fixation position. This condition was effectively the same as the egocentric condition used in Experiment A5.

If body-centred information is the more important frame of reference of the two, there should be little difference between priming in the body-centred condition and priming in the body- and eye-centred condition. Likewise, if eye-centred information is the most relevant, then the eye-centred and body- and eye-centred priming effects should be similar

One further aim of Experiment B2 was to investigate whether egocentric priming effects could also be found in other forms of visual search. Therefore, the conjunction search paradigm that was used in Experiment B1 was used here (i.e. the target was defined by a combination of features, i.e. orientation and colour) to extend the previous findings, which were obtained with a simple feature search paradigm (i.e. the target was defined by a single feature, namely orientation).

Method

Participants

Twenty seven participants (5 male) took part in this experiment (age range 18 – 28 years, mean age 21.0).

Apparatus

The apparatus used was the same as described in the General Methods.

Stimuli

As in Study A, two sets of stimuli were presented in each trial. First a letter was presented which participants were instructed to report the identity of. The font sizes used varied between 8 and 16 (corresponding to visual angles 0.3˚ and 0.7˚ respectively). For each participant it was established that for letters of such a small font size, accuracy of letter identification dropped below 20% when they fixated on any location other than the location at which the letter was presented.

During the second part of a trial a search array was presented. The search arrays were the same as those presented in Experiment B1; however, in this experiment all the search arrays consisted of 13 lines. In target present trials there were 12 distractors (6 red backslashes and 6 green forward slashes) and one target (a green forward slash), and in target absent trials there were 13 distractors (6 red backslashes and 7 green forward slashes), thus there were the same number of red and green items in present and absent displays (6 red, 7 green). In all search arrays, two green distractors were placed close together and acted as a landmark for the allocentric priming condition (see Figure 17A).

The stimuli were projected onto a blank wall and were observed from a distance of 2.2 metres. The search arrays measured approximately 20˚ both horizontally and vertically. These were placed onto black backgrounds so the whole stimulus display measured 50˚ horizontally and 40˚ vertically.

There were four priming conditions: Allocentric, Egocentric-Body, Egocentric-Eyes, and Egocentric-Body-Eyes Combined (see Figure 17A). In the allocentric (A) condition the location of the target was positioned relative to the landmark but at different positions relative to the observer's body and the fixation spot. In the egocentric-body (EB) condition the target maintained the same position relative to the observer's body but it occupied different positions relative to the landmark and the fixation spot. In the egocentric-eyes (EE) condition the target maintained the same position relative to the fixation spot, while occupying different locations relative to the landmark and the observer's body. In the egocentric-body-eyes combined (EBE) condition, the target occupied the same location relative to both the observer's body and the fixation spot, but at different positions relative to the landmark. In this condition it was necessary that the fixation spot stayed in the same location for all the trials of a particular sequence. Figure 17C shows examples of the placement of the search arrays on the black backgrounds.

Procedure

The trial procedure was similar to that used in the previous study. A fixation cross was presented for 1000 ms, a letter presented for 500 ms before the fixation cross was again presented for 500 ms. Next, the search display was presented, and once participants had pressed a response button, the projected display went blank for 500 ms and the next trial was initiated. Thus, there was a minimum of 2500 ms between two consecutive search displays. The trial procedure is shown in Figure 17C.

The target stimulus was present in 71% of trials. To induce position-priming, sequences of trials, where a given target position was presented 5 times within a given sequence, were designed. Interspersed within a sequence there were also 2 target absent trials, thus each sequence consisted of 7 trials. For each priming condition there were 20 different sequences, with a new priming position being used for each sequence, making a total of 140 trials per priming condition (100 present, 40 absent). The experimental trials were divided into 5 blocks, with each block containing 4 sequences (28 trials) of each priming condition (the 28 trials were grouped together, with a 3 second blank screen separating the different priming conditions). The orders of the priming conditions within a block, and the order of the blocks, were randomised across participants.

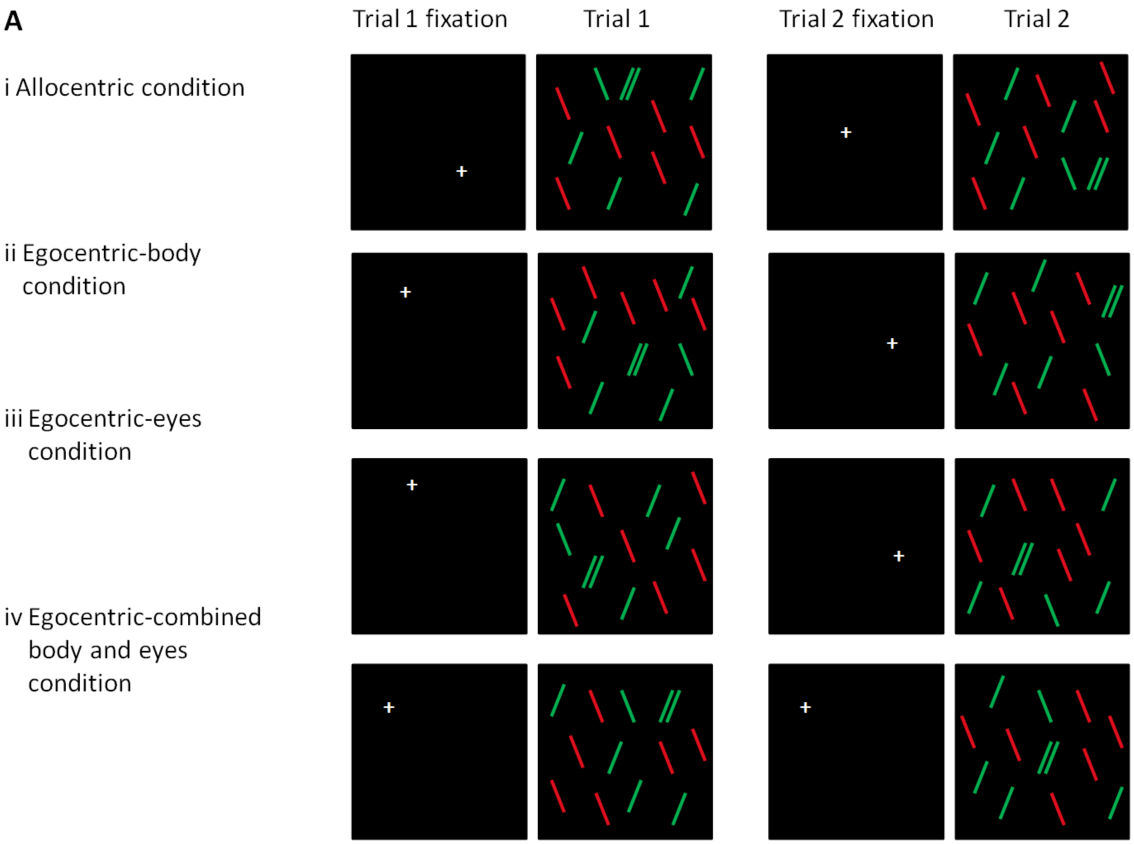


Figure 17. Priming conditions and trial sequence in Experiment B2.

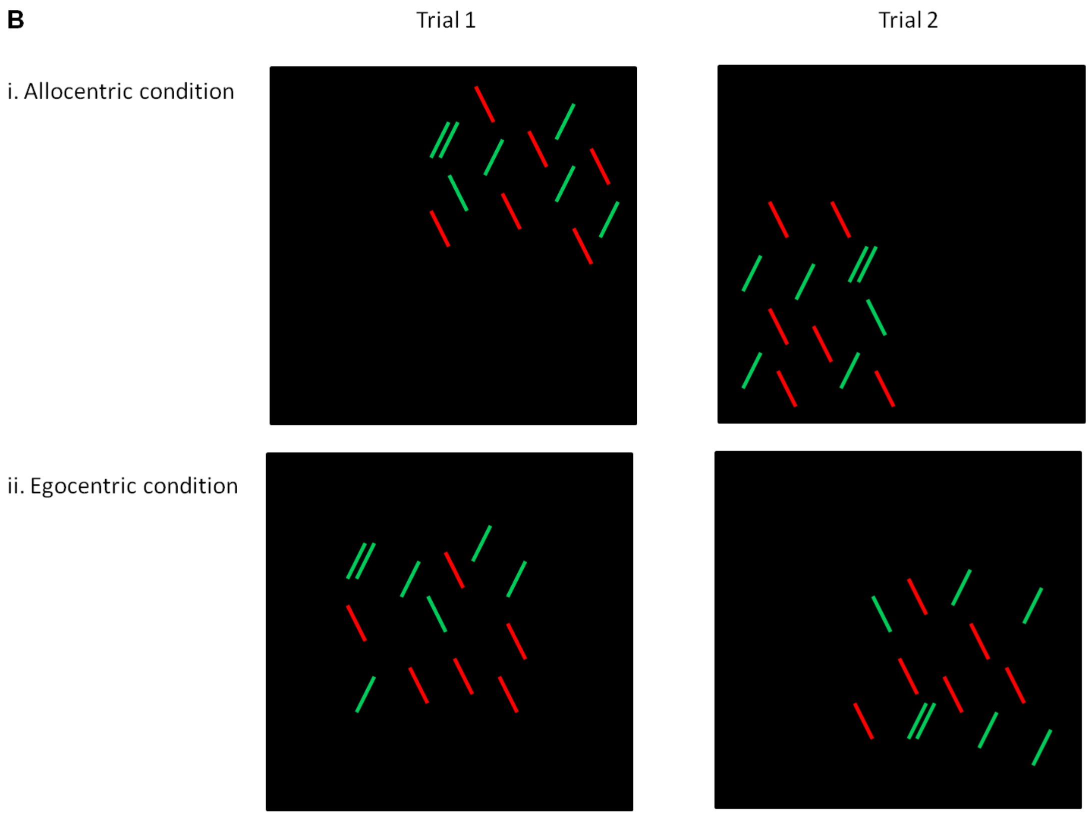
(A). Priming conditions in Experiment B2. Please note the target stimulus is a green, backward slash.

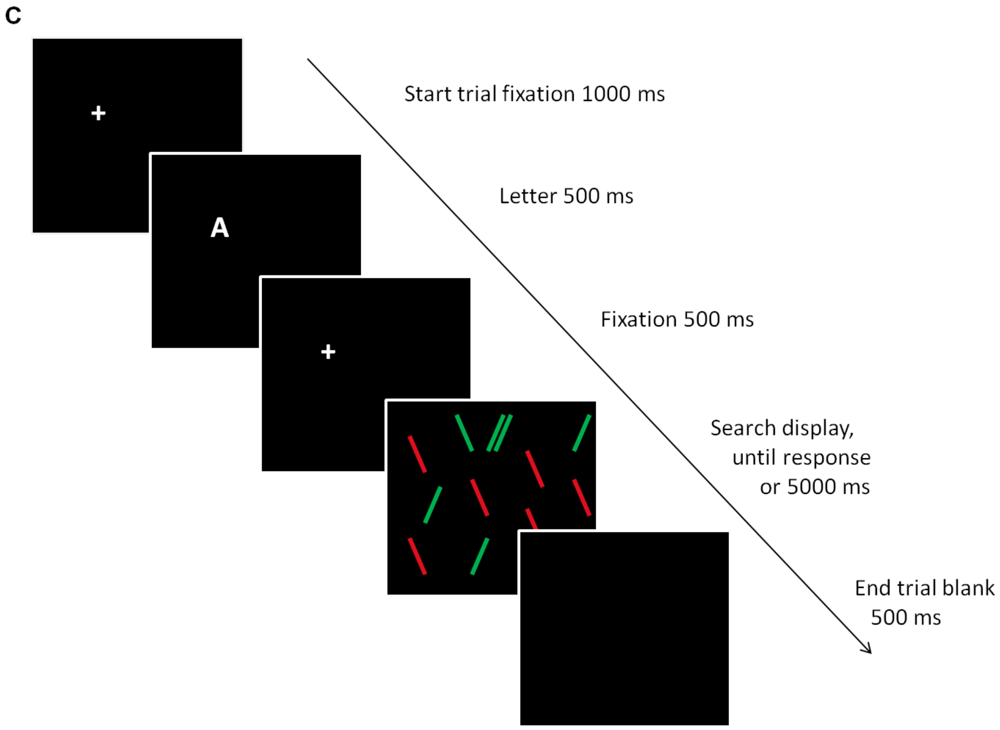
i) Allocentric (A) priming condition. In trial 1 and trial 2 the target is to the left of the anchor but it occupies different positions relative to the observer and the fixation spot.

ii) Egocentric-body (EB) priming condition. When the egocentric body position is repeated, the target occupies the same absolute position on the screen, but it has no constant relationship with either the anchor or the fixation spot.

iii). Egocentric-eyes (EE) priming condition. The position of the target relative to the fixation spot is the same in trial 1 and trial 2 but the target has a different position relative to the anchor and the observer's body.

iv). Egocentric- body and eyes combined (EBE). The target occupies the same absolute position on the screen and has the same location relative to the fixation spot. The target has no relationship with the location of the anchor.





(B). Schematic of the placement of allocentric and egocentric search arrays on the black backgrounds.

(C). Sequence and timing of each trial in Experiment B2.

Results

Analyses

The first analysis of the data from this experiment is concerned with the immediate priming effects and involved performing a repeated measures ANOVA, with the variables Priming Condition (Allocentric, Egocentric-Body, Egocentric-Eye, Egocentric Body-Eye) and Repetition (First present trial, Second present trial). This is followed by post-hoc t-tests evaluating a) the immediate priming effects for each frame of reference and b) the speed of responses in each priming condition. The cumulative priming effects were then evaluated with a global ANOVA (Priming Condition: Allocentric, Egocentric-Body, Egocentric-Eye, Egocentric Body-Eye; Presentation Number: 1 - 5). Simple effects analyses, in the form of an ANOVA for each priming condition, were then performed, and paired samples t-tests were used to compare search times to the first and last target present trials of a sequence for each priming condition. Finally, Wilcoxon Signed Ranks tests compared the magnitudes of the priming effects between the priming conditions.

Letter Reporting

For each participant the smallest font size they could read when fixating on it was established prior to the experimental trials (8 participants used font size 8; 9 used font size 10; 2 used font size 12; 4 used font size 14; 4 used font size 16). The accuracy of letter reporting was recorded during the experimental trials and was 99.4% across all participants, indicating that subjects fixated correctly at the beginning of each trial. Trials where the participant failed to report the letter correctly were not included in the analysis (this resulted in the removal of 93 out of 15120 trials).

Accuracy

Participants were highly accurate in their responding to the visual search stimuli (present trials 93% correct, absent trials 92% correct, thus 654 trials out of 15120 trials were incorrect). Trials that were classified as outliers (search times more than two standard deviations above or below the mean) were also removed (665 trials out of the 14466 correct trials were classed as outliers and removed).

Present and absent searches

Search times to target absent trials (*M* = 1083.31, *SD* = 363.7) were significantly slower than those to target present trials (*M* = 901.02, *SD* = 284.2), *t*(26) = 10.13; *p* < .05 (normalised data). This was observed in all four priming conditions (see Table 6).

Table 6. Mean Search Times (ms) to Present and Absent Searches in Experiment B2.

	Present	Absent
Allocentric	858.7 (272.4)	1063.8 (360.8)
Egocentric – Body	915.8 (305.3)	1108.6 (389.4)
Egocentric – Eyes	956.5 (307.2)	1094.8 (384.8)
Egocentric – Body and Eyes Combined	873.1 (260.3)	1066.1 (329.4)

Note. Standard deviations are shown in parentheses.

Immediate priming effects

Figure 18 compares the search times to the first two present trials of a sequence when they directly followed one another (i.e. when there were no intervening absent trials). A 2 x 4 repeated measures ANOVA (normalised data) with the factors Repetition (First present trial, Second present trial) and Priming Condition (A, EB, EE, EBE) revealed a significant main effect of Repetition, $F(1,26) = 10.88$; $p < .05$, such that search times were faster on the second presentation of a target position, a significant main effect of Priming Condition, $F(3,78) = 16.36$; $p < .05$, and a significant Repetition by Priming Condition interaction, $F(3,78) = 7.51$; $p < .05$.

Post-hoc tests (2-tailed t-tests) revealed that the difference in search times between the first presentation and the second presentation of a target location was only significant in the EBE condition, $t(26) = 5.15$; $p < .0125$, with a mean reduction of 97.46 ms (EB: $p = .288$, reduction of 19.69 ms; EE: $p = .130$, increase of 12.73 ms; A: $p = .132$, reduction of 24.70 ms). This suggests that the interaction between Repetition and Priming Condition was driven by significantly greater priming in the EBE condition compared to the other conditions (EBE vs. A: $Z = -2.64$; $p < .016$, $r = -.359$; EBE vs. EE: $Z = -3.27$, $p < .016$, $r = -.445$; EBE vs. EB: $Z = -2.81$, $p < .016$, $r = -.382$). Figure 18 illustrates this interaction.

With regards to the significant main effect of Priming Condition, post-hoc tests (2-tailed t-tests) revealed that participant’s responses were faster in the A condition compared to the other three priming conditions (A vs. EBE: $t(26) = -4.60$; $p < .008$; A vs. EB: $t(26) = -4.52$; $p < .008$; A vs. EE: $t(26) = -7.50$; $p < .008$). Search times to the three egocentric priming condition were not different from one another (EBE vs. EB: $p = .273$; EBE vs. EE: $p = .011$; EB vs. EE: $p = .109$).

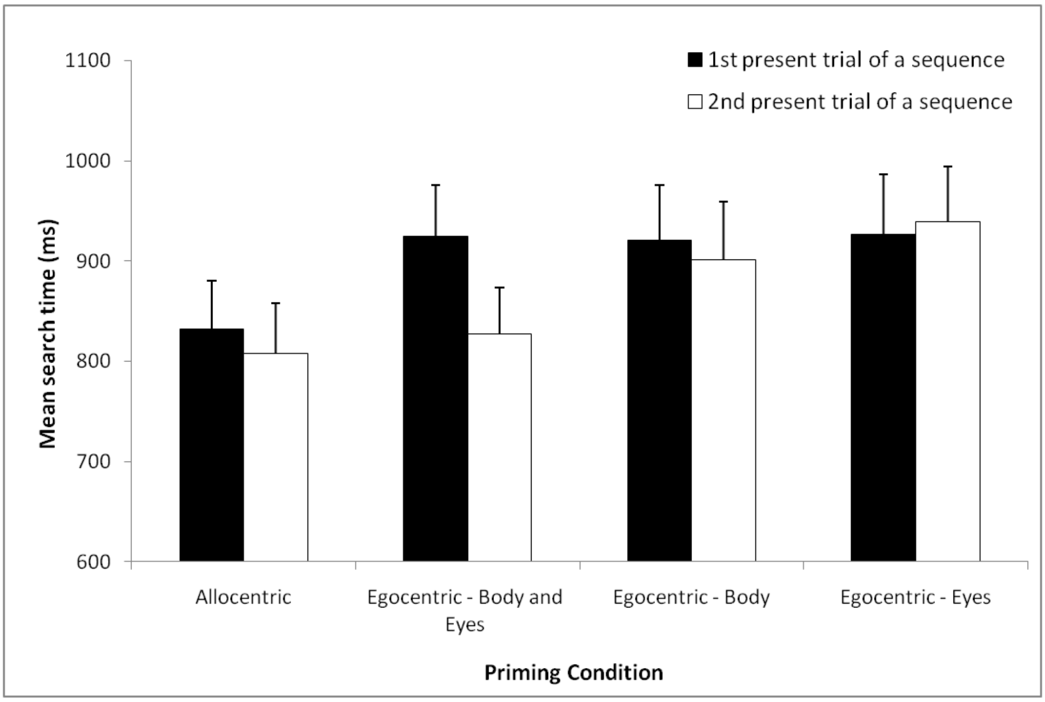


Figure 18. Mean search times (ms) to the first two target present trials of a sequence when they directly followed each other in Experiment B2. Error bars represent the standard error (+1 SE).

Cumulative priming effects

Within each sequence of trials, the target stimulus was at a given position 5 times. Search times to non-primed trials (1st trials of a sequence, *M* = 886.77, *SD* = 266.8) were significantly slower than those to the primed trials (trials 2 - 5 in a sequence, *M* = 836.75, *SD* = 255.6), *t*(26) = 5.98; *p* < .05 (normalised data). This indicates cumulative priming. This was true for all conditions except the EE condition, where there was no difference between the two (Table 7).

Figure 19 shows the search times to the 5 presentations of a target position for the four priming conditions. Search time data were subjected to a 5 x 4 repeated measures ANOVA (normalised data) with the factors Presentation Number (1 - 5) and Priming Condition (A, EB, EE, EBE). This analysis revealed a significant main effect of Presentation Number, *F*(4,104) = 17.07; *p* < .05; a significant main effect of

Priming Condition, *F*(3,78) = 39.27; $p < .05$; and a significant Priming Condition by Presentation Number interaction, *F*(12,312) = 8.00; $p <.05$.

With regards to the significant main effect of Priming Condition, post-hoc tests (2-tailed t-tests) revealed that participant's responses were slower in the EE condition compared to the other conditions (EE vs. A: *t*(26) = -9.47; $p < .008$; EE vs. EB: *t*(26) = -6.71; *p* < . 008; EE vs. EBE: *t*(26) = -8.62; $p < .008$). Participants were also slower in the EB condition compared to both the EBE and A conditions (*t*(26) = -3.22; $p < .008$ and *t*(26) = -4.70; $p < .008$ respectively). There was no difference in search times in the EBE and the A conditions ($p = .226$).

Post-hoc tests, in the form of repeated measures ANOVAs for each priming condition, revealed that the main effect of Presentation Number was significant in the EBE condition, *F*(4,104) = 22.61; $p < .05$; the EB condition, *F*(4,104) = 14.00; $p < .05$, and the EE condition, *F*(4,104) = 3.84; $p < .05$, but not in the A condition ($p = .358$). Inspection of Figure 19 suggests that, search times decreased as the number of presentations of a target location increased in the EBE and EB conditions, but not in the A or EE condition.

Direct comparisons between the search times to the first and fifth target present trials of a sequence provided a measure of cumulative priming for each of the conditions, and are shown in Table 7. The differences between the first and fifth present trials of a sequence were approaching significance in the A condition, *t*(26) = 2.30; $p = .030$[15]; the EBE condition, *t*(26) = 8.62; $p < .0125$; and the EB condition, *t*(26) = 6.59; $p < .0125$. This comparison was not significant in the EE priming condition ($p = .130$). Given that the priming effect was not significant in the EE condition, the following comparisons are restricted to the other three conditions.

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[15] The critical value for this test was $p < .125$ owing to a Bonferroni correction being applied.

Cumulative priming was significantly greater in the EBE condition compared to the A condition (*Z* = -4.11, *p* < .017, *r* = -.791); however, there was no significant difference between the magnitude of cumulative priming in the EBE condition and the EB condition (*p* = .456). There was greater priming in the EB condition compared to the A condition (*Z* = -3.41, *p* < .017, *r* = -.657).

Table 7. Mean Search Times (ms) to Non-Primed Trials and Primed Trials and the Difference Between Trials 1 and 5 of a Sequence in Experiment B2.

	Non primed trials (1)	*Primed trials (2 to 5)*	*Difference between trials 1 and 5*
Allocentric	818.8 (249.2)	798.7 (245.5)	27.17 (65.0)
Egocentric – Body	922.6 (293.6)	841.33 (273.0)	110.79 (91.9)
Egocentric – Eyes	908.4 (296.7)	912.0 (277.3)	-19.66 (85.4)
Egocentric – Body and Eyes Combined	897.3 (253.1)	795.0 (238.8)	118.57 (78.7)

Note. Standard deviations are shown in parentheses.

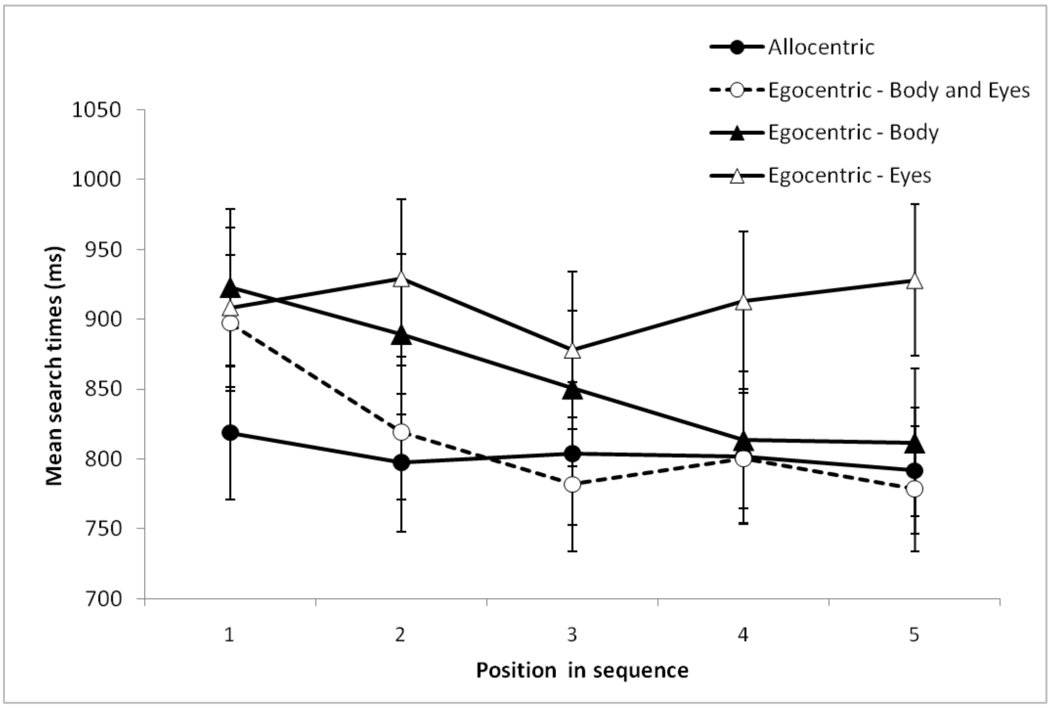

Figure 19. Mean search times (ms) to target present trials as a function of presentation number in Experiment B2. Error bars represent that standard error (+/- 1 SE).

Initial search times

It could be argued that the differences in the magnitudes of the cumulative priming effects are a result of the variable initial search times (see Figure 19). While search times to the first present trial of a sequence are faster in the allocentric condition compared to those in the three egocentric conditions, *F*(3,78) = 14.31; $p <$ .05 (normalised data), at this point there is no difference between the search times in the three egocentric conditions ($p = .566$). Therefore, the search times at the start of a sequence cannot explain the different amounts of priming observed in the three egocentric priming conditions. Additionally, there is no difference between the four priming conditions when only the first present trial of the first sequence of a group of four sequences are compared ($p = .505$, normalised data).

Given that a significant allocentric cumulative priming effect was found in Experiment A5, the lack of significant allocentric cumulative priming in this study came as a surprise. It was observed that there was greater variability, in the form of higher standard deviations, in participants' search times to the conjunction searches in this experiment compared to the features searches reported in Experiment A5. It is plausible that this increase in variability was sufficient to mask the allocentric priming effect. However, the main focus of this study was to examine egocentric priming and to establish which specific egocentric frame of reference was used.

Experiment B2 Summary

The aim of this experiment was to investigate which specific egocentric frame of reference was responsible for driving the priming effects that were reported in Experiment A5. Indeed, the finding that an egocentric frame of reference can drive spatial priming in visual search (the EBE condition here is equivalent to the egocentric condition in the previous experiment) were replicated. As there was a minimum delay of 2500 ms between search arrays, and the priming effects were cumulative, building up over sequences of six target present trials interspersed with target absent trials, the data therefore confirm that egocentric representations can be stored for at least a few seconds. In this experiment, two egocentric conditions were compared: one where the target location was specified in body-centred coordinates and one where the target location was defined using eye-centred coordinates. Significantly greater priming was observed when body-centred coordinates defined the target location. When the target had the same location relative to the fixation spot, and thus to the position of the observer's eye, repetition had no consistent effect on search times; therefore, the proposal that participants learnt that a specific saccade from the fixation spot would take them to the target location is rejected. There was no difference between the body-centred condition and the combined condition (body- and eye-centred); therefore, it is proposed that the most relevant frame of reference seems to be the body. In light of these findings, Study C went onto investigate the nature of this egocentric-body frame of reference further.

Chapter 4 – Study C: Body-centred frames of reference

Experiment B2 evaluated which specific egocentric frame of reference was responsible for driving the priming effects that were observed in Experiment A5. In comparing two egocentric conditions it was found that while repeating the location of a the target relative to the observer's body led to significant reductions in search times, repeating the location of the target relative to the fixation cross, and thus relative to the position of the observer's eye, did not have a consistent effect on search times. Furthermore, there was no difference between the body-centred condition and the combined condition (body- and eye-centred). Therefore, having established that the most relevant frame of reference seems to be the body, Study C sought to investigate this egocentric-body frame of reference further.

Despite going to great lengths to minimise the influence of allocentric cues in the egocentric priming conditions (i.e. by projecting the stimuli onto a blank wall in a darkened room), participants may have been able to use some landmark in the room which the Experimenter was unaware of rather than their own body. In this case it would be expected that if their robust performance in "egocentric" condition in reality reflects the use of some allocentric cue within the room, the priming effect should be destroyed by changing the location of the display within the room. However, if participants used their body, or a specific part of their body, as the reference point, then changing their location within the room should not affect the priming effects, as long as the body was moved so that the location of the target relative to the body remained constant.

Study C evaluated search performance in two egocentric-body conditions. The first of these was the same as that used in Experiment B2: the location of the target was repeated with respect to the position of the observer. This condition was compared with a second condition where the observers were required to move between trials. In this condition, the stimuli were designed so that the location of the target had the same location relative to the observer's body despite the participant moving to occupy a different location. Therefore, this egocentric-move condition would test the strongest version that the frame of reference being used to define the location of the target in the experiments presented in this thesis is the observer's body. If the frame of reference that is being used in our experiments is truly a body-centred frame of reference then spatial priming will still be observed when participants are required to move between trials.

Method

Participants

20 naïve participants (3 male) took part in this experiment (age range 18 – 34 years, mean age 22.7).

Apparatus

The apparatus used was the same as described in the General Methods with the following exceptions. Two projectors were used in this study, as opposed to one projector in the previous studies. This meant that the stimuli could be presented on one of two screens, of equal size and located side by side, on a blank wall. Participants were required to stand 290 cm from the wall. The increased distance between the participants and the wall in this experiment reflected the need for participants to stand in order to allow efficient moving between the screens and to avoid blocking the projected image they were required to stand further back. The exact locations of the standing area were marked on the floor. The set up was designed so that the standing position for each screen corresponded to the centre of that screen.

Stimuli

As in the previous studies, each trial consisted of two sets of stimuli. First, a letter was presented which participants had report the identity of. The font sizes used varied between 10 and 16 (corresponding to visual angles 0.3˚ vertically and horizontally, and 0.4˚ vertically and horizontally, respectively).

During the second part of a trial a search array was presented. The search arrays were the same as those presented in Study B. There were two priming conditions: Egocentric-Still and Egocentric-Move. In both priming conditions the location of the target was positioned relative to the observer's body. In the egocentric-still condition participants remained standing in front of one of the screens for all the trials of a sequence, whereas in the egocentric-move condition participants were required to move between the two screens after each trial of a sequence (see Figure 20A). The search arrays measured 14˚ vertically and 15˚ horizontally and these were placed onto black backgrounds so that the whole image measured 29˚vertically and 40˚horizontally.

Procedure

At the beginning of each trial a fixation cross was presented at a random location for 1000 ms, and this was replaced with a letter (presented for 500 ms). The fixation cross was re-presented for 500 ms before the search display was presented. The search array remained on screen until participants made their button press response. Once participants had responded a blank screen was presented for 500 ms, before the next trial was initiated. A screen instructing participants whether they were required to move to the other screen or stay in front of the same screen was presented. When the instruction was to stay in front of the screen, the instructions were presented for 2000 ms before the next trial was initiated automatically. If the instruction was to move to the other screen, participants were required to move to the new location and press a button when they were in the correct position. This button press would then start the next trial. In piloting the experiment it was found that moving from one screen to the other took approximately 2 seconds, hence the presentation of the stay instructions for 2000 ms meant that the two conditions were balanced in terms of the length of the inter-trial interval. Therefore, there was a minimum of 4500 ms between the presentation of two consecutive search arrays. The timing information for a trial is shown in Figure 20B.

To induce position-priming, sequences of trials whereby a given target position was used 5 times within a given sequence were designed. Interspersed within a sequence were also 2 target absent trials, thus each sequence consisted of 7 trials, and the target stimulus was present in 71% of trials. The experiment was divided into four blocks of trials. Each block contained five sequences of move trials and five sequences of stay trials. Therefore, for each priming condition, 20 different sequences were used, with a new priming position being used for each sequence. Participants completed a total of 140 trials of each priming condition (100 target present and 40 target absent trials). The order of the blocks alternated between the two priming conditions (half the participants started with a stay block). Both the order of the sequences within blocks, and the order of the blocks, was randomised across participants and sessions. The experiment took approximately 45 minutes to complete.

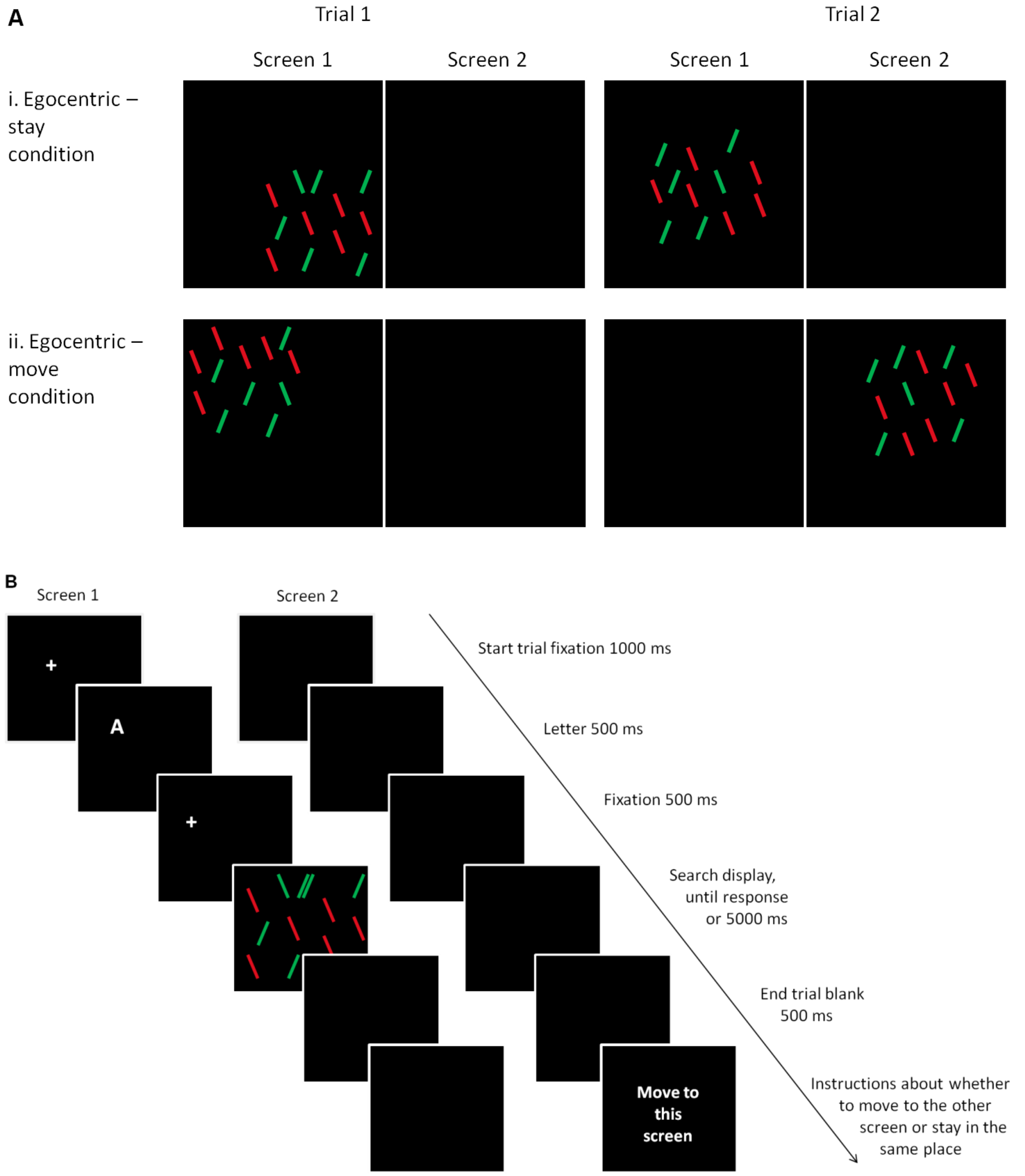

Figure 20. Priming conditions and trial sequence in Study C.

(A). Priming conditions in Study C.

i). Egocentric-stay condition. In trial 1 and trial 2 the participant stands in front of screen 1. The target occupies the same absolute position on the screen.

ii) Egocentric-move condition. In trial 1 the participant stands in front of screen 1 and moves to stand in front of screen 2 for trial 2. The target has the same location relative to the participant on both screens.

(*B*). Sequence and timing of each trial in Study C.

The example given is for a move trial. After participants had moved they were required to press a button to initiate the next trial. For a stay trial, at the end of the trial the instruction to stay in the same place would be presented on screen 1 for 2000 ms.

Results

Analyses

The first analysis of the data from this experiment is concerned with the immediate priming effects and involved performing a repeated measures ANOVA, with the variables Priming Condition (Egocentric-Move, Egocentric-Still) and Repetition (First present trial, Second present trial). This is followed by post-hoc t-tests evaluating the immediate priming effects for each priming condition. The cumulative priming effects were then evaluated with a global ANOVA (Priming Condition: Egocentric-Move, Egocentric-Still; Presentation Number: 1 - 5). Simple effects analyses, in the form of an ANOVA for each priming condition, were then performed, and paired samples t-tests were used to compare search times to the first and last target present trials of a sequence for each priming condition. Finally, a paired samples t-test compared the magnitudes of the priming effects between the two priming conditions.

Letter Reporting

For each participant the smallest font size they could read when fixating on it was established prior to the experimental trials: 13 used font size 10; 5 used font size 12; 2 used font size 16). The accuracy of letter reporting was recorded during the experimental trials and was 99.8% across all participants. Trials where the participant failed to report the letter correctly were not included in the analysis; this resulted in the exclusion of 10 trials out of 5600.

Accuracy

Participants were highly accurate in their responding to the visual search stimuli (target present trials 98% correct, target absent trials 93% correct, overall 213 trials out of 5600 trials were incorrect). Accuracy was the same in the Egocentric-Move condition and the Egocentric-Still condition (96% correct, *p* = .614, Wilcoxon signed Ranks Tests). Trials that were classed as outliers were also removed (248 trials out of the 5387 correct trials).

Present and absent searches

Search times to target absent trials (*M* = 861.77, *SD* = 192.5) were significantly slower than search times to target present trials (*M* = 710.60, *SD* = 143.6), *t*(19) = 5.66; *p* < .05. This was observed in both priming conditions (see Table 8).

Table 8. Mean Search Times (ms) to Present and Absent Searches in Study C.

	Target Present	Target Absent
Egocentric – Move	732.22 (146.6)	890.55 (191.9)
Egocentric – Still	689.00 (143.0)	832.99 (219.5)

Note. Standard deviations are shown in parentheses.

Immediate priming effects

Figure 21 compares the search times to the first two target present trials of a sequence when they directly followed one another, that is, there were no intervening target absent trials. A 2 x 2 repeated measured ANOVA with the factors Repetition (First present trial, Second present trial) and Priming Condition (Egocentric-Move, Egocentric-Still) revealed a statistically significant main effect of Repetition, *F*(1,19) = 18.54; *p* < .05, such that search times were faster on the seconds presentation of a target position; a marginally non significant main effect of Priming Condition (*p* = .088); and a non significant Repetition by Priming Condition interaction (*p* = .443).

Post-hoc tests (2-tailed t-tests) revealed that the difference in search times between the first presentation and second presentation of a target location was significant in both priming conditions: Egocentric-Move: $t(19) = 2.61$; $p < .025$, with a mean reduction of 33.40 ms ($SD = 57.3$); and Egocentric-Still: $t(19) = 3.31$; $p < .025$, with a mean reduction of 49.05 ms ($SD = 66.2$). There was no difference between the amount of priming (i.e. the reduction in search times) in the two priming conditions ($p = .443$).

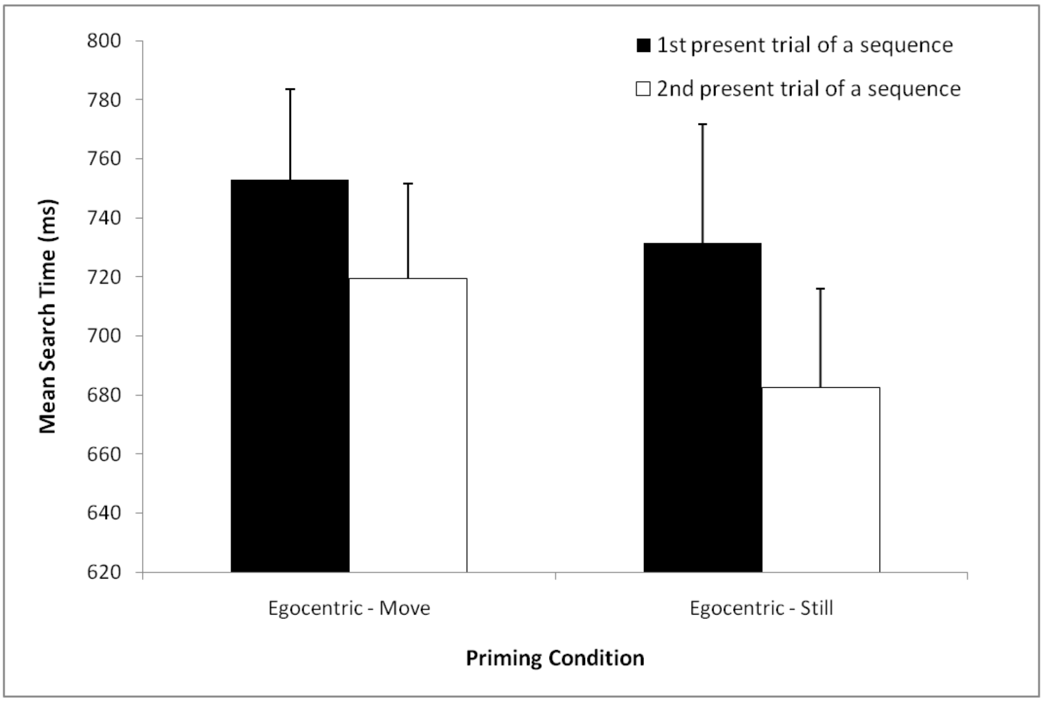

Figure 21. Mean search times (ms) to the first two target present trials of a sequence when they directly followed each other in Study C. Error bars represent +1 standard error.

Cumulative priming

Within each sequence of trials the target stimulus was at a given position 5 times. Search times to non-primed trials (1st trials of a sequence, $M = 752.72$, $SD = 146.2$) were significantly slower than those to primed trials (trials 2 - 4 in a sequence, $M = 700.36$, $SD = 144.3$), $t(19) = 8.96$; $p < .05$. This difference indicates that priming of target locations and was observed in both the Egocentric-Move and Egocentric-Still conditions (Table 9).

Table 9. Mean Search Times (ms) to Non-Primed Trials and Primed Trials and the Difference Between Trials 1 and 5 of a Sequence in Study C.

	Non-primed trials (1)	Primed trials (2 - 5)	Difference between Trials 1 and 5
Egocentric – Move	758.75 (139.9)	725.17 (149.6)	44.30 (49.2)
Egocentric – Still	746.69 (161.1)	675.54 (141.3)	92.32 (73.9)

Note. Standard deviations are shown in parentheses.

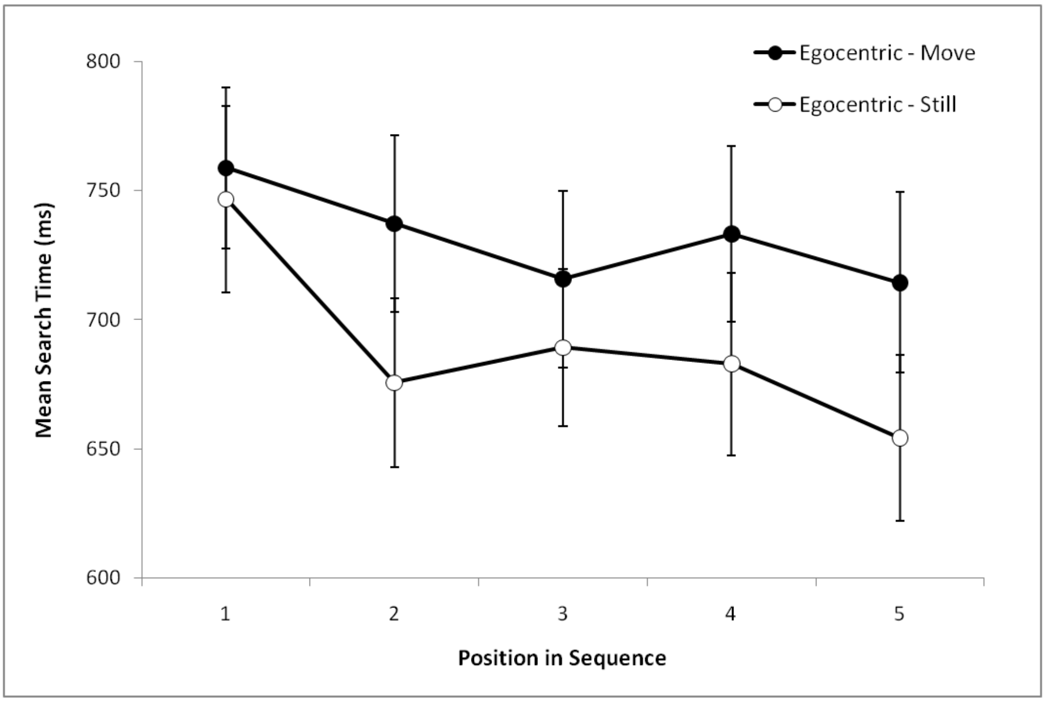

Figure 22. Mean search times (ms) to target present trials as a function of presentation number in Study C. Error bars represent the standard error (+/- 1 SE).

Figure 22 shows the search times to the 5 presentations of a target position in both of the priming conditions. Search time data were subjected to a 5 x 2 repeated measures ANOVA with the factors Presentation Number (1 - 5) and Priming

Condition (Egocentric-Move, Egocentric-Still). This analysis revealed a significant main effect of Presentation Number, $F(4,76) = 16.36$; $p < .05$; a significant main effect of Priming Condition, $F(1,19) = 29.04$; $p < .05$; and a marginally non significant Presentation Number by Priming Condition interaction ($p = .068$).

Analyses of simple effects, in the form of repeated measures ANOVA for each priming condition, revealed that the main effect of Presentation Number was significant in the Egocentric-Still condition, $F(4,76) = 11.81$; $p < .025$, and likewise in the Egocentric-Move condition, $F(4,76) = 4.00$; $p < .025$. Inspection of Figure 22 shows that search times decreased as the number of presentations of a target location increased.

Direct comparisons between the search times to the first and fifth target present trials of a sequence provided a measure of cumulative priming for the two priming conditions and are shown in Table 9. In the Egocentric-Still condition there was mean reduction of 92.32 ms between the first and last presentation and this difference was statistically significant, $t(19) = 5.59$; $p < .025$. In the Egocentric-Move condition there was mean reduction of 44.30 ms between the first and last presentation and again this difference was statistically significant, $t(19) = 4.02$; $p < .025$. The difference between the amount of cumulative priming observed in the two conditions was not significant ($p = .060$).

With regards to the main effect of Priming Condition, post-hoc tests (2-tailed t-tests) revealed that participants' responses were faster in the Egocentric-Still priming condition ($M = 689.77$, $SD = 144.1$) compared to the Egocentric-Move priming condition ($M = 731.89$, $SD = 146.7$), $t(19) = 5.39$; $p < .05$. It can be seen from Figure 22 and Table 9 that there is little difference between the search times to the first target present trial of a sequence in the two priming conditions, and this difference is not statistically significant (*p* = .476). Therefore, the trend for greater priming effects in the Egocentric-Still condition cannot be explained by a difference in the initial search times.

Study C Summary

The aim of this study was to investigate whether priming of a target location was observed when participants moved to occupy a new location in between trials while the location of the target relative to their body was maintained. The analysis of the immediate priming effects revealed that search times became speeded when two present trials directly followed one another, both when participants stayed in the same location between trials and when they moved to a new location. Furthermore, significant cumulative priming (over five target present trials) was also observed in both the Egocentric-Still and the Egocentric-Move priming conditions. Therefore, the findings from this experiment demonstrate that the location of the target is being coded relative to the observer's body, and that this coding holds even when the observer moves to occupy a new location.

The movement element of this experiment increased the minimum inter-trial interval between the two consecutive search arrays to 4500 ms (in Experiment B2 the minimum inter-trial interval was 2500 ms). In the trials where no movement was required, the instruction screen telling participants to remain in the same position was presented for 2000 ms; therefore, ensuring that the trial procedures in the two conditions were equivalent (on average it took participants two seconds to move between the two screens). In view of the extended period of time between trials, and the observation of significant priming effects in this experiment, it is now possible to argue that egocentric representations can be stored for more than just a couple of seconds. Furthermore, owing to the finding that the priming effects built up over the five target present trials of a sequence, which were also interspersed with target absent trials, the proposal that egocentric representations are highly transient can be rejected.

Chapter 5 – Study D: Temporal delays and spatial priming

As egocentric priming effects have been established using two different visual search tasks, namely a feature search task in Experiment A5 and a conjunction search task in Studies B and C, it is necessary to now investigate the temporal characteristics of the frame of reference information more formally. While in Study C the minimum time between the presentation of two search arrays was 4500 ms which was longer than in previous experiments (Experiment B2: 2500 ms; Experiment A5: 2200 ms), the aim of Study D was to determine how long egocentric information can persist for by varying the length of the delay between the presentation of two search arrays. If egocentric representations can be stored for more than a couple of seconds then priming will be observed across the delay conditions. The magnitude of the priming effects will be plotted as a function of delay to determine how and when the information deteriorates. If egocentric representations can be stored for the longest delay, egocentric priming will be observed and this will have implications for the perception-action model which argues that egocentric information is highly transient (Milner & Goodale, 1993, 2006).

Method

Participants

30 naïve participants (10 male) took part in this experiment (age range 19 – 51 years, mean age 26.4).

Apparatus

The apparatus used was the same as described in the General Methods.

Stimuli

Each trial consisted of two sets of stimuli. First, a letter was presented which participants had report the identity of. The font sizes used varied between 6 and 16 (corresponding to visual angles 0.2° both vertically and horizontally, and 0.7° vertically and horizontally, respectively).

During the second part of a trial a search array was presented. The search arrays were the same as those presented in Studies B and C. There were two priming conditions: Allocentric and Egocentric-Body. In the allocentric priming condition the location of the target was positioned relative to the landmark (two distractors close together) but at different positions relative to the observer's body. In the egocentric-body priming condition, the target maintained the same position relative to the observer's body but it occupied different positions relative to the landmark (see Figure 23A, also see Figure 17B, page 125 for examples of the placement of the search arrays onto the black backgrounds).

Procedure

A beep sounded for 100 ms at the start of each trial. Owing to the manipulation of the length of the delay between trials it was necessary to include a beep in order to signal to participants that the next trial was starting. As the three delay conditions were randomly presented in blocks of three sequences (one sequence of each delay) participants were not able to anticipate when each trial would be starting. Therefore, the sounding of a beep would orient their attention back to the task and ensure that any differences between the delay conditions were not the result of participants not being ready for the trials. While a beep was not included in previous studies it is not thought that it would affect search performance as after the beep the regular trial sequence resumed before the search array was presented. A fixation cross was then presented at a random location for 500 ms, and this was replaced with a letter presented for 500 ms. The fixation cross was then re-presented for 500 ms before the search display was presented. The search array remained on screen until participants made their button press response. Once participants had responded, a blank screen was presented for 400 ms, 2400 ms, or 6400 ms, before the next trial was initiated. The varying blank screen lengths created minimum delays between two consecutive search displays of 2000 ms, 4000 ms, or 8000 ms. The trial procedure is shown in Figure 23B.

To induce position-priming, sequences of trials, whereby a given target position was used 4 times within a given sequence, were designed. Interspersed within a sequence there were also 2 target absent trials, thus each sequence consisted of 6 trials, and the target stimulus was present in two thirds of trials. For each priming condition, 21 different sequences were used, with a new priming position being used for each sequence. These 21 sequences were divided into 7 blocks of three sequences, with each block containing one sequence of each temporal delay.

Owing to the periods of delay between the presentations of search arrays it was necessary that participants completed three testing sessions in order to get a sufficient number of trials for statistical analysis. Each testing session contained 126 trials of each priming condition (84 present, 42 absent) and as participants completed three sessions of experimental trials, a total of 378 trials for each priming condition (126 trials of each temporal delay) were completed. The blocks alternated between the two priming conditions (half the participants started with an allocentric block in the first session, an egocentric in the second session, and an allocentric in the third session). Both the order of the sequences within blocks, and the order of the blocks, was randomised across participants and sessions.

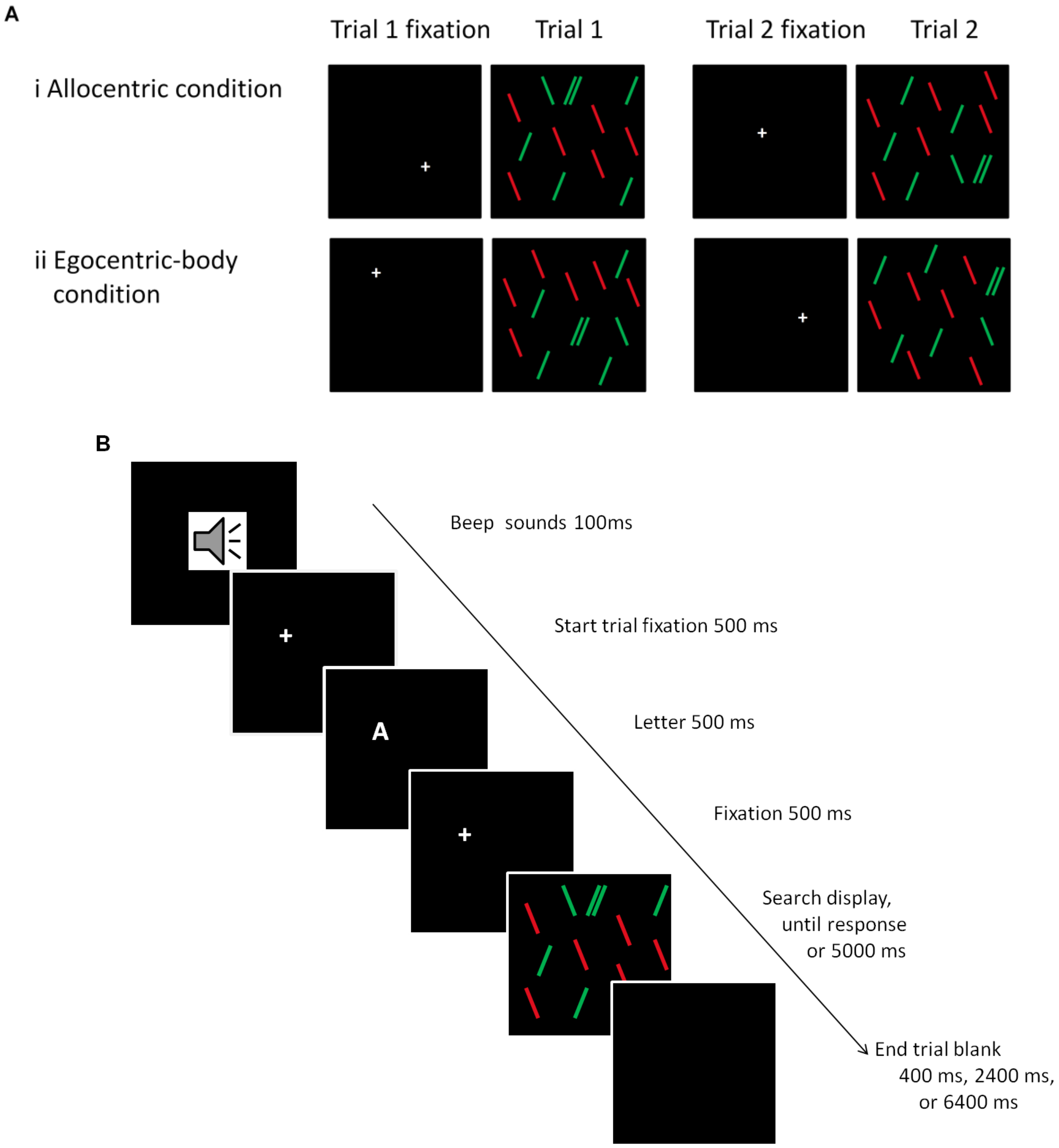

Figure 23. Priming conditions and trial sequence in Study D.

(A). Schematic of stimuli for the two priming conditions.

i) Allocentric (A) priming condition. In trials 1 and 2 the target is to the left of the anchor but it occupies different positions relative to the observer and the fixation spot.

ii) Egocentric-body (EB) priming condition. When the egocentric body position is repeated, the target occupies the same absolute position on the screen, but it has no constant relationship with either the anchor or the fixation spot.

(B). The sequence and timing of each trial.

Results

Analyses

Data from the egocentric and allocentric priming conditions were analysed separately. The first analysis is concerned with the immediate priming effects and involved performing a repeated measures ANOVA, with the variables Repetition (First present trial, Second present trial) and Delay Condition (Short, Medium, Long). This is followed by post-hoc t-tests evaluating the immediate priming effects for each delay condition. The cumulative priming effects were then evaluated, again using a repeated measures ANOVA, with the factors Presentation Number (1 - 4) and Delay Condition (Short, Medium, Long). Paired samples t-tests and Wilcoxon Signed Ranks tests were then performed to evaluate the main effects of Presentation Number and Delay Condition further.

Letter Reporting

For each participant the smallest font size they could read when fixating on it was established prior to the experimental trials (2 participants used font size 6; 6 used font size 8; 13 used font size 10; 6 used font size 12; 3 used font size 16). The accuracy of letter reporting was recorded during the experimental trials and was 99.7% across all participants, indicating that participants fixated correctly at the beginning of each trial. Trials where participants failed to correctly report the letter were excluded from the analysis; this resulted in the exclusion of 58 trials out of 22176 trials.

Accuracy

Participants were highly accurate in their responding to the visual search stimuli (present trials 97% correct, absent trials 94% correct, overall 1081 trials out of 22176 trials were incorrect)[16]. Outlier analysis resulted in the removal of 886 trials out of 21221 correct trials.

Present and absent trials

Search times to target absent trials (M = 1010.89, SD = 319.1) were significantly slower than those to target present trials (M = 737.94, SD = 150.1), Z = -4.78, $p < .05$, r = -.617 (Wilcoxon Signed Ranks test). This was observed for all delay conditions in both allocentric and egocentric searches (see Table 10).

Table 10. Mean Search Times (ms) to Present and Absent Searches in Study D.

	Allocentric		Egocentric	
	Present	Absent	Present	Absent
Short Delay	687.53	935.29	759.69	977.31
	(117.3)	(302.9)	(171.0)	(318.6)
Medium Delay	711.92	993.81	769.15	1033.39
	(153.1)	(321.4)	(163.3)	(315.5)
Long Delay	716.98	1050.49	782.33	1075.03
	(158.8)	(370.2)	(154.2)	(305.2)

Note. Standard deviations are shown in parentheses.

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[16] One participant only completed one session of trials; therefore, the total number of trials is 29 participants x 756 trials and 1 participant x 252 trials.

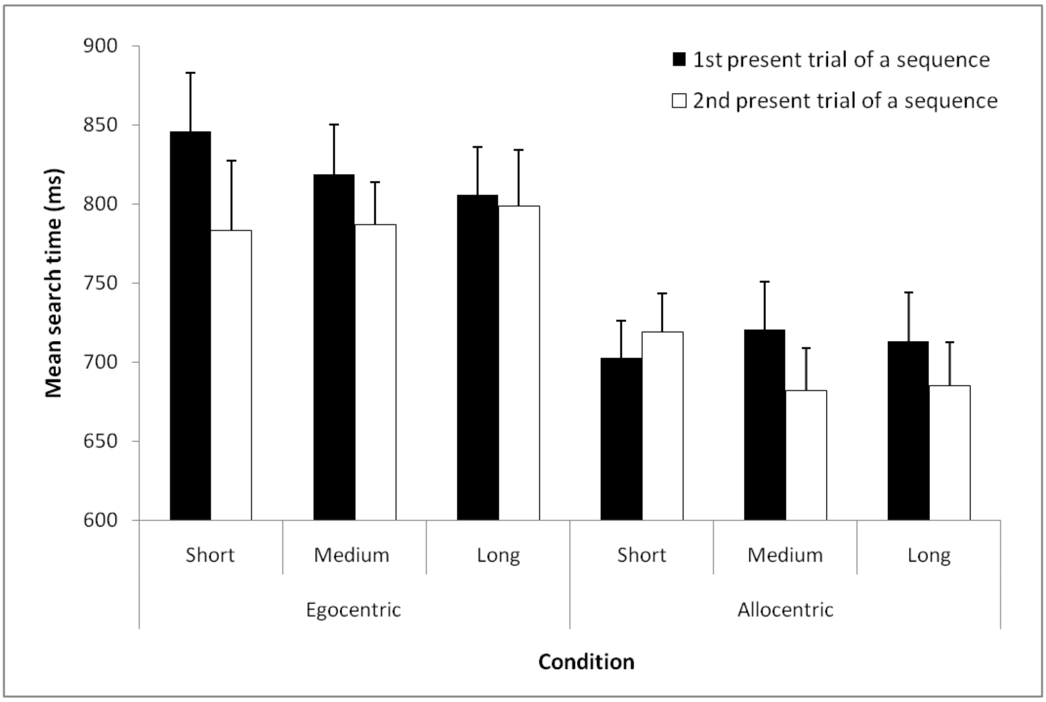

Figure 24. Mean search times (ms) to the first two target present trials of a sequence when they directly followed each other in Study D. Error bars represent + 1 standard error.

Egocentric priming condition: Immediate priming effects

The left half of Figure 24 compares the search times to the first two present trials of a sequence when they directly followed one another (i.e. when there were no intervening target absent trials) for the egocentric priming condition. A 2 x 3 repeated measures ANOVA (normalised data) with the factors Repetition (First present trial, Second present trial) and Delay (Short, Medium, Long) revealed a non significant main effect of Repetition (p = .064), such that there was only a trend for search times to the first present trial of a sequence (M = 823.63, SD = 173.6) to be slower than those to the second present trial of a sequence (M = 789.76, SD = 175.7); a non significant main effect of Delay (p = .899); and a non significant Repetition by Delay interaction (p = .247).

For all three delay conditions, post-hoc tests (paired samples t-tests) did not reveal significant differences between search times for first and second presentations.

Allocentric priming condition: Immediate priming effects

The same analysis (normalised data) for allocentric searches revealed that while the main effect of Repetition was not statistically significant (p = .111), search times to the first present trial of a sequence (M = 712.15, SD = 150.6) were slower than those to the second present trial of a sequence (M = 695.44, SD = 133.6). The ANOVA also revealed a non significant main effect of Delay (p = .180), while the Repetition by Delay interaction was statistically significant, $F(2,58) = 5.92$; $p < .05$. This is shown in the right half of Figure 24.

Post-hoc tests (2-tailed t-tests) revealed that the difference in search times to the first presentation and second presentation of a target location was only significant in the Medium delay condition, $t(29) = 4.12$; $p < .017$, with a mean reduction of 38.4 ms (Short delay condition: p = .359, increase of 16.4 ms, Long delay condition: marginally non significant, p = .051, reduction of 28.1 ms).

Egocentric priming condition: Cumulative priming effects

Within each sequence of trials the target stimulus was at a given position four times. This data is shown in Figure 25 for the egocentric priming condition. Search times to primed trials (where the target was presented at the same position as in a previous trial within a sequence, M = 746.35, SD = 157.0) were faster than those to the non-primed trials (the first present trial of a sequence, M = 834.21, SD = 183.3), $t(28) = 10.10$; $p < .05$. This is shown in Table 11 for all delay conditions.

The data were subjected to a 4 x 3 repeated measures ANOVA (normalised data) with the factors Presentation Number (1 - 4) and Delay (Short, Medium, Long). The analysis revealed a significant main effect of Delay, $F(2,58) = 5.24$; $p < .05$; a significant main effect of Presentation Number, $F(3,87) = 79.98$; $p < .05$; and a significant Presentation Number by Delay interaction, $F(6,174) = 11.86$; $p < .05$.

With regards to the main effect of Delay, post-hoc tests (2-tailed t-tests) revealed that search times were faster in the Short delay condition ($M = 760.65$, $SD = 172.7$) compared to the Long delay condition ($M = 781.15$, $SD = 153.6$, $t(29) = 2.66$; $p < .017$). The difference between the Medium delay ($M = 769.58$, $SD = 162.4$) and Long delay conditions was not statistically significant ($p = .102$), as was the difference between Short delay and Medium delay ($p = .186$).

As can be seen from Figure 25 search times decreased as a function of Presentation Number. Direct comparisons between search times to the first and fourth target present trials of a sequence provided a measure of cumulative priming for the three delay conditions. Post-hoc tests revealed that this difference was significant in all three delay conditions. In the Short delay condition there was a mean reduction of 165.5 ms (SD = 97.8), $t(29) = 9.27$; $p < .017$), between the first and fourth target presentation; in the Medium delay condition this difference was 150.31 ms (SD = 84.3), $t(29) = 9.77$; $p < .017$; and in the Long delay condition the reduction was 61.89 ms (SD = 82.3), $t(27) = 4.12$; $p < .017$.

Wilcoxon signed ranks tests revealed that whilst the difference between the amount of cumulative priming in the Short condition and the Medium condition was not significant ($p = .465$), it was between the Medium and Long delay conditions, $Z = -3.92$, $p < .017$, $r = -.506$, and between the Short and Long delay conditions, $Z = -4.39$, $p < .017$, $r = -.567$.

Allocentric priming condition: Cumulative priming effects

Search times to primed trials (*M* = 700.44, *SD* = 143.4) were slightly faster than those to non-primed trials (*M* = 708.89, *SD* = 147.9); however, this difference was not significant (*p* = .278). Table 11 shows this for the different temporal delays. The repeated measures ANOVA (normalised data) with the factors Presentation Number (1 - 4) and Delay (Short, Medium, Long) revealed a statistically significant main effect of Delay, *F*(2,58) = 5.91; *p* < .05; a marginally non significant main effect of Presentation Number (*p* = .064); and a significant Presentation Number by Delay interaction, *F*(6,174) = 3.55; *p* = < .05. This data is shown in Figure 26.

With regards to the main effect of Delay, post-hoc tests (2-tailed t-tests) revealed that search times were faster in the Short delay condition (*M* = 687.58, *SD* = 118.0) than in both the Medium delay condition (*M* 710.27, *SD* = 152.7, *t*(29) = 2.53; *p* < .017); and the Long delay condition (*M* = 715.66, *SD* = 159.2, *t*(29) = 2.61; *p* < .017). The difference between search times in the Medium and Long delay conditions was not significant (*p* = .411).

In comparing the absolute differences in search times to the first present trial and fourth present trial of a sequence, post-hoc analysis (paired samples t-tests) revealed that the difference was approaching significance in the Short delay condition (*p* = .039), with a mean reduction of 27.40 ms (*SD* = 76.2) and in the Long delay condition (*p* = .024) with a mean increase of 24.27 ms (*SD* = 59.0). The difference in the Medium delay condition was not significant (*p* = .402, mean reduction 7.28 ms, *SD* = 65.6).

Figure 27 collates the magnitude of the priming effects (immediate and cumulative) for both priming conditions across the three delay intervals.

Table 11. Mean Search Times (ms) to Non-Primed trials and Primed trials in Study D.

	Allocentric		Egocentric	
	Non-Primed	Primed	Non-Primed	Primed
Short Delay	701.48	679.29	849.52	727.05
	(139.8)	(117.9)	(209.2)	(165.8)
Medium Delay	717.45	705.23	846.51	742.83
	(161.2)	(154.4)	(191.4)	(158.7)
Long Delay	707.70	716.74	806.61	769.17
	(160.6)	(164.6)	(168.8)	(154.4)

Note. Standard deviations are shown in parentheses.

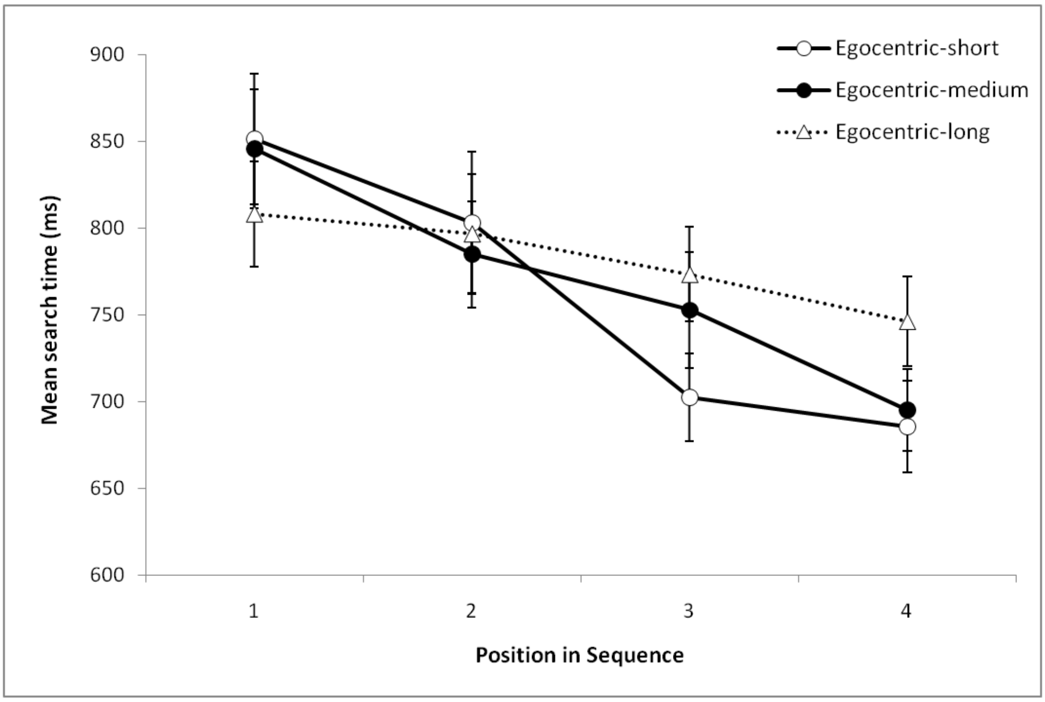

Figure 25. Mean search times (ms) to target present trials in the egocentric condition as a function of presentation number in Study D. Error bars represent the standard error (+/- 1 SE).

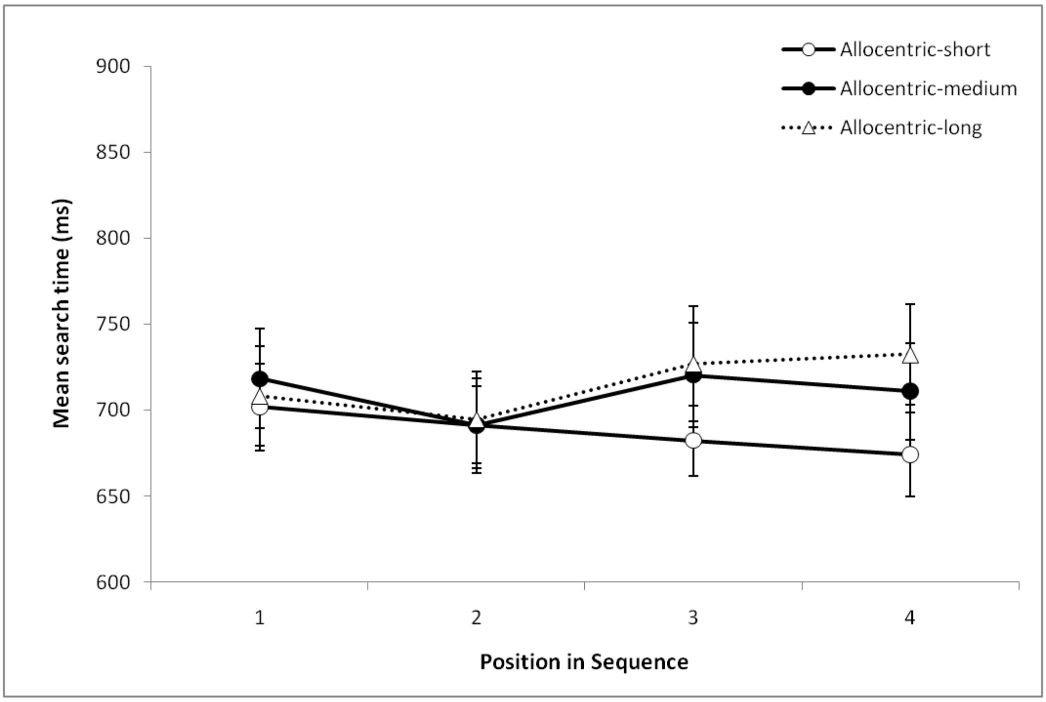

Figure 26. Mean search times (ms) to target present trials in the allocentric condition as a function of presentation number in Study D. Error bars represent the standard error (+/- 1 SE).

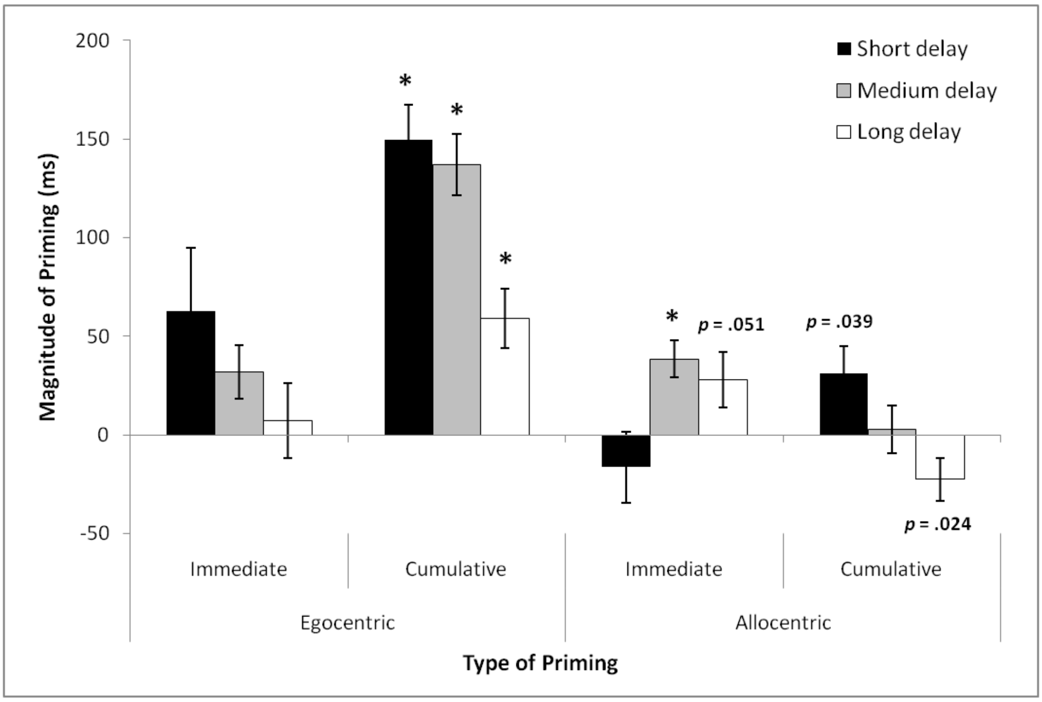

Figure 27. Amount of immediate and cumulative priming for egocentric and allocentric searches by delay in Study D. Error bars represent the standard error (+/- 1 SE). * demotes significant difference at p <.017 (Bonferroni correction applied).

First present trials

It could be argued that the differences in the magnitudes of the priming effects, that is, greater cumulative priming in the egocentric condition relative to the allocentric condition, are a result of the variable initial search times. Search times to the first present trial of a sequence are faster in the allocentric searches (*M* = 709.51, *SD* = 145.3) compared to those in the egocentric searches (*M* = 834.97, *SD* = 180.1), *t*(29) = 10.30; *p* < .05. However, the accuracy of responses to the first present trial of a sequence is significantly reduced in the allocentric condition (89.3%) compared to the egocentric condition (93.3%), *Z* = 3.17, *p* < .05, *r* = .410; therefore, suggesting a speed-accuracy trade off.

When only the first present trials of a block are analysed (normalised data), there is still a speeding for allocentric searches (*M* = 748.11, *SD* = 165.4) compared to egocentric searches (*M* = 844.33, *SD* = 190.8), *t*(29) = 6.00; *p* < .05. However, when looking at only the first present trials of each session, there is no difference between allocentric (*M* = 823.22, *SD* = 293.4) and egocentric (*M* = 829.04, *SD* = 248.0) *p* = .777 (normalised data).

Overall, search times to allocentric present searches (*M* = 705.48, *SD* = 141.1) were faster than those to egocentric present searches (*M* = 770.39, *SD* = 160.3, *t*(29) = 10.49; *p* < .05. This difference may be explained by the observation that there is an overall difference between the participant's accuracy to the searches in the two priming conditions: a Wilcoxon Signed Ranks test found a significant difference between the accuracy of present and absent searches to allocentric and egocentric searches, *Z* = 4.26, *p* < .05, *r* = .569 (data could not be normalised using a log transformation), such that accuracy was greater in the egocentric condition (96.4 % of trials correct) compared to the allocentric condition (94.2 %).

Study D Summary

The aim of this study was to investigate the time period over which previously presented information of a target location can persist for; therefore, the effect of delay on egocentric and allocentric priming was evaluated. The finding of significant cumulative priming, whereby search times decreased over the course of the four repetitions of a target location, interspersed with target absent trials, in the shortest delay condition (minimum time between two consecutive search arrays was 2000 ms), in the egocentric priming condition replicates findings from previous experiments presented in this thesis (Experiments A5 and B2). With regards to the egocentric priming condition, significant priming effects were also observed for the two longer delay conditions (minimum time between two search arrays of 4000 ms and 8000 ms). While the reduction in search times between the first and fourth presentations of a target location were still significant at the longest delay, the reduction at this point was less than at the other two delays. This therefore indicates some diminishing of the information at this time point. There was no difference between the egocentric priming at the short delay and the medium delay conditions. The observations of this study therefore extend both the findings of previous experiments and the time for how long egocentric information is available for.

With regards to the allocentric priming condition, there was only a trend for a reduction in search times with repetition of a target location at the shortest delay. Indeed, there was a trend for an increase in search times in the long delay over the four presentations of a target location.

Discussion of Studies B, C, and D

In the experiments presented in Chapters 3 - 5 the target that participants were searching for was made up of a conjunction of features, namely, orientation and colour, whereas in Chapter 2 (Study A) the target was defined solely by its orientation. The significant priming effects that were observed in Studies B - D provide evidence that the priming effects observed in Study A are not specific to a feature search paradigm. Interestingly, for targets defined using an egocentric frame of reference the cumulative priming effects were greater in the experiments using the conjunction search paradigm compared to those using the feature search paradigm. It is thought that this might reflect the increased difficulty of the conjunction search, as shown by the systematic increase in search times as the number of distractor items increases for this type of search (Experiment B1). Therefore, the longer search times to conjunction searches, shown by the statistically significant main effect of Search Type (Feature vs. Conjunction) in Experiment B1 means that during a conjunction search there was greater scope for search time reductions with repetition. In addition to response times being extended in the conjunction search task compared to the feature search task, responses were also more variable, illustrated by greater standard deviations. In Study D in particular, the allocentric priming effects only approached significance, and while the magnitude of the priming effects were similar to those in Study A where statistical significance was reached. It is thought that the increased variability in the data may offer some explanation for the marginal effects in the studies employing a conjunction search.

Temporal characteristics

The observations of Experiment B2 confirm the previous finding (Experiment A5) that egocentric information can be stored for a couple of seconds, as in this experiment the minimum period of time between the presentation of two search arrays was 2500 ms. Furthermore, as the cumulative priming effects built up over the presentation of five present trials, which were interspersed with target absent trials, the findings suggest that the egocentric information can persist for considerably longer than a couple of seconds. Moreover, when the inter-trial interval was extended to 4500 ms in Study C, statistically significant egocentric priming effects were still observed (see Table 12).

Study D went onto show that while the magnitude of egocentric priming does diminish with the passage of time, by finding that at the longest of three inter-trial intervals the egocentric priming effects were smaller relative to those for the two shorter inter-trial intervals (Table 12) the priming effects are still significant, with the average reduction in search times approaching 60 ms. What is surprising is that the longest inter-trial interval in this experiment was 8000 ms, and again the priming effects built up over the presentation of four trials, interspersed with target absent trials.

In summary, not only have the egocentric priming effects that were observed in Study A been replicated consistently across Studies B - D with a second visual search paradigm, but Study D provides the strongest evidence that egocentric representations can be stored for considerably longer than a couple of seconds.

Table 12. Cumulative Priming Effects across Studies B - D.

			Priming Condition				
	Seq	Min delay (ms)	Body + Eyes	Body only	Eyes only	Body move	Allo
Study B Exp 2	6	2500	118.6	101.8	-19.7 (ns)		
Study C	5	4500		92.3		44.3	
Study D Short delay	4	2000		149.4			31.2 (ns)
Study D Medium delay	4	4000		137.0			2.7 (ns)
Study D Long delay	4	8000		59.9			-22.4

Note. Seq demotes sequence and is the number of target present trials in a sequence.

Frame of reference specificities

In addition to exploring the temporal characteristics of the egocentric frame of reference that has been used, Studies B and C sought to determine which specific egocentric frame of reference was responsible for driving the spatial priming effects observed in Study A. It was not clear from Experiment A5 whether participants were remembering the location of the target relative to the position of their body or relative to the location of the fixation spot that appeared before the search arrays were presented, and thus they were using the same eye movement across trials to locate the target. Therefore, in Experiment B2, these two egocentric frames of reference were investigated separately and in combination. It was found that when the location of the target was repeated relative to the location of the fixation spot there was no consistent effect of search times. This therefore suggested that participants were not relying on an eye-centred frame of reference. Conversely, statistically significant priming effects were observed when the location of the target was defined relative to the observer’s body alone. Taken together, the absence of priming in the eye-centred condition and the presence of priming in the body-centred condition, suggests that the most relevant egocentric frame of reference in the studies presented here is the body. This conclusion is further strengthened by the observations of the priming effects in the third egocentric condition in Experiment B2. It was found that the priming effects in the egocentric-body condition were not statistically different from those in the combined egocentric body- and eye condition (see Table 12).

Having established that the egocentric frame of reference responsible for driving the priming effects was the body in Experiment B2, Study C sought to evaluate the robustness of this frame of reference. This was achieved by assessing the effect of moving participants between when the location of a target position was first presented and when it was re-presented. The experimental set up was such that while the target occupied the same location relative to the observer, its absolute location changed between the two presentations. There was a reduction in search times between the first presentation and the second presentation of a target location both when the observer was required to stay in the same location and when they were required to move to a new location between the two trials, thus indicating immediate priming effects. Furthermore, statistically significant cumulative priming effects were observed, in that search times continued to decrease when the location of the target relative to the body was repeated across a sequence of five trials. Again, these effects were observed both when participants did not move location between trials and when they did. Therefore, in summary, both Experiment B2 and Study C provide evidence that the egocentric information being used in the experiments is being coded relative to the observer’s body.

In conclusion, the findings from Studies B, C, and D suggest that both egocentric and allocentric information are used in spatial priming during a conjunction visual search task, in addition to being used in the feature visual search task presented in Study A. Furthermore, it has been established that the most relevant egocentric frame of reference appears to be the body, and that the priming effects still hold when the observer moves to occupy a new location. It has also been found that egocentric representations can be stored for considerably longer than a couple of seconds, a finding that is in opposition to the premise that egocentric information is of a highly transient nature made by the perception-action model (Milner & Goodale, 1993, 1995, 2006). In depth discussion of how the findings from Studies A – D relate to the current literature and their implications for the perception-action model will be presented in Chapter 7.

Chapter 6 – Study E: Transcranial magnetic stimulation and spatial priming.

Spatial priming has been established for visual search targets defined in egocentric (body) and allocentric frames of reference in the studies presented in this thesis. In investigating the brain areas involved in both spatial priming and conjunction visual search *transcranial magnetic stimulation* (TMS) has been invaluable. This is because it transiently disrupts activity in a specific brain region, and thus allows inferences to be made about whether a specific brain area is necessary in the completion of the cognitive of sensorimotor function that is being tested (Hallett, 2000).

PPC and conjunction searches

There is a considerable body of research that suggests that the *posterior parietal cortex* (PPC) is involved in conjunction visual search tasks. For example, it has been observed that patients with lesions to right hemisphere parietal brain regions are impaired at completing visual search tasks when a combination of features are used to define the target (Arguin, Cavanagh, & Joanette, 1994; Friedman-Hill, Robertson, & Treisman, 1995; Kanwisher & Wojciulik, 1998). Conversely, the same group of patients perform normally on feature based searches (Arguin, et al., 1994), that is, where only one feature defined the target. Additionally, data from imaging studies supports the view that the PPC is involved in conjunction searches (for example, Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991, using positron emission tomography, PET; and Donner et al., 2002, using fMRI).

The use of TMS on healthy participants has permitted further investigation into the functional role of the right PPC in feature binding in conjunction search. It has been shown that while TMS to the PPC does not affect performance on feature search tasks, it significantly increases search times to conjunction searches (Ashbridge, Walsh, & Cowey, 1997; Ellison, Rushworth, & Walsh, 2003). Furthermore, the effects of disrupting PPC activity are modulated by the amount of practice the observer has had with a specific search task: Walsh, Ashbridge, and Cowey (1998) observed that once participants had become experienced with a conjunction search task, TMS to the PPC no longer increased search times; therefore, they concluded that the PPC is selectively involved in novel conjunction visual search tasks.

However, it could be argued that the differential affects of TMS on feature and conjunction searches are explained by task difficulty. It has typically been found that search tasks where one feature defines the target are easier than when a conjunction of features define the target, owing to the fact that in the former the target and the distractors do not share any features, whereas in the latter type of search the target shares one feature with all the distractors (Humphreys, Riddoch, & Quinlan, 1985; Wolfe, 1998b). Likewise, the search times to the feature search used in Study A were faster than those to the conjunction searches in Studies B – D[17]. Therefore, it could be argued that the selective slowing with TMS to the PPC to search times in conjunction searches but not in feature searches may reflect a difference in search difficulty. However, in comparing the effect of TMS to the right PPC on search times to both easy and difficult feature and conjunction searches, Ellison et al. (2003) found that the level of search difficulty did not explain the differential effects of PPC disruption on the two types of search tasks. It was also observed that increasing the number of distractor items in the search array did not increase the PPC slowing to search times (Ellison, et al., 2003).

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[17] Experiment B1 found that the average search times to feature searches was 560.86 ms (*SD* = 160.8) and to conjunction searches was 1065.09 ms (*SD* = 270.5).

In summary, there is substantial evidence that the right PPC is involved in conjunction search tasks that have not been extensively practiced, and that disruption to this area with TMS has detrimental effect on search performance, in the form of increased search times.

PPC and spatial priming

The second component of the visual search paradigms used in this thesis is spatial priming, that is, the observation that search times become faster when the location of a target is repeated. Experiment B2 found there was the greatest benefit to search times when the location of the target was repeated relative to the observer's body, and Experiments A5, B2, and Study D found priming for targets defined allocentrically, although the effects were smaller than those for egocentric priming. There has been some research using TMS to establish which brain areas are important for spatial priming in visual search. Campana, Cowey, Casco, Oudsen, and Walsh (2007) found that applying TMS to the left frontal eye fields (FEFs) significantly reduced the spatial priming effects that were observed when no TMS was applied to this area. The researchers suggests that this is evidence that the FEFs, particularly the left FEFs, are involved when information pertaining to spatial location is required to be stored for a short period of time (Campana, et al., 2007). Further evidence for the role of the FEFs in spatial priming was provided by O'Shea, Muggleton, Cowey, and Walsh (2007) who observed that when the left FEF was subjected to TMS stimulation, priming for target location was significantly reduced. They found that the same TMS application did not have any effect on feature priming effects, namely, with colour; therefore, they concluded that the "FEFs integrate a spatial memory signal that facilitates saccades to a recently inspected location (O'Shea, et al., 2007, p. 1150). Therefore, there is a body of research implicating the crucial role of the frontal eye fields, specifically, the left FEFs, in spatial priming (see also Kalla, Muggleton, Juan, Cowey, & Walsh, 2008; O'Shea, Muggleton, Cowey, & Walsh, 2006, for a review of the FEFs in visual search tasks).

While there has been extensive research implicating the posterior parietal cortex in conjunction visual searches, there has been little research looking at the role of this area in the spatial priming of targets in such searches. Instead, research has been weighted into looking at the role of the frontal eye fields in spatial priming. The purpose of this study was to investigate whether the PPC would be involved in spatial priming, and furthermore examine whether its involvement is specific to either egocentric or allocentric priming. In line with the previous experiments, targets were defined in either allocentric or egocentric (body-centred) frames of reference. This study could possibly provide a direct test of the involvement of dorsal stream areas in spatial priming, and therefore allow examination of whether persistent visual information is found and can be disrupted. Therefore, this experiment coupled the conjunction visual search paradigm used in Studies B – D with the application of TMS to the posterior parietal cortex.

Method

Participants

Twelve participants (6 male) from Durham University took part in this experiment (age range 21 – 51 years, mean age 31.9). Participants all had normal or corrected-to-normal vision and 7 were right handed. Participants were required to complete a questionnaire assessing their suitability for participating in a TMS study and their general health prior to both testing sessions (see Appendix C for a copy of the consent form).

Apparatus

This experiment was programmed using E-prime, version 2.0 professional, and this software was also used to present the stimuli, control the presentation timing of the stimuli, and to record participant's responses and reaction times. The program was run on an IBM compatible personal computer with a 15-inch monitor (1280 by 1024 resolution, refresh rate 60 Hz). The stimuli used in the localisation of the posterior parietal cortex were presented on this monitor (viewing distance 57 cm), whereas a projector was used to present the stimuli onto a blank wall in the experimental trials (viewing distance 220 cm). Participants made their responses to the stimuli using a button box.

Transcranial magnetic stimulation

The TMS was delivered using a Magstim Rapid TMS machine. During both the posterior parietal cortex (PPC) localisation task and the experimental trials, 5 pulses, separated by 100 ms, were applied at the onset of the visual search arrays. The machine was set at 65% of the stimulator's maximum power (i.e. 1.3 Tesla). A

70 mm figure-of-8 coil was used, which was placed tangential to the participant's skull. The sites of interest were the right posterior parietal cortex (PPC) and the right visual motion area V5. There was also a sham condition where the 'live' TMS coil was placed on the floor behind the participants while the Experimenter held an unconnected coil over the PPC site.

Posterior parietal cortex localisation

The right PPC was functionally localised in each participant prior to the experimental trials. The method of PPC localisation involved administering TMS to a number of different sites (a 3 by 3 grid) which centred on a point 9 cm dorsal and 6 cm lateral to the mastoid-inion. The PPC site selected for each participant was the one where the application of TMS increased search times to target present trials by approximately 100 ms, compared to when no TMS was applied (sham blocks, where the coil connected to the TMS machine was placed on the floor behind the participant and the Experimenter held a second, unconnected coil over a PPC site). This method of PPC localisation has been used previously; for example, by Ellison, Lane, and Schenk (2007) and Ellison et al. (2003). The search times to the Sham condition and the selected PPC area for each participant are shown in Appendix D.

For the PPC localisation trials the visual search stimuli were presented on a 320 mm by 240 mm computer monitor, from which participants were seated 57 cm, and the visual angle of the whole screen measured approximately 30˚ horizontally and 23˚ vertically. The search arrays consisted of 12 red and green lines presented on black backgrounds. In target present trials there was one target (a green backslash) and 11 distractors (6 red backslashes and 5 green forward slashes), and in target absent trials there were 12 distractors (6 red backslashes and 6 green forward slashes). Each item in the search array measured 1.3˚ horizontally and 2.1˚ vertically.

At the start of each trial a white central fixation cross was presented for 500 ms (visual angle 0.5˚). This was followed by the search array, which was presented until participants made their key press response indicating whether the target was present or absent. A blank screen was then presented for 4000 ms, before the next trial was initiated. Participants completed blocks of 10 trials (5 target present, 5 target absent) of either PPC or Sham stimulation, the order of which was decided by the Experimenter. On average participants completed 8 conjunction hunting blocks before the Experimenter had localised the principle PPC site. This PPC localisation was completed at the start of the first testing session (each participant completed two testing sessions), and the measurements of the principle PPC were recorded and used to locate the area of interest in the second testing session.

V5 localisation

Area V5 was chosen as the control TMS site. A control site was necessary in order to distinguish between the effects of disrupting activity to an area needed in certain tasks and more general effects that the application of TMS can result in. For example, a slowing in performance when TMS is applied might simply be explained by participants being distracted by the sensation and noise of the TMS compared to when they complete the task when no TMS is applied. Area V5 was chosen as the control site for two reasons. First, it is easy to anatomically localise: it was measured as being 3 cm above and 5 cm lateral to the right from the mastoid-inion of each participant. Second, V5 is only involved in visual search tasks that have an element of motion (Ellison, et al., 2007); therefore, TMS to this area would not interfere with the search task being used.

This site was tested with 1 pulse of TMS prior to experimental trials to ensure stimulation did not result in the participant experiencing twitches. If this was the case, the coil was re-oriented to avoid this. In one participant varying the orientation of the coil did not improve the twitching effects so this participant only completed the PPC and Sham conditions.

Experimental stimuli

The nature and arrangement of the stimuli used in the experimental trials were different to those used in the PPC localisation trials. As in the previous studies, the experimental trials consisted of two sets of stimuli. First, a letter (font size 10, visual angle 0.4˚) was presented and participants had to foveate and report the identity of this letter. During the second part of a trial a search array, consisting of red and green lines on black backgrounds, was presented. The target line was always a green backslash (oriented at -20˚ from vertical) and distractors were green forward slashes (oriented at 20˚ from vertical) and red backslashes (see Figure 28A). Each search array consisted of 13 lines: in target present trials there were 12 distractors (6 red backslashes and 6 green forward slashes) and one target, and in target absent trials there were 13 distractors (6 red backslashes and 7 green forward slashes). In all search arrays, two distractors were placed close together and acted as a landmark for the allocentric priming condition. The anchor provided no predictive information about the location of the target in the egocentric condition.

The stimuli in the experimental trials were projected onto a blank wall. The search arrays measured approximately 20˚ both horizontally and vertically, and each search item was 1.2˚ horizontally and 3.5˚ vertically. The search arrays were placed onto black backgrounds so the whole stimulus display measured 50˚ horizontally and 40˚ vertically.

There were two priming conditions: Allocentric and Egocentric-Body. In the allocentric priming condition the location of the target was positioned relative to the landmark (two distractors close together) but at different positions relative to the observer's body. In the egocentric-body priming condition, the target maintained the same position relative to the observer's body but it occupied different positions relative to the landmark. Examples of allocentric and egocentric stimuli are shown in Figure 28A (see also Figure 17B, page 125 for examples of the placement of the search arrays onto the black backgrounds). The position of the fixation spot changed between trials so there was no fixed relationship between the location of the target and the location of the fixation spot.

Procedure

At the beginning of each trial a fixation cross was presented at a random location for 1000 ms. This was replaced with a letter, presented for 500 ms. The fixation cross was then re-presented for 500 ms before the search display was presented. During the first 100 ms that this display was presented for, a small grey square was included at the top right hand corner of the display. This was detected by an LED attached to a computer monitor unseen by the participant and triggered the TMS pulse. This ensured that the TMS pulse was delivered at the onset of the search array for every trial. Participants were not aware of the presence of this grey square as it was presented at the point where the wall met the ceiling. Participants had to decide whether the target line was present in the search array, and the search array remained on screen until either participants made their button-press response or 4000 ms had passed and no response was made. Once participants had responded/time had elapsed, a blank screen was presented for 2000 ms, before the next trial was initiated. Therefore, there was a minimum delay of 4100 ms between two consecutive search arrays. The timing procedure for each trial is illustrated in Figure 28B.

To induce position-priming, sequences of trials whereby a given target position was used 4 times within a given sequence were designed. Interspersed within a sequence there were also 2 target absent trials, thus each sequence consisted of 6 trials, with the target stimulus being present in two thirds of trials. For each priming condition, 21 different sequences were used, with a new priming position being used for each sequence. The experiment was divided into blocks of trials and for each block 6 sequences were randomly sampled, thus there were 42 trials in each block (28 present, 14 absent).

Participants completed two sessions of experimental trials, with each session consisting of 12 blocks. As there were two priming conditions in this experiment (Allocentric and Egocentric) and three TMS conditions (PPC, V5, and Sham) participants completed 4 blocks of each condition (168 trials per condition, 1008 trials in total). The order of the blocks alternated between the two priming conditions (half the participants started with an allocentric block in the first session and an egocentric in the second session). The order of the TMS conditions was randomised between both participants and testing sessions.

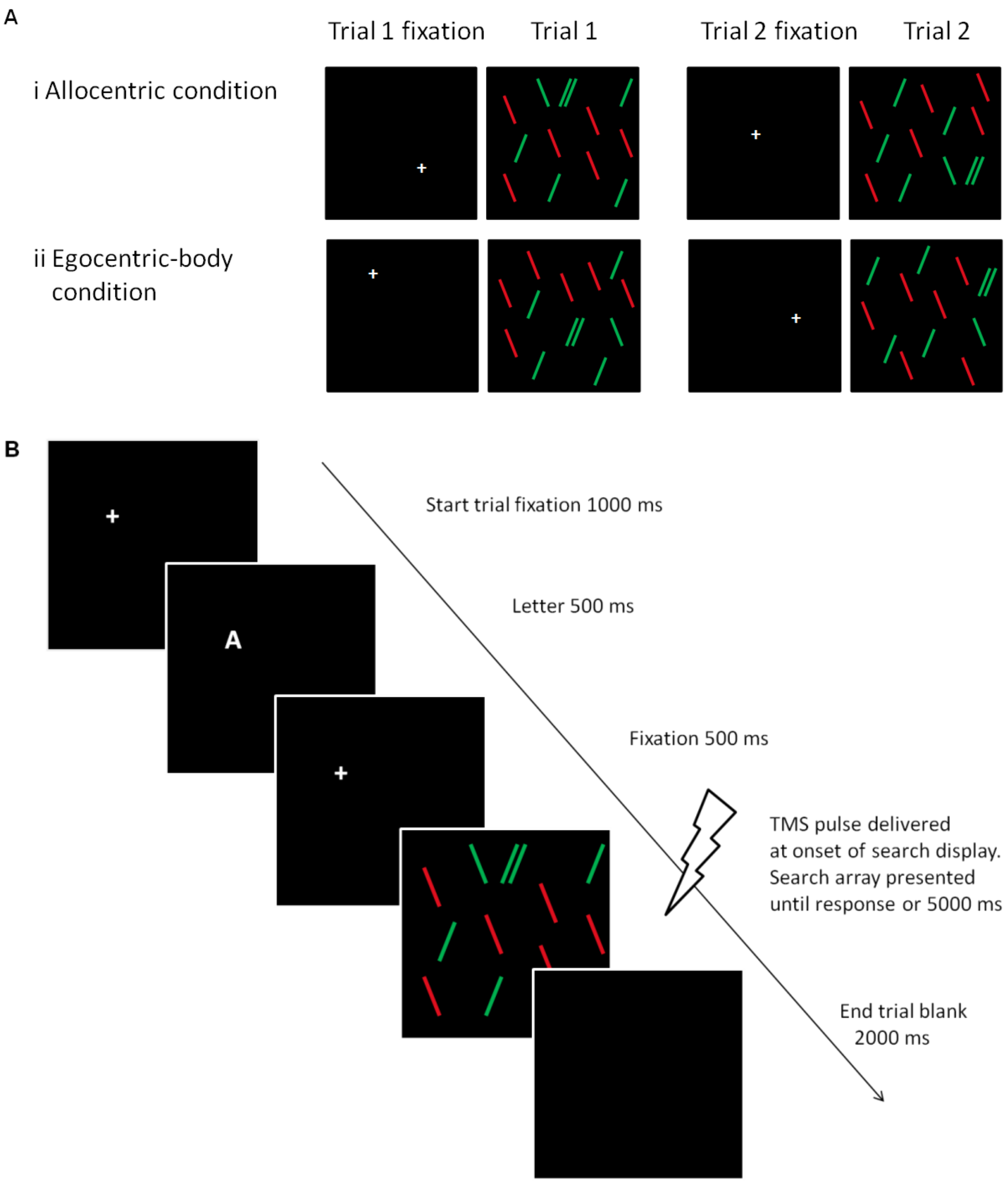

Figure 28. Priming conditions and trial sequence in Study E.

(A). Schematic of stimuli for the two priming conditions.

i) Allocentric priming condition. In trial 1 and trial 2 the target is to the left of the anchor but it occupies different positions relative to the observer and the fixation spot.

ii) Egocentric-body priming condition. When the egocentric body position is repeated, the target occupies the same absolute position on the screen, but it has no constant relationship with either the anchor or the fixation spot.

(B). The sequence and timing of each trial.

Results

Analyses

Data from the egocentric and allocentric priming conditions were analysed separately. The first analysis is concerned with the immediate priming effects and involved performing a repeated measures ANOVA, with the variables Repetition (First present trial, Second present trial) and TMS Condition (PPC, V5, Sham). Where necessary, this was followed by post-hoc t-tests to evaluate the immediate priming effects for each TMS condition. The cumulative priming effects were then evaluated, again using a repeated measures ANOVA for each priming condition, with the factors Presentation Number (1 - 4) and TMS Condition (PPC, V5, Sham). Simple effects analyses, in the form of an ANOVA for each TMS condition, were then performed. Post-hoc t-tests followed up the main effect of Priming Condition and the Presentation Number by Priming Condition interaction. Paired samples t-tests were then performed to evaluate the difference between search times to the first and last presentation of a target location within a sequence.

In order to evaluate the overall TMS effects a global analysis with the factors TMS Condition (PPC, Sham), Priming Condition (Allocentric, Egocentric)[18], and Presentation Number (1 – 4) was performed. The effect of TMS to the PPC was evaluated by considering only the first present trials of a sequence, again using a repeated measures ANOVA (TMS Condition: PPC, Sham; Priming Condition: Allocentric, Egocentric). Further analysis of the TMS effects to PPC were considered by comparing search times to the PPC and Sham conditions at the start of the experiment with those at the end of the experiment (allocentric and egocentric

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[18] Evaluating TMS effects is the only analysis in this study where the data from the allocentric and egocentric priming conditions were analysed together.

were averaged together), again using a repeated measures ANOVA and post-hoc tests, in the form of paired samples t-tests..

Data from all 12 participants was analysed. One participant was not able to receive TMS to area V5, so for that participant only PPC and Sham data was obtained. All analyses are concerned with participants' reaction times to decide whether the target stimulus was present or absent. Incorrect answers and outliers (responses with reaction times more than two standard deviations above or below the mean) were removed.

Accuracy

Participants were highly accurate in their responding to the visual search stimuli (present trials 95% correct, absent trials 92% correct). Overall, 696 trials were incorrect out of 11760 trials[19]. Outlier analysis resulted in the removal of 581 trials out of the 11064 correct trials.

Present and absent trials

Overall, search times to target absent trials ($M = 814.77$, $SD = 148.2$) were significantly slower than those to target present trials ($M = 636.42$, $SD = 105.8$), $t(11) = 8.39$; $p < .05$. This was observed in all six experimental conditions (see Table 13). Search times to the allocentric and egocentric priming conditions are now analysed separately.

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[19] One participant did not complete the V5 trials; therefore, the total number of trials is 11 participants x 1008 trials and 1 participant x 672 trials.

Table 13. Mean Search Times (ms) to Present and Absent Searches in Study E.

		Target Present	Target Absent
Allocentric	Sham	607.71 (107.1)	801.55 (158.7)
	PPC	618.96 (87.3)	798.61 (133.5)
	V5	618.67 (92.6)	812.04 (148.4)
Egocentric	Sham	646.02 (108.7)	813.15 (143.3)
	PPC	664.79 (125.5)	828.36 (164.0)
	V5	661.16 (143.8)	842.08 (166.4)

Note. Standard deviations are shown in parentheses.

Egocentric priming condition: Immediate priming effects

Figure 29 compares the search times to the first two present trials of a sequence when they directly followed one another in the egocentric priming condition. A 2 x 3 repeated measures ANOVA with the factors Repetition (First present trial, Second present trial) and TMS Condition (PPC, V5, Sham) did not reveal any significant main effects or interactions (main effect of Repetition: p = .551; main effect of TMS Condition: p = .349; and Repetition by TMS Condition interaction: p = .953). As can be seen from Figure 29 there is very little difference between search times to the first and second presentations of a target position, thus suggesting an absence of immediate priming in the three TMS conditions.

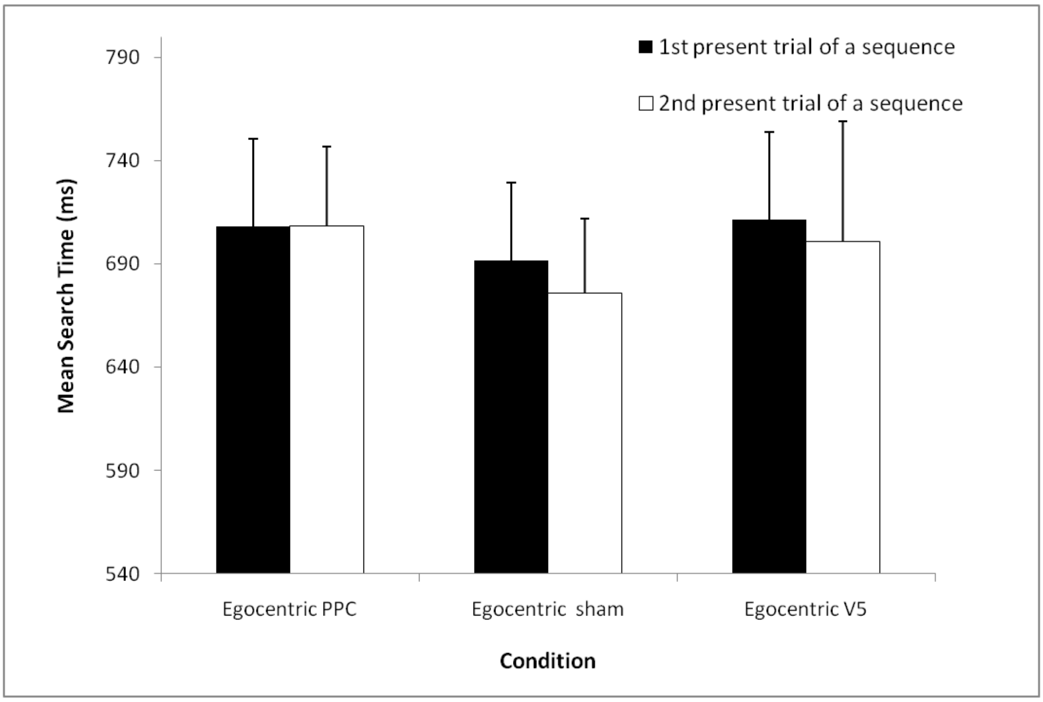

Figure 29. Mean search times (ms) to the first two target present trials of a sequence in the egocentric condition when they directly followed each other in Study E. Error bars represent + 1standard error (SE).

Allocentric priming condition: Immediate priming effects

Figure 30 compares the search times to the first two present trials of a sequence when they directly followed one another (i.e. there were no intervening target absent trials). A 2 x 3 repeated measured ANOVA with the factors Repetition (First present trial, Second present trial) and TMS Condition (PPC, V5, Sham) revealed a significant main effect of Repetition, $F(1,10) = 7.64$; $p < .05$, such that search times were faster on the second presentation of a target position, a non significant main effect of TMS Condition ($p = .252$), and a non significant Repetition by TMS Condition interaction ($p = .732$).

Post-hoc tests (2-tailed t-tests) revealed that the difference in the search times between the first presentation and the second presentation of a target location was not statistically significant in the Sham condition ($p = .077$, with a mean reduction of

27.18 ms). In the PPC condition there was an average reduction of 6.77 ms between the first and second presentation of a target location (*p* = .658) and in the V5 condition, the average reduction was 27.14 ms (*p* = .178, ms). On inspection of Figure 30, it can be seen that this difference is the smallest in the PPC condition.

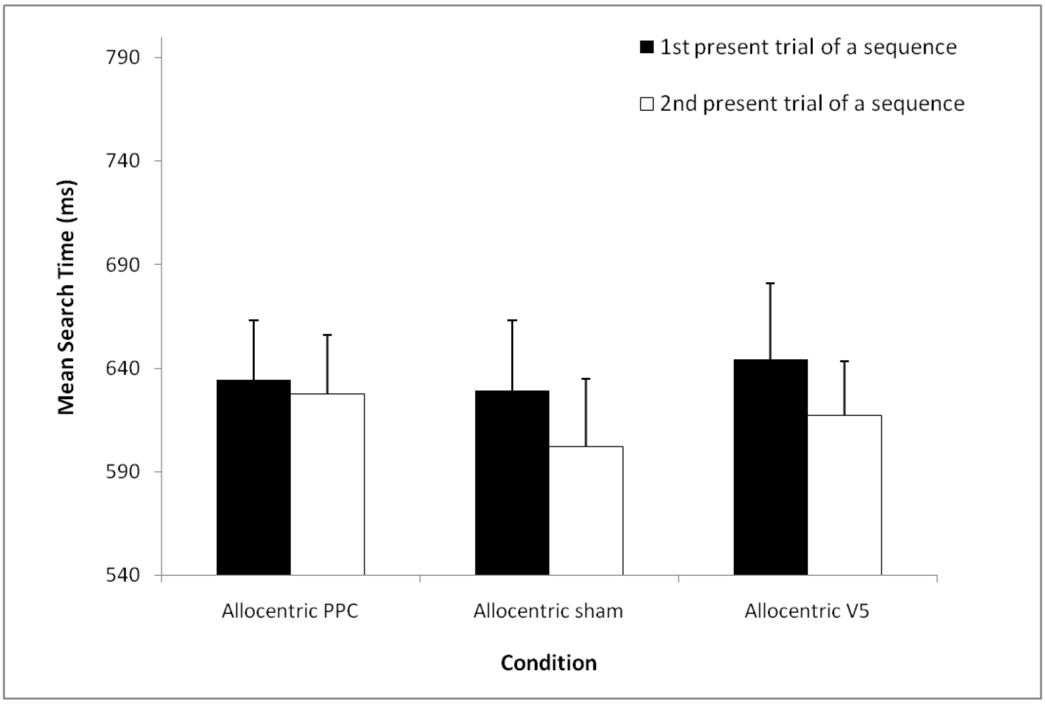

Figure 30. Mean search times (ms) to the first two present trials of a sequence in the allocentric condition when they directly followed each other in Study E. Error bars represent +1 standard error.

Egocentric priming condition: Cumulative priming effects

Search times to non-primed trials (first trials of a sequence, *M* = 712.22, *SD* = 143.6) were significantly slower than those to primed trials (trials 2 - 4 in a sequence, *M* = 647.85, *SD* = 118.9), *t*(11) = 5.21; *p* < .05; indicating cumulative priming. This was true for the three TMS conditions (see Table 14).

Figure 31 shows the search times to the 4 presentations of a target position for the three TMS conditions. Search time data were subjected to a 4 x 3 repeated measures ANOVA with the factors Presentation Number (1 - 4) and TMS Condition

(PPC, Sham, V5). This analysis revealed a statistically significant main effect of Presentation Number, *F*(3,30) = 25.47; $p < .05$, a non significant main effect of TMS Condition ($p = .335$), and a non significant Presentation Number by TMS Condition interaction ($p = .915$).

Post-hoc tests, in the form of a repeated measures ANOVA for each TMS condition, revealed that the main effect of Presentation Number was significant in the Sham condition, *F*(3,33) = 15.83; $p < .017$; significant in the PPC condition, *F*(3,33) = 11.90; $p < .017$; and in the V5 condition, *F*(3,30) = 8.39; $p < .017$. Inspection of Figure 31 shows that search times decreased as the number of presentations of a target position increased in all three TMS conditions.

Direct comparisons between search times to the first and fourth present trials of a sequence provided a measure of cumulative priming for each of the three TMS conditions and are shown in Table 14. The differences between the first and the fourth present trials were significant in all three TMS conditions: PPC: reduction of 94.10 ms, *t*(11) = 5.08; $p < .017$; Sham: reduction of 105.69, *t*(11) = 5.13; $p < .017$; and V5: reduction of 83.79 ms, *t*(10) = 3.56; $p < .017$. There were no significant differences between the three TMS conditions in terms of the amount of cumulative priming observed.

Table 14. Mean Search Times (ms) to Non-Primed Trials and Primed Trials and the Difference Between Trials 1 and 4 of a Sequence for Egocentric Searches in Study E.

	Non-primed trials (1)	Primed trials (2 - 4)	Difference between trials 1 and 4
PPC	716.55 (157.6)	653.47 (144.1)	94.10 (64.2)
Sham	707.29 (140.4)	631.89 (107.8)	105.69 (71.4)
V5	716.17 (149.5)	658.97 (124.6)	83.79 (78.0)

Note. Standard deviations are shown in parentheses.

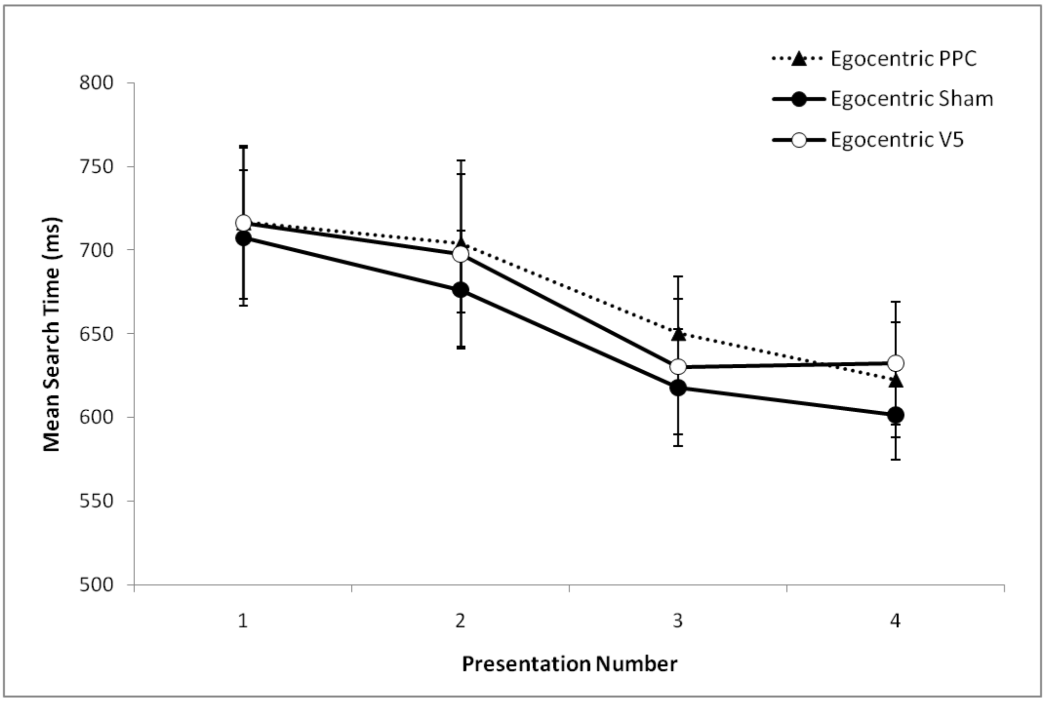

Figure 31. Mean search times (ms) to target present trials in the egocentric condition as a function of presentation number in Study E. Error bars represent the standard error (+/- 1 SE).

Allocentric priming condition: Cumulative priming effects

Within each sequence of trials the target stimulus was at a given position four times. Search times to non-primed trials (first trials of a sequence, M = 634.84, SD = 102.3) were significantly slower than those to primed trials (trials 2 - 4 in a sequence, M = 614.92, SD = 93.1), $t(11) = 2.82$; $p < .05$; indicating cumulative priming. This was true for the three TMS conditions (see Table 15).

Figure 32 shows the search times to the 4 presentations of a target position for the three TMS conditions. Search time data were subjected to a 4 x 3 repeated measures ANOVA with the factors Presentation Number (1 - 4) and TMS Condition (PPC, Sham, V5). The analysis revealed a statistically significant main effect of Presentation Number, $F(3,30) = 5.16$; $p < .05$, a non significant main effect of TMS Condition ($p = .254$), and a non significant Presentation Number by TMS Condition interaction ($p = .657$).

Post-hoc tests, in the form of a repeated measures ANOVA for each TMS condition, revealed that the main effect of Presentation Number was significant in the Sham condition, $F(3,33) = 4.07$; $p < .017$, but not in the PPC condition ($p = .696$) or the V5 condition ($p = .198$).

Direct comparisons between search times to the first and fourth present trials of a sequence provided a measure of cumulative priming for each of the three TMS conditions and are shown in Table 15. The difference was marginally non significant in the Sham condition ($p = .03$), non significant in both the PPC condition ($p = .403$) and the V5 condition ($p = .264$).

Table 15. Mean Search Times (ms) to Non-Primed Trials and Primed Trials and the Difference Between Trials 1 and 4 of a Sequence for Allocentric Searches in Study E.

	Non-primed trials (1)	Primed trials (2 to 4)	Difference between trials 1 and 4
PPC	632.37 (100.9)	621.81 (93.8)	14.15 (56.4)
Sham	631.18 (116.7)	602.93 (108.5)	23.50 (32.7)
V5	640.28 (107.6)	618.42 (86.7)	22.16 (62.2)

Note. Standard deviations are shown in parentheses.

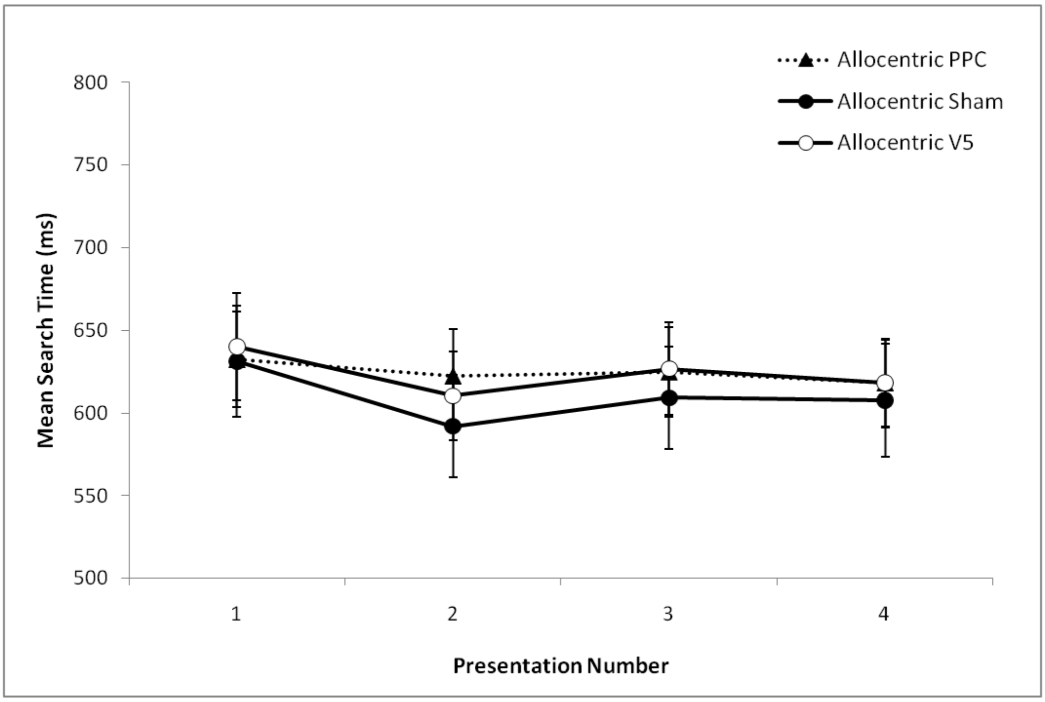

Figure 32. Mean search times (ms) to target present trials in the allocentric condition as a function of presentation number Study E. Error bars represent the standard error (+/- 1SE).

TMS effects, spatial priming, and frames of reference

A global analysis was performed on the data which looked at overall TMS effects, and as the primary interest of this experiment was the role of the PPC on priming, this analysis was restricted to the PPC and Sham conditions. As such, a 2 x 2 x 4 repeated measures ANOVA was performed on the data with the factors TMS Condition (PPC, Sham), Priming Condition (Allocentric, Egocentric), and Presentation Number (1 - 4). The analysis found a statistically significant main effect of TMS Condition, $F(1,11) = 5.95$; $p < .05$, such that search times were slower in the PPC ($M = 648.91$, $SD = 110.8$) condition compared to the Sham condition ($M = 630.37$, $SD = 110.3$)[20]; and a significant main effect of Priming Condition, $F(1,11) = 21.35$; $p < .05$, with search times to allocentric searches ($M = 617.22$, $SD = 100.4$) being faster than search times to egocentric searches ($M = 662.05$, $SD = 120.7$). The main effect of Presentation Number was also statistically significant, $F(3,33) = 15.91$; $p < .05$. Search times were slowest on the first presentation of a target location ($M = 671.84$, $SD = 123.2$) and became faster as the number of presentations increased (2nd presentation: $M = 648.67$, $SD = 112.2$; 3rd presentation: $M = 625.5$, $SD = 107.2$; 4th presentation: $M = 612.49$, $SD = 102.3$).

Of the 2-way interactions, only the interaction between Priming Condition and Presentation Number was significant, $F(3,33) = 15.91$; $p < .05$. The reduction in search times as a function of Presentation Number was greatest in the egocentric priming condition (1st presentation: $M = 711.92$, $SD = 146.8$; 4th presentation: $M = 612.02$, $SD = 103.6$), with a mean reduction of 99.90 ms, compared to that in the allocentric priming condition (1st presentation: $M = 631.78$, $SD = 103.9$; 4th presentation: $M = 612.95$, $SD = 103.0$), with a mean reduction of 18.83 ms.

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[20] The mean search time (ms) to trials when TMS was applied to V5 was 646.52 ($SD = 112.1$)

However, it could be argued that this is because search times in the egocentric searches were slower at the first presentation of a target position compared to the allocentric searches, thus providing greater scope for a reduction in search times in the egocentric priming condition.

The 3-way interaction between TMS Condition, Priming Condition, and Presentation Number was not significant ($p = .892$).

TMS effects

While the global analysis found that overall search times were slower in the PPC condition compared to the Sham condition, the analysis presented now considers only the first target present trials of a sequence for the two TMS conditions. At this point in a sequence the target appears in a new location, and thus there are no priming effects; therefore, it is able to provide a clean picture of the TMS effects. Table 16 shows the average search times to the first present trials of a sequence for the two TMS conditions for the two priming conditions, both separately and averaged together. A 2 x 2 repeated measures ANOVA with the factors TMS Condition (PPC, Sham) and Priming Condition (Allocentric, Egocentric) revealed that the main effect of TMS Condition was not significant ($p = .677$). It can be seen from Table 16 that there is no difference between the search times at this point for the different TMS conditions.

The analysis found a statistically significant main effect of Priming Condition, $F(1,11) = 19.49$; $p < .05$. Search times in the allocentric condition ($M = 631.77$, $SD = 103.9$) are faster than those in the egocentric condition ($M = 711.92$, $SD = 146.8$) for both TMS conditions. Owing to the nature of the organisation of the trials within the experiment, each block of trials consisted of seven sequences;

therefore, it is only the first present trial of the first sequence of a block that is truly free from any frame of reference information. When only these trials are compared the difference between allocentric search times (*M* = 675.01, *SD* = 128.66) and egocentric search times (*M* = 743.83, *SD* = 174.1) only approaches significance (*p* = .068)[21].

The interaction between TMS Condition and Priming Condition was not significant (*p* = .755).

Table 16. Mean Search Times (ms) to the First Present Trial of a Sequence for each TMS Condition in Study E.

	Allocentric	Egocentric	Average of two priming conditions
PPC	632.37 (100.9)	716.55 (157.6)	674.46 (124.6)
Sham	631.18 (116.7)	707.29 (140.4)	669.23 (125.3)

Note. Standard deviations are shown in parentheses.

Of particular interest is the similarity in search times to the first present trial of a sequence for the PPC and Sham conditions (see Figure 32 and Figure 31for allocentric and egocentric priming conditions respectively), as this in not in line with the well reported finding that TMS to the PPC increases search times (Ashbridge, et al., 1997; Ellison, et al., 2003). However, owing to the many conditions and variables that were involved in this experiment (three TMS conditions, two Priming Conditions, and four levels of Presentation Number) in order to get sufficient numbers of trials per condition for valid statistical analysis, it was necessary that

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[21] The search time for the allocentric condition represents the average search times of the first present trial of a block for the PPC and Sham TMS conditions, and likewise for the egocentric priming condition.

participants completed a total of 24 blocks of trials over two testing sessions. Therefore, owing to the length of this experiment, it is possible that some of the TMS effects may have been reduced with the averaging of search times across all 24 blocks. To investigate a possible reduction in TMS effects between the start and the end of the experiment, the average search times to target present trials in the first PPC block of the experiment are compared with the average search times to the target present trials in the first Sham block of the experiment. The same comparison was also completed for the last TMS and Sham blocks of the experiment[22].

A 2 x 2 repeated measures ANOVA with the factors Block (First, Last) and TMS Condition (PPC, Sham) revealed a significant main effect of Block, $F(1,11) = 21.38$; $p < .05$; a marginally non significant main effect of TMS Site ($p = .061$); and a non significant Block by TMS Condition interaction ($p = .222$). It can be seen from Figure 33 that search times to target present trials are slower in both TMS conditions during the first block of trials ($M = 666.07$, $SD = 119.0$) compared to the target present trials in the last block of trials ($M = 615.12$, $SD = 110.3$).

Post-hoc tests in the form of paired samples t-tests (normalised data), revealed that the difference in search times between the first block of PPC and Sham trial ($M = 51.55$, $SD = 96.6$) was approaching significance ($p = .092$) whereas the same comparison ($M = 7.61$, $SD = 48.7$) was not significant for the last block of trials ($p = .599$). This can be seen in Figure 33, and therefore suggests that the effect of TMS to the PPC reduced as a function of practice.

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[22] As the order of both the priming conditions and TMS conditions was randomised across participants the first TMS PPC block could be either allocentric or egocentric (for 7 participants it was egocentric and for 5 it was allocentric). The block selected as the last block of the experiment matched the first in terms of priming condition, and may not have been the last TMS block of the experiment. This controlled for differences between search times to the two frames of reference.

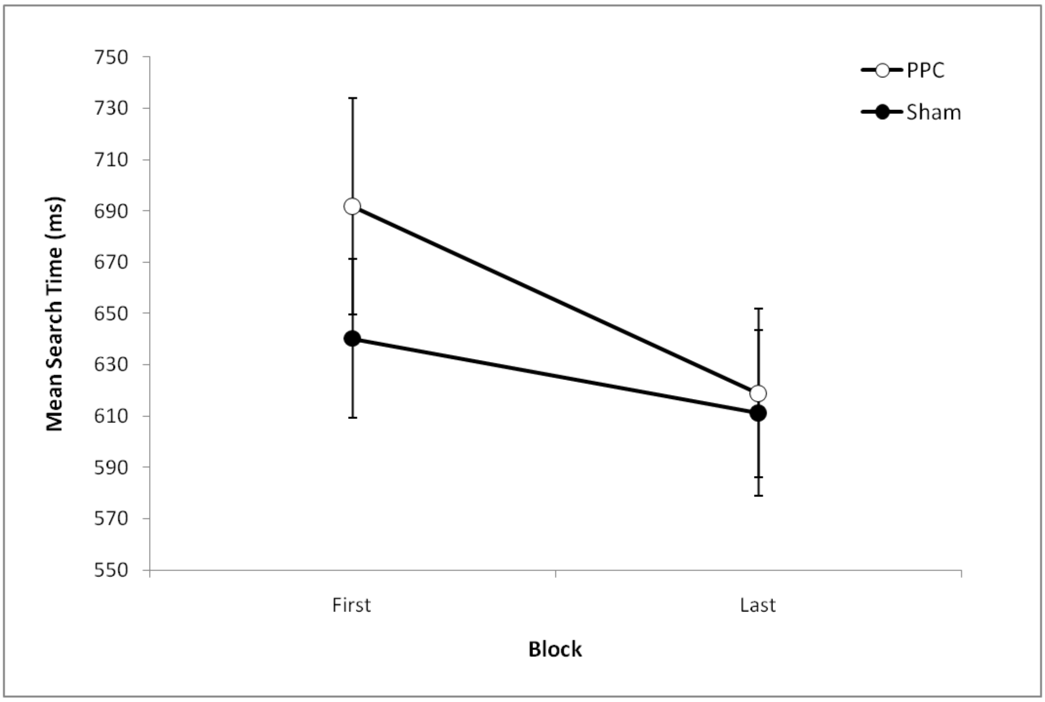

Figure 33. Mean search times (ms) to target present trials in the first and last TMS and Sham blocks in Study E. Error bars represent the standard error (+/- 1 SE).

Study E Summary

In the egocentric priming condition, no immediate priming effects were observed, but significant cumulative priming was obtained for all three TMS conditions. However, the amount of priming did not significantly differ between TMS conditions. In contrast, significant cumulative priming was only observed in the allocentric sham condition. These findings therefore confirm once more that egocentric priming is consistent and more robust than allocentric priming. The main surprise of the findings from this study was the absence of a PPC-TMS effect on visual search performance in general. This is in striking contrast to earlier findings (Ashbridge, et al., 1997; Ellison, et al., 2003) and will be discussed further.

Discussion of Study E

The aim of this study was to investigate the effect of applying transcranial magnetic stimulation to the posterior parietal cortex on performance in a conjunction visual search task where the location of the target was repeated either in terms of its allocentric position (relative to an anchor in the display) or its egocentric position (relative to the observer's body). When no TMS was applied (i.e. the Sham condition) the previous finding that an egocentric-body frame of reference can drive spatial priming in conjunction visual search was replicated. Significant priming effects for targets defined using an allocentric frame of reference were also observed (cumulative priming, sham condition). Of the two, across the studies presented in this thesis, the allocentric priming effects have consistently been less than the egocentric priming effects; therefore, to find significant cumulative allocentric priming in this experiment with only twelve participants adds considerable weight to the previous findings.

Furthermore, in the previous studies, with the exclusion of Study D where the inter-trial interval was manipulated, the longest minimum delay between two consecutive search presentations was 2500 ms (Experiment B2)[23]. Owing to the introduction of TMS in this experiment, the minimum time between two search arrays was 4100 ms, and as the priming effects were cumulative, building up over sequences of four target present trials which were interspersed with target absent trials, the findings from this experiment extend those of Studies A and B and replicate those of Study C.

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[23] The minimum delay between trials in Study C (body move experiment) was 4500 ms but in this study the set up was different and involved participants standing and moving between two screens. Only the inter-trial interval in Experiment B2 is directly comparable to this TMS study.

It was observed that TMS to the PPC did not have a detrimental effect on the magnitude of the cumulative priming effects. It was found that search times were generally slower when TMS was applied to the PPC compared to those in the Sham condition; however, and although not statistically significant ($p = .133$), this trend was also observed when TMS was applied to area V5 (see footnote 20, page 190). Therefore, the difference between search times in the PPC and the Sham conditions may reflect a general slowing when TMS is applied to the participant. By comparing the TMS effects (the difference between TMS and Sham search times to present trials) at the start of the experiment with those at the end of the experiment, the data suggests that the TMS effects decrease with practice, which is in line with the findings of Walsh et al. (1998) who reported that with practice TMS to the PPC no longer has a detrimental effect on the speed of participant's search times.

No evidence that TMS to the PPC disrupted search performance when the target location was not repeated, that is, for the first present trials of a sequence, was found: at this point there was no difference between search times in the Sham and the PPC conditions. The crucial role of the PPC in conjunction visual search has been consistently reported (Ashbridge, et al., 1997; Ellison, et al., 2003); therefore, this finding is quite surprising. However, in the PPC localisation task in which TMS was applied to a number of different sites which centred on an area known to be in the vicinity of the PPC (9 cm dorsal and 6 cm lateral to the mastoid-inion) a slowing in search times relative to when no TMS was applied was observed for all participants (see Appendix D). This suggests that it was not the characteristics of the stimuli that were used that undermined the TMS effects, and therefore there must be some other explanation. As such, it is thought that the way in which the stimuli were presented, as opposed to the nature of the stimuli, may account for the absence of TMS effects in this study.

Spatial priming experiments have often solely focused on repeating the absolute location of a target and have not been concerned with the frame of reference that the target is defined in. Therefore, the most common method of stimuli presentation is on a computer monitor (for example, Ellison, et al., 2003; Kristjansson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Kumada & Humphreys, 2002; Maljkovic & Nakayama, 1996; Muggleton, Juan, Cowey, & Walsh, 2003; Walsh, et al., 1998). However, as the aim of the experiments presented in this thesis was to investigate how specific reference frames influence spatial priming, presenting the visual searches on a computer monitor was not sufficient. By presenting the stimuli onto a blank wall in a darkened room and asking participants to sit/stand between two and three metres away from them, it was possible to ensure that no other stable visual cues could be used instead of the frames of reference that were under investigation. For example, in the allocentric priming condition, where the target was defined relative to a salient item in the search array, the edge of a computer monitor would have provided additional information over the target location but this confound was avoided in the studies presented here owing to the method of presentation. Additionally, by presenting the search arrays on a blank wall it was possible to manipulate the various egocentric frames of reference more than would be possible with using a computer monitor as the search area was larger; for example, target locations could be more varied and the eye movements required to locate the target from fixation could be bigger.

The projected stimuli used in this experiment were '*beyond arms reach'* of the participants, and are therefore said to be in extra-personal space, that is, in far space; conversely, when stimuli are presented on a computer monitor, as they were in the experiments by Ellison et al. (2003) and Walsh et al. (1998), they are usually '*within arm's reach'* of the participants, which is known as peri-personal space, or near space (Berti & Rizzolatti, 2002; Yang & Kapoula, 2004). A number of researchers have reported that there is a dissociation between performance on tasks presented in extra-personal and peri-personal space. While there is limited research into the influence of viewing distance on visual search performance, there has been a great deal of research into this space dissociation using a line bisection task. Fink et al. (2000) and Fink, Marshall, Weiss, and Zilles (2001), found the line bisection task to involve the PPC, and therefore deemed relevant to the current discussion.

Healthy subjects often exhibit what is called *pseudoneglect*, which is a tendency to bisect a line to the left of the centre; for example, Bowers and Heliman (1980), Jewell and McCourt (2000), and McCourt and Jewell (1999). It has been found that the degree of this pseudoneglect is influenced by the distance from which the stimuli are observed from. When McCourt and Garlinghouse (2000) manipulated the viewing distance of stimuli they found that participants were more accurate at bisecting lines when they were observed from a greater distance, that is, the stimuli were presented in far space. Likewise, Bjoertomt, Cowey, and Walsh (2002) found that participants were more erroneous on a line bisection task when the stimuli were presented in near space.

With regards to brain function, using PET, Weiss et al. (2000) observed that the patterns of activity for tasks, namely, manual line bisection and pointing to dots, completed in near and far space were different. It was found that for near judgements activation was in the parietal cortex along the intraparietal sulcus and the dorsal occipital cortex, while for judgments made in far space, the ventral occipital cortex and the right medial temporal cortex were activated (Weiss, et al., 2000). Furthermore, Weiss, Marshall, Zilles, and Fink (2003) evaluated performance in near and far space of both a manual and a perceptual line bisection tasks; therefore, investigating potential differences as a function of nature of the task (motor or perceptual). Weiss et al. (2003) concluded that "differential neural mechanisms are implicated when processing stimuli in near versus far space irrespective of the particular task demands" (p. 844). Therefore, under normal viewing conditions, the accuracy of performance, as well as the brain areas that are involved, is different for stimuli presented in near and far space.

Further supporting this, when Bjoertomt et al. (2002) applied TMS to either the right PPC or the right ventral-occipital lobe it was found that TMS to the right PPC resulted in a significant shift in participant's perception of the mid-point of the line, thus the degree of pseudoneglect increased. However, this was only the case when the stimuli were presented in near space. The opposite pattern of results was observed with TMS to the right ventral occipital lobe: this shift in perception was observed for stimuli presented in far space only. These findings therefore further suggest that there is a difference in the neurology underlying spatial processing in near and far space and that the PPC might be selectively involved in tasks performed in near space (Bjoertomt, et al., 2002).

This dissociation in near and far space has also been reported with spatial neglect patients, and again implicates PPC areas. For example, Halligan and Marshall (1991) evaluated the performance of stroke patient (T.M.) who had an infarct to his posterior parietal cortex, with his superior and medial parietal cortex being spared. Halligan and Marshall (1991) found that patient T.M. displayed visual neglect for line bisection in peri-personal space (i.e. near space) but not in extra-personal space (i.e. far space), and the authors concluded that “severe left visual neglect in peripersonal space can coexist with minimal or no neglect in extrapersonal space” (1991, p. 500). This dissociation in near and far space is further supported by Vuilleumier, Valenza, Mayer, Reverdin, and Landis (1998) who observed that a patient with a right temporo-occipital hematoma displayed neglect for stimuli presented in far space while not showing this deficit for those presented in near space

Therefore, taken together, the observations of both neurologically intact individuals and those with brain damage strongly suggest that there is dissociation between processing stimuli presented in near and far space, and that posterior parietal areas are involved in processing stimuli presented in near space, or within arm’s reach. Data from imaging studies suggests that the differential anatomical localisation of near and far space also maps onto the location of the ventral and dorsal steams respectively (Bjoertomt, et al., 2002; Milner & Goodale, 1993; Weiss, et al., 2003).

In conclusion, this current study has raised a number of interesting questions. The PPC has long been implicated in visual search; however, the existing research is restricted to stimuli displays being presented in peri-personal space (i.e. on a computer monitor). Conversely, the findings from this study, as well as the observations of the effect of viewing distance on a line bisection task, would suggest minimal involvement of this area in visual search stimuli presented in extra-personal space. Therefore, further research into this, as well as determining which areas are involved in far visual search would greatly add to the literature.

Chapter 7 – General Discussion

The two frames of reference that are commonly used are egocentric, whereby the location of an object is defined relative to the observer, or to a specific part of the observer's body; and allocentric, where the location of the object is defined relative to another item or landmark in the visual scene (Burgess, et al., 2004; Mou, et al., 2008). The ventral and dorsal processing streams in the primate brain have long been thought to subserve perception and action respectively (Milner & Goodale, 1993, 2006) and the observations that a patient with ventral stream damage (D.F.) is impaired in perceptual tasks but not visuomotor tasks have supported this distinction. More recently it has been found that D.F. was impaired on tasks, both perceptual and visuomotor, when allocentric information was required, while her performance on the same tasks was unaffected when egocentric information was required in their completion (Schenk, 2006). Further support for an allocentric processing deficit in this patient has also been reported in other studies (Carey, et al., 2009; Carey, et al., 2006; Murphy, et al., 1998). This thesis sought to investigate allocentric and egocentric frames of reference in greater detail, and specifically whether egocentric information is available after a temporal delay. This was achieved by evaluating spatial priming in visual search, and determining how search performance is modulated by the frame of reference that the target is defined in. Spatial priming refers to a speeding in the time taken to locate a specified target when the location of the target is repeated from one trial to the next (Huang, et al., 2004; Kristjansson, et al., 2002; Shore & Klein, 2001).

The experiments presented in this thesis used either a simple feature search task (Study A) or a conjunction search task (Studies B – E) to investigate the consequences of repeating the egocentric and allocentric information of the location of the target on search performance. While a short discussion of the results was presented after each experiment, in this section I will attempt to integrate the findings across the different studies which form my thesis. I will start with a summary of the findings, followed by a discussion of their implications for an understanding of spatial priming in visual search and the implications for the perception-action model. Finally, the limitations and opportunities for further research will be discussed.

Summary of results

Experiment A1 investigated the effect of repeating either the absolute location of a target (egocentric condition) or the relative location of the target with regards to a landmark in the search array (allocentric condition). A significant reduction in search times as a function of repetition was observed in both conditions. The minimum period of time between the presentation of two consecutive search arrays was 3500 ms; therefore, this experiment provided the first indication that egocentric information is still available a few seconds after initial presentation. However, the comparison between the priming effects in the two conditions was complicated by an overall speeding of search times to the egocentric displays; therefore, from the findings of Experiment A1 it was not possible to conclude whether allocentric or egocentric information is the most effective in spatial priming.

Experiment A2 sought to determine the reason for the faster search times in the egocentric condition observed in Experiment A1, and evaluated the influence of the allocentric anchor (two distractors placed close together) on search performance. It was found that when the anchor was present in the search array, search times were considerably longer compared to when the anchor was absent. This finding is important for two reasons. Firstly, it provided an explanation of the differences in initial search times between the egocentric and allocentric conditions in Experiment A1; and secondly, it indicated the need for the anchor to be present in all priming conditions in subsequent experiments, even though only has a functional role in the allocentric priming condition.

Experiment A3, having controlled for the presence of the anchor, while replicating the findings of Experiment A1 of significant cumulative priming effects in the egocentric condition, failed to find evidence of priming in the allocentric condition. As the nature of the allocentric displays had not changed between Experiments A1 and A3, it is thought that the absence of priming effects may be explained by the reduced number of sequences in Experiment A3. Furthermore, search times levelled off after five or six repetitions of a target location; therefore, in future experiments the number trials in a sequence would be reduced, allowing a greater number of target positions to be investigated.

Experiment A4 evaluated the effectiveness of the letter identification task prior to the presentation of search arrays at ensuring participant's gaze returned to the centre of the display between trials. It was found that when participants were not allowed to foveate the centrally presented letter, accuracy of identification fell to below 50%. Consequently, in future experiments, when participants failed to correctly report the letter the search time data from that trial would not be included in the analysis, as this would indicate that they had not correctly foveated the letter.

Experiment A5 investigated whether egocentric or allocentric information is responsible for driving the priming effects, and extended an experiment by Maljkovic and Nakayama (1996). Significant allocentric and egocentric priming was observed, and furthermore, there was no difference in the magnitude of the priming effects in the egocentric condition and in the condition where allocentric information and egocentric information both defined the location of the target. Therefore, it was concluded that egocentric information is the most relevant frame of reference in spatial priming in visual search.

As Study A used a feature search task and the subsequent experiments would employ a conjunction search task, Experiment B1 evaluated the effect of set size on these two search types. On finding a differential effect of set size on the two, in that, set size incrementally increased search times only in the conjunction search, it was concluded that different search mechanisms were required in the completion of these two searches, namely, that the feature search (Study A) was an easy “pop-out” search while the conjunction search required more laborious, serial search mechanisms.

Using the conjunction search task, Experiment B2 investigated which specific egocentric frame of reference was responsible for the previously observed priming effects: an eye-centred or a body-centred frame of reference. Repeating the location of the target relative to the fixation spot, and thus eye position, did not have any consistent effect on search times, whereas, repeating the location relative to the observer’s body yielded significant priming effects. There was also no difference between the priming effects when the target location was repeated relative to the body and when it was repeated relative to the body and the eye simultaneously; therefore, it was concluded that participants were coding the location of the target relative to their bodies.

Study C followed up the previous studies by investigating the body-centred frame of reference further. When participants were required to move to a new location in between trials, and the location of the target maintained the same position relative to the participants’ bodies, search times were once again speeded. This therefore demonstrates that the priming effects are the result of the information being coded relative to the body.

Having demonstrated that egocentric representations, centred on the body, can be stored for a few seconds (the minimum delay between the presentation of two consecutive search arrays in the previous experiments ranged between 2200 ms and 4500 ms) Study D investigated the time course of these representations more formally by manipulating the inter-trial interval. Of interest, egocentric priming was observed at the longest delay, that is, when there was a minimum delay of eight seconds between two consecutive search arrays. As these priming effects built up over the presentation of four target present trials, which were interspersed with the presentation of target absent trials, this study provides evidence that egocentric information is available for a considerable period of time.

Finally, Study E coupled the spatial priming paradigm with transcranial magnetic stimulation (TMS) to investigate the functional role of the posterior parietal cortex (PPC) in allocentric and egocentric priming. While TMS to the PPC has previously been found to disrupt spatial priming effects (Ashbridge, et al., 1997; Ellison, et al., 2003), significant priming was observed for both allocentric and egocentric frames of reference in this experiment. It was proposed that the presence of priming effects may be explained by a methodological factor: in previous experiments the stimuli were presented in near space, i.e. on a computer monitor, while in this experiment, the stimuli were presented in far space, i.e. on the wall. There has been some research indicating a near/far dissociation in the role of the PPC, in that the PPC is selectively involved in near space processing (Bjoertomt, et al., 2002; Weiss, et al., 2003).

Interpretation of findings

There are two findings from this thesis which are important. Firstly, contrary to the assumption of Milner and Goodale's perception-action model (1993, 2006), egocentric representations are not highly transient but are still available after a temporal delay (upwards of eight seconds, Study D). Secondly, the most important egocentric frame of reference was found to be body-centred, as when participants moved to occupy a new location, priming effects were still observed (Study C). The implications of these findings will be presented, after considering how the findings fit more generally within the visual search field.

Visual search literature

This thesis investigated memory for egocentric representations using spatial priming in visual search. Significant priming effects were observed for both a simple feature search task (Study A) and a conjunction search task (Studies B – E), thus, demonstrating that the egocentric and allocentric priming effects are not specific to either a feature or a conjunction search paradigm. Interestingly, the cumulative priming effects were greater in the egocentric condition when using the conjunction rather than the feature search paradigm. This might reflect the increased difficulty of the conjunction search (Duncan & Humphreys, 1989, 1992; Treisman & Gelade, 1980). In this case, greater difficulty translated into longer search times (as shown in Experiment B2), meaning that during a conjunction search there was greater scope for search time reductions with repetition.

More specifically, the experiments presented here add to the existing literature on priming, and are particularly informative in determining what is actually primed in location priming. In position priming experiments it was often the case that while the absolute location of a target was repeated, the formation of the search array was also maintained across trials; for example, Geyer, Müller, and Krummenacher (2006) presented the search elements in a four by four grid (see also Hilstrom, 2000: Maljkovic & Nakayama, 2000). Therefore, the target's location relative to the other items (allocentric position) was also repeated. While Maljkovic and Nakayama (1996) went some way to addressing whether the target's relative location or absolute location was being primed, their results were inconclusive. However, evidence has been provided here (Experiment A5) that when both the relative coordinates (allocentric) and the absolute coordinates (egocentric) of a target location are repeated, it is the egocentric information that drives the priming effects.

While search times have been found to become faster with repetition; for example, either repeating a feature of the target (Hilstrom, 2000; Huang, et al., 2004; Maljkovic & Nakayama, 1994) or the location of the target (Kristjansson, et al., 2005; Kumada & Humphreys, 2002), and also in the experiments presented in this thesis, it is believed that there are two independent and opposing processes that may account for the overall speeding: facilitation and inhibition. Indeed, both Maljkovic and Nakayama (1996) and Geyer, Müller, and Krummenacher (2007) observed that while participants were faster at detecting a target if it appeared in a location that it previously appeared in, relative to a neutral location (i.e. facilitation), search times were slower if the target was presented in a location that was previously occupied by a distractor item (location-based inhibition of return, Danziger, et al., 1998; Posner & Cohen, 1984; Tipper, et al., 1994). It is thought that the spatial arrangement of the stimuli in search arrays impacts the effect of distractor inhibition on search times (Geyer, et al., 2007). Position priming research has to some degree presented stimuli in random locations across trials; however, frequently this is achieved by placing the stimuli randomly in an invisible grid (Kumada & Humphreys, 2002, for example); therefore, making the likelihood of targets appearing in the locations that formally held a distractor high. Conversely, in the search arrays presented in the experiments in this thesis, there was no fixed spatial arrangement of the stimuli; therefore, while the target would have been in the same location in the egocentric condition across trials, the distractor stimuli would not have occupied the same formation as they did in previous trials. Therefore, it is possible to argue that the observed priming effects are the result of the target location being facilitated and not the locations of the distractors being inhibited. Supporting this, Geyer et al. (2007) found no inhibitory influence of the distractors on position priming when the spatial configuration of the stimuli was not predictable, that is, when the placement of stimuli was random.

With regards to the observation that search times in the allocentric condition were faster than those in the egocentric conditions, the only difference between the search arrays was that the location of the target was repeated relative to the position of the anchor in the allocentric searches. It is thought that this coupling between the target and the anchor reflects *contextual cueing*, whereby search performance is facilitated if all, or part, of the stimulus configuration is repeated across trials (Chun, 2000; Chun & Jiang, 1998). Chun and Jiang (1998) argue that “memory of visual context can guide spatial attention towards task-relevant aspects of a scene” (p. 28), thus potentially offering an explanation as to why searches in the allocentric priming condition were consistently faster than those in the egocentric conditions.

Egocentric representations can be stored

It is argued that visuomotor performance depends on the use of egocentric representations, that is, in order to interact with a certain item, the subject must know where the target is in relation to their effector that will perform the action (Milner & Goodale, 1995, 2006; Rains, 2002; Wang & Spelke, 2000); for example, a footballer must know the exact location of the ball relative to their foot in order to accurately strike the ball. The perception-action model (Milner & Goodale, 1995, 2006) argues that the dorsal stream is responsible for visuomotor processing; therefore, Milner and Goodale assumed that the dorsal stream relies on egocentric representations. As this information changes with every movement of the observer, they therefore assumed that egocentric representations in the dorsal stream are not stored. Contrary to this assumption, the findings presented in this thesis suggest that egocentric information can persist for more than a few seconds.

While it is not possible to directly show that the egocentric information used in the experiments presented here derives from the dorsal stream, there is some evidence that this is the case. Schenk (2006) found that the allocentric processing abilities of a patient with ventral stream damage were impaired, while both her dorsal stream and egocentric coding were intact and unaffected. Furthermore, research into the neural correlates of spatial coding suggests that different mechanisms are involved in making allocentric and egocentric judgements; for example, the posterior parietal cortex, and thus dorsal stream areas, has been associated with egocentric representations (Committeri, et al., 2004; Galati, et al., 2000; Vallar et al., 1999). Zaehle et al. (2007) found that the precuneus, an area which is involved in the control of visually guided hand movements and has been linked with optic ataxia (Karnath & Perenin, 2005), was selectively associated with egocentric representations. Furthermore, Weniger et al. (2009) observed that there was a negative relationship between the volume of the precuneus and performance on the egocentric orientation task. The symptoms of optic ataxia patients, who have damage to dorsal stream areas, manifest themselves in degraded visuomotor coordination abilities (Ellis & Young, 1996; Jakobson, et al., 1991), suggesting an impairment in using egocentric representations. It has also been found that patients with parietal lobe damage show greater impairments at completing a spatial navigation task from an egocentric perspective compared to frontal patients (Seubert, Humphreys, Muller, & Gramann, 2008), and that they are selectively impaired on a task requiring egocentric performance while their performance on an allocentric version of the task is the same as that of healthy controls (Weniger, et al., 2009). Therefore, research from a variety of sources suggests that egocentric information derives from the dorsal stream, and thus it is tempting to conclude that the egocentric information is derived from dorsal stream structures.

However, it should be noted that while there is a great amount of research implicating the dorsal stream's responsibility for egocentric processing, there is some evidence to suggest that the ventral stream is involved in egocentric as well as allocentric representations. For example, Zaehle et al. (2007) observed activation in ventral stream areas, namely, the inferior temporal gyrus, the calcarine sulci, and the superior occipital gyrus when egocentric judgements were made.

While the studies in this thesis are not able to provide direct evidence that the dorsal stream was involved in egocentric priming after a delay, it has shown the egocentric information is not as transient as previously thought. The observation that egocentric information is not highly transient it at odds with the perception-action model (Milner & Goodale, 1993, 2006). However, evidence that the dorsal stream is active for tasks completed after a temporal delay has been found, which is therefore supportive of the conclusions developed in this thesis. For example, using fMRI, Connolly et al. (2003) observed activation in dorsal stream areas when participants were required to complete a motor action after a delay of nine seconds. Counter intuitively, the visuomotor deficits of optic ataxia patients are reduced with the onset of a temporal delay (Goodale, Jakobson, et al., 1994; Milner, et al., 2003; Milner, et al., 2001). In light of this, as well as the assumption that dorsal stream representations are short lived (Westwood, et al., 2003), it was proposed that the improvement in the visuomotor performance of optic ataxia patients with a delay was the result of a shift from using dorsal stream representations to using ventral stream representations (Goodale, Jakobson, et al., 1994; Himmelbach & Karnath, 2005; Milner, et al., 2001). However, on observing "robust and indistinguishable activation of intact dorsal occipital and parietal areas adjacent to the patient's lesions" (p. 1508) for both immediate and delayed actions in patient I.G, Himmelbach et al. (2009) concluded that there was no evidence of reduced dorsal activity after a temporal delay of five seconds. There was also overlap of the dorsal areas involved in immediate and delayed reaching in healthy subjects.

Likewise, Singhal, Kaufman, Valyear, and Culham (2006) found that the anterior intraparietal sulcus (AIP), which is located in the dorsal stream and is thought to be involved in grasping movements (Binkofski, et al., 1998), was activated in action execution after a delay; therefore, suggesting contributions of the dorsal stream in delayed movement. Additionally, Singhal et al. (2006) found that the lateral occipital complex (LOC), an area of the ventral stream involved in object recognition (Grill-Spector, Kourtzi, & Kanwisher, 2001), was not only activated at the time of the presentation of the stimulus to be reached, but that it was reactivated when the motor action was performed after a delay. This therefore suggests that delayed action requires both the ventral stream and the dorsal stream. Confirming this, Cohen, Cross, Tunik, Grafton, and Culham (2009), using transcranial magnetic stimulation, found that not only is the AIP involved in immediate grasping but it is also required in the completion of the same movements after a delay. Therefore, it was concluded that the ventral stream is not solely responsible for mediating grasping movements after a delay, but that the dorsal stream has some involvement (Cohen, et al., 2009). Furthermore, Cohen et al. (2009) observed that the lateral occipital cortex (LOC), a ventral stream area, was selectively involved in the completion of an action after a delay.

Further supporting the involvement of AIP after a temporal delay is the study of single unit recordings in monkeys. Murata, Gallese, Kaseda, and Sakata (1996) found that many of the neurons in this area were active during a delay period of two seconds between seeing an object and making the corresponding hand movement to that object. This again suggests the involvement of dorsal activity during a delay period.

Additionally, research that had been used to support the perception-action model in saying that dorsal stream representations are short lived, namely the finding that with the introduction of a delay, visual illusions have an effect on visuomotor performance whereas when there is no delay they do not (Westwood & Goodale, 2003), has been questioned. While it has been thought that with the onset of a delay there is a switch to using the ventral stream, rather than the dorsal stream, to provide the visual information for the control of the movements, and perceptual information is susceptible to visual illusions (Hu & Goodale, 2000; Westwood & Goodale, 2003), an alternative explanation has now been offered. Franz et al. (2008) observed that when there is no delay, visual feedback is available throughout, whereas in the delay condition this is not the case. When Franz et al. (2008) systematically varied the amount of visual feedback that participants received, it was observed that the effects of the illusion were reduced when greater amounts of visual feedback were available. Therefore, Franz et al. (2008) concluded that it is the availability of visual feedback, which allows on-line corrections to be made, that reduces the apparent effects of the illusion, and not necessarily a switch from dorsal to ventral processing. Furthermore, Hesse and Franz (2009) comment that there are “no qualitative differences between movements executed after a delay and movements executed under full vision” (p. 1543).

In summary, the conclusion from the experiments presented in this thesis that egocentric information, thought to originate from the dorsal stream, can persist for several seconds, is consistent with recent findings, that the dorsal stream is involved during a delay (for example, Cohen, et al., 2009; Connolly, et al., 2003; Singhal, et al., 2006). The conclusion that egocentric representations can be stored raises an interesting question. If egocentric visual representations can persist for several seconds then they should be available to the motor system. In this case, how can the degrading effects of visual delays on visuomotor performance (Bradshaw & Watt, 2002; Elliott & Madalena, 1987; Westwood, et al., 2003) be explained? One explanation for this degradation of performance is that the internal representation of a visual scene or an object is never as rich as the real visual scene or object. Importantly, once the source of the internal representation is removed, probing eye or head movements can no longer be used to provide new and more reliable information; for example, while the object is present, slight head movements can be used to obtain more accurate information about the distance between the object and observer. This information is clearly important in producing an accurate reaching or pointing movement. It is therefore not surprising that once we have to rely on an internal representation, some aspects of motor control may degrade. Furthermore, alternative explanations have recently been offered for the reduced visuomotor performance with temporal delays, namely, that the amount of visual feedback is critical in determining the degradation of visuomotor accuracy after a period of delay (Franz et al., 2008).

While it may be thought that the temporal aspects of dorsal and ventral processing have previously been investigated (for example, Franz, et al., 2008; Hesse & Franz, 2009; Himmelbach, et al., 2009), it is believed that this thesis is able to make a specific contribution on this issue. While the behavioural results of Franz et al. (2008) and Rogers, Smith, and Schenk (2009) show that visuomotor control survives delays, it remains unclear how this is achieved, and a number of alternatives are possible. For example, visuomotor performance after a delay may rely on additional input from the ventral stream, or be explained by allocentric information in the dorsal stream, or likewise, egocentric information in the ventral stream, or it may be that egocentric information is more persistent than assumed. Similarly, data from imaging research has shown that the dorsal stream is involved in visuomotor performance after a delay (Connolly, et al., 2003; Singhal, et al., 2006), but it is not known whether this is the result of the persistence of egocentric information or because of an allocentric/ventral stream contribution.

The studies presented in this thesis have found the egocentric information can persist for several seconds. On this basis it can be argued that egocentric representations are not as transient as previously thought, and therefore it is suggested that in explaining the findings above, additional ventral stream or allocentric information does not necessarily have to be recruited. Furthermore, it has been shown for the first time that Milner and Goodale's (1995, 2006) assumption of the transient nature of egocentric coding is not correct.

The conclusion that egocentric information is not as highly transient as assumed by the perception-action model is challenged by observations of visuomotor performance after a delay. It has been found that the visuomotor performance of visual agnosia patient D.F. is impaired after a period of delay (Goodale, Jakobson, et al., 1994) and her performance at making memory guided eye movements was less accurate compared to when making stimulus-driven eye movements (Rossit, Szymanek, Butler, & Harvey, 2010). The degradation in D.F.'s performance has been explained by the assumption that, since egocentric information cannot persist, her performance after a delay relies upon allocentric information from the ventral stream, which is damaged. Furthermore, Cohen et al. (2009) reported that the application of TMS to both ventral and dorsal stream areas affects delayed visuomotor performance; therefore, suggesting that the ventral stream is involved to some degree in the execution of delayed movements.

However, if egocentric information can persist, as suggested by the experiments that have been presented in this thesis, why is the ventral stream more critical for delayed performance than for non-delayed performance, as shown by D.F. being more impaired in delayed tasks compared to non-delayed tasks? It is thought that there are two possible answers to this question. Firstly, that the ventral stream is critical in maintaining the egocentric reference during delay, and thus its absence in patient D.F. means that her performance worsens after a delay. Supporting this, there is some evidence that the ventral stream is involved in egocentric representations, as well as allocentric representations (Zaehle, et al., 2007). Secondly, and again indicating a role of the ventral stream after a delay, while egocentric information is not transient, it may be the case that this source of information becomes noisier with delay. Sensory information from the receptors of the bodies' muscles and joints provide a sense of the relative position of different parts of the body at any given time, which is known as proprioceptive information (Riemann & Lephart, 2002). It has been observed that most of the bodies' receptors become less sensitive when stimulation is constant or continual, a process commonly known as adaptation (Carlson, 2001; Lindsay, Bone, & Callender, 1997). Therefore, proprioceptive signals have a tendency to die down; for example, if you do not move for a long time, you lose the sense of where your limbs are, and you lose the body-centred reference points. Accordingly, it becomes necessary to draw on other resources to provide this information. In order to know where body parts are in relation to each other, it could be argued that the ventral stream uses allocentric information to create an egocentric representation. Thus, to maintain egocentric position, ventral contributions, using in part allocentric information, might become more critical after a delay. The stability of the egocentric representation is achieved by using allocentric information, and suggests the involvement of the ventral stream after a delay; therefore, offering an explanation as to why D.F. displays degraded visuomotor abilities after a delay.

Egocentric information is coded relative to the body

In addition to establishing that egocentric information can persist for more than a couple of seconds, it was also found that in this condition the location of the target was being coded relative to the participants' bodies, as when participants were required to move to a new location and the relationship between the location of the target and observer was maintained, search times were still speeded. Conversely, when the location of the target was repeated relative to the fixation point, and thus the position of the participants' eyes, there was no consistent effect of search times; therefore, suggesting that participants were not relying on an eye-centred frame of reference.

While the absence of eye-centred coding in the experiments here appears to contradict the finding of McKyton and Zohray (2008), who reported a cost in changing the retinotopic coordinates of the target between trials, their effects were highly specific. A cost to performance was observed when target positions were shifted horizontally; however, there was no difference when they were translated vertically by the same amount (McKyton & Zohray, 2008). Furthermore, while McKyton and Zohray (2008) took a cost when the information changed to represent learning, the experiments here were concerned with spatial priming and the benefits of repeating target location.

The finding here that body-centred information can persist and influence search performance in subsequent trials is in-line with findings from topographical memory research, and specifically those that have evaluated the ability for egocentric representations to be updated. These studies often involved whole body movements, and with finding that changing position does affect recall, it has been concluded that there is memory for egocentric representations. For example, Shelton and McNamara (2004) found facilitation of recognition performance when the object array was presented from the same viewpoint in both the learning and testing phases, and both Diwadkar and McNamara (1997) and Christou and Buelthoff (1999) found that response times were faster when the test viewpoint matched the learnt viewpoint compared to when they did not match, suggesting memory for that egocentric viewpoint. Of interest, Diwadkar and McNamara (1997) found that response times increased as a function of the degree of displacement of the participant’s position: the greater the degree of displacement, the longer the response times. These observations suggest that “a novel view of a familiar scene is recognized by effecting a transformation between the novel view and the view represented in memory. This transformation consumes more time as the angular distance over which it must be carried out increases” (Diwadkar & McNamara, 1997, p. 304). Finlay et al. (2007) also observed an incremental decrease in recognition performance (response times became longer and responses were less accurate) as the distance between learnt view and test view increased. Furthermore, these effects were observed indiscriminately across three temporal delay conditions (the longest being 12 seconds); therefore, providing evidence that the egocentric representations of scenes are still available after a period of delay (Finlay, et al., 2007). This not only supports the finding here that egocentric representations can persist, but as participants made whole body movements, it is in line with the finding that the egocentric information is coded relative to the observers’ bodies. In summary, the observations from topographical memory research support the findings of this thesis of the importance of body-centred information.

There is also a body of research looking at which is the most relevant egocentric frame of reference in patients with spatial neglect. A robust finding seems to be that neglect can be trunk-centred, with left neglect patients failing to report stimuli presented to the left of the midline of their body (Beschin, Cubelli, Della Sala, & Spinazzola, 1997; Karnath, Christ, & Hartje, 1993; Karnath, Schenkel,

& Fischer, 1991). Furthermore, when the patient's body is rotated to the left, the extent of neglect is reduced, suggesting the relevance of coding information relative to the body, which is in line with the findings here. While the study of head-centred neglect has yielded inconclusive results, support that spatial neglect is based on retinotopic coordinates has also been provided (Behrmann, Ghiselli-Crippa, Sweeney, Dimatteo, & Kass, 2002; Patrik Vuilleumier et al., 1999). When looking at reference frames in spatial neglect there appears to be a great amount of variation, and which is the critical frame of reference for the neglect depends both on the patient and the demands of the task.

Visual persistence versus motor persistence

The phenomenon of motor priming is relevant to understanding the contribution of the findings of this thesis. Motor priming refers to the observation that ongoing visuomotor acts are affected by previous visuomotor acts. That is, when a motor action is repeated the kinematic aspects of that movement are influenced by those of the previous movement (Dixon & Glover, 2009; Jax & Rosenbaum, 2007, 2009). For example, Dixon and Glover (2009) observed that grip aperture was affected by the size of the target in the previous trial. This suggests a lingering effect of the motor program used in the first movement. Likewise, here, it was found the search performance (i.e. search times) were influenced by the preceding search arrays, that is, participants were consistently faster at locating a target when it appeared in the same location that it previously appeared in. Priming effects are argued to be the result of representations still being available at a subsequent point in time (Huang, et al., 2004; Shore & Klein, 2001). It is thought that there are two potential sources of information that are available when the motor action is completed for a second time that can explain motor priming: a motor representation and a visual representation. If motor priming effects are based on the persistence of visual information then the observations would contradict the assumptions of the perception-action model, as the model argues that visuomotor representations are highly transient. Conversely, the findings of motor priming research would not be in opposition to the model if they are based motor persistence, as Milner and Goodale (1995, 2006) have never denied that previous motor acts are capable of having an effect on subsequent motor acts. However, it is not possible to disentangle whether motor priming represents visual persistence or motor persistence, as in order to address this question a paradigm which isolates the visual source was required.

Indeed, this was achieved by the experimental paradigm employed in this thesis. Furthermore, spatial priming in visual search allowed allocentric and egocentric frames of reference to be separated from one another and this is critical. The visuomotor priming paradigms were not specific with respect to the spatial basis of the persistence, that is, if the visual representations are based on allocentric input from the ventral stream or if they are based on persistence of egocentric information from the dorsal stream. Therefore, the approach used in this thesis is clearer and more specific than that of motor priming research.

A final implication of this research more generally is that it provides evidence that egocentric coding is relevant, not just for visuomotor control, as is widely known; for example, Goodale and Haffenden (1998), Milner and Goodale 1995, 2006), and Wang and Spelke (2000), but that it is also involved in a number of other cognitive functions, including attentional control and memory. The work here with visual search adds to the existing literature on the use of egocentric coding in a variety of other cognitive tasks; for example, scene and object recognition, mental imagery and rotation, and number line processing (Conson, Mazzarella, & Trojano, 2009; Creem-Regehr, Neil, & Yeh, 2007; Sterken, Postma, de Haan, & Dingemans, 1999; Tao et al., 2009; Waller, 2006). Taken together, the findings contradict Milner and Goodale's thesis that egocentric information is not relevant for typical perceptual tasks.

Limitations and future directions

Here consideration will be given to some of the general limitations of the experiments presented in this thesis, along with suggestions for the future direction of this program of research to further advance the field.

Spatial priming in visual search was selected as the most appropriate method to investigate egocentric coding for a number of reasons; one of these being that it was an implicit task, and thus ensured that participants were not prompted towards using either allocentric or egocentric information over the other. Similarly, no specific instructions about how the target should be coded were provided. While it was felt that this was a necessary characteristic of the chosen paradigm, it only allows inferences to be made about which frame of reference participants used to complete the search task. During the course of the experimental trials participants may have become aware of how the location of the target was being coded; for example, they may have learnt that the target always occupied the same location for a few trials in a row (i.e. the egocentric-body condition), thus they may have developed a search strategy to locate the target. It would have aided the interpretation of the behavioural data, if, after the experiment, participants were asked to report whether they were aware of the different frames of reference and if they had used any strategies. Anecdotally, on de-briefing and explaining the design of the experiment, participants generally reported that they were not aware of the frame of reference manipulation; however, formal questioning would have proved insightful on this point.

Many of the participants tested in the experiments of this thesis took part in order to meet a requirement of their course. Owing to the demographic of students enrolled on the Psychology course, there was a consistent sex bias throughout the experiments, with participants being predominantly female. Of interest, some researchers have reported differences in the strategies that males and females use in spatial navigation tasks. For example, Kim, Lee, and Lee (2007) found that males performed better in a spatial recognition task than females, and Lawton (2001) observed that when giving directions, while males relied more heavily on cardinal directions, females used landmarks, such as buildings, more frequently than males did. However, it has also been reported that there are no differences between the spatial memory of males and females (Dabbs, Chang, Strong, & Milun, 1998; Lavenex & Lavenex, 2010). Therefore, the gender of participants should be controlled in future experiments with equal numbers of males and females participating. Furthermore, it would be interesting to analyse the data according to gender to evaluate if there is a differential frame of reference preference in males and females.

A second point related to the selection of participants is that some participants completed more than one experiment. While it is thought that the potential effects of learning on task performance may be problematic, Study D is able to provide some indication of the effects of becoming familiar with the visual search task. In Study D participants completed three experimental sessions on different days and when the data was analysed as a function of testing session, it was found that while overall search times decreased across the testing sessions, this reduction was not different in the allocentric and egocentric priming conditions (see Appendix E for this analysis).

A third limitation of the experiments presented in this thesis is that eye-movements were not recorded. It is thought that this would have been able to provide a wealth of information about the nature of the saccades that participants used to locate the target, such as the frequency of saccades and their magnitude. This would have been particularly useful in early experiments when there was speculation about whether participants were using body-centred information or eye-centred information during the search task. However, the absence of eye tracking does not negate the findings presented here. Indeed, the introduction of a secondary task into the search paradigm, namely, the letter identification task prior to the presentation of the search arrays, was sufficient to ensure that participants foveated the letter in order to accurately report it, and thus eye movements had to be restricted for successful completion of this task. Nevertheless, eye tracking would have been able to provide irrefutable evidence about whether this was the case or not. Eye tracking would also have been informative about the nature of the scan paths that participants used to locate the target; for example, whether these changed with the repeated presentation of a target location and searching behaviour through distractor stimuli, from which inferences about memory capacity can be made (Gilchrist & Harvey, 2000; Peterson, et al., 2001). Furthermore, eye tracking would have allowed the visual impact of the allocentric anchor to be assessed, that is, whether it automatically captured attention. Therefore, recording eye movements is suggested as a consideration in investigating frames of reference in visual search further.

Across all the experiments reported here the stimuli were presented onto a blank wall to prevent any frames of reference, other than those being manipulated, from contributing to the visual display and being used as additional visual cues of the target location. However, in Study E, where the spatial priming paradigm was coupled with TMS, localising the optimal posterior parietal site (the site at which the application of TMS led to a slowing in search performance), was conducted on a computer monitor. There were two reasons for this. Firstly, this method of PPC localisation has been used previously (Ellison, et al., 2007; Ellison, et al., 2003); and secondly, the localisation search task was only concerned with participants' search times to conjunction search stimuli and had no regard for position priming (i.e. the target appeared in a random location on every trial), so carefully controlling the frame of reference information (e.g. the edge of the computer monitor) was not necessary. Owing to these different methods of presentation, the visual density of the search arrays varied between the PPC localisation trials (presented on a computer monitor) and the experimental trials (projected onto the wall). While it is thought that this dissociation can offer an explanation for the data not replicating the finding that the application of TMS to the PPC slows search times when no frame of reference is involved (Ashbridge, et al., 1997; Ellison, et al., 2003), it is felt that the visual characteristics of the search arrays should have been considered and controlled between PPC localisation and experimental trials.

On a related note, it would be interesting to investigate the near and far space distinction in visual search formally. The PPC has been found to be selectively involved in line bisection tasks that are completed in near space but not in far space

(Bjoertomt, et al., 2002; Weiss, et al., 2000). While past research has found disruption to conjunction search performance when the stimuli are presented on a computer monitor, and thus in near space (Ashbridge, et al., 1997; Ellison, et al., 2003), there have been no reports evaluating the effects in far space, and this is therefore proposed as a future extension of this current research. Furthermore, the performance on allocentric and egocentric tasks has been found to be influenced by the visual field the stimuli are presented in. For example, Sdoia, Couyoumdjian, and Ferlazzo (2004) found that participants were faster at making allocentric judgments when the stimuli were presented in the upper visual field compared to when the same stimuli were presented in the lower visual field. Conversely, for egocentric judgments, the advantage was observed when the stimuli were presented in the lower visual field (see also Dyde & Harris, 2008). Therefore, it is suggested that investigating visual field differences and frames of reference in spatial priming is an additional avenue for further research.

A number of suggestions, mainly drawn out of considering the short comings of the research presented in this thesis, of how the research into spatial priming and frames of reference could be extended, have been proposed. It is thought that the most important future direction is to consider the nature of the task being used. Spatial priming was selected to investigate egocentric coding as it was felt that as egocentric representations are associated with motor functions (Milner & Goodale, 1993, 2006), their use in a perceptual task such as visual search would provide the strongest test of the hypothesis that egocentric information is unavailable after a temporal delay. Since a perceptual task might bias against the use of egocentric information any evidence of its use after a delay needs important consideration. Having established that egocentric representations are relevant in a perceptual task where the stimuli comprised of two dimensional lines, a future direction for research would be to evaluate search performance when the stimuli are instead three dimensional objects. It has been found that the presentation of graspable and pliable objects is sufficient to activate motor related areas (Chao & Martin, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997); therefore, this would allow the comparison of more relevant egocentric representations to be made with allocentric representations within the same perceptual task.

Furthermore, investigating the roles of the different spatial frames in a motor task would be highly valuable. This could be achieved by using a visual search task with a motor component, whereby participants are required to point towards the target. Additionally, the use of real-world, and therefore graspable, objects would transform the task to an appropriate motor task that would certainly engage the visuomotor processing networks of the brain. Finally, it would be of great interest to follow up the research by Schenk (2006) and evaluate the performance of optic ataxia patients on perceptual and visuomotor tasks that require allocentric and egocentric representations. Specifically, it would be interesting to appraise whether this group of patients are impaired in utilising an egocentric frame of reference.

Concluding remarks

In summary, this thesis investigated frames of reference in spatial priming within two visual search tasks. The experiments revealed that egocentric information, coded relative to the body, is central to defining target location, and thus demonstrating that egocentric information is useful in the completion of perceptual tasks, as well as being involved in visuomotor tasks. Moreover, as the priming effects were driven by information that was presented more than a couple of seconds before, it has demonstrated that egocentric representations are not as transient as originally thought. This finding has implications for our understanding of spatial priming in visual search and for our interpretation of the perception-action model. Previous research on spatial priming in visual search has used allocentric landmarks. Such visual landmarks can become perceptually fused with the target itself, so that they effectively create a new and, owing to its combination with a unique visual feature, more salient target. This means that with allocentric priming it remains to some extent unclear whether the facilitation reflects the perceptual emergence of a more salient target or true spatial priming. Egocentric priming allows us to avoid this problem, since in this case the reference point is not another visual stimulus but the body. Finding clear evidence of egocentric priming therefore shows that true spatial priming exists in visual search.

Most importantly this thesis provided a test of the perception-action model, or more precisely, one of its most basic assumptions, namely that egocentric representations are transient and cannot persist for more than a second. This assumption has been used to explain numerous findings, ranging from the decrement of visuomotor performance with delay in healthy subjects, to the paradoxical improvement of delayed motor performance in optic ataxia patients, and the finding of increased illusory effects on visuomotor performance when a delay is introduced. Clearly these findings now require new explanations.

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Appendix

Appendix A: General Consent Form

Consent to participate in a research study
Psychology Department, University of Durham

Title of study: Investigating visual search

Investigator's names: Keira Ball (Ph.D. student), and Dr. Thomas Schenk (supervisor).

Please circle as appropriate:

Have you read the participant information sheet? YES NO

Have you had the opportunity to ask question and discuss this study? YES NO

Have you received enough information about this study? YES NO

Do you understand that you are free to withdraw from the study YES NO
At any time
Without giving a reason
Without any adverse affect of any kind

Were you given enough time to consider whether you want to participant? YES NO

Do you agree to take part in this study? YES NO

Signature of participant ___________________________	Signature of investigator ___________________________
Name in block letters ___________________________	Name in block letters ___________________________
Date______________________	Date______________________

Appendix B: Example participant information sheet.

Title of Study: Investigating the differences between action and perception: A visual search study.

Investigator's names: Keira Ball (Ph.D. student) and Dr. Thomas Schenk (supervisor). This research is funded by the Wolfson Research Institute.

Purpose: You have been asked to participate in a research study that uses a visual search paradigm to investigate the influence of visual search mechanisms that can be applied to everyday behaviour. This work will form part of the Ph.D. research of Keira Ball.

Procedures: The study involves responding to the presentation of stimuli by making a present/absent discrimination. The stimuli will be projected onto a blank wall so you will be required to sit facing the wall holding a button box, on which you will make your response. Each trial will start with the presentation of a letter in the centre of the screen. You have to verbally report this letter to the researcher, who will be sitting in the corner of the room throughout the experiment. After this, you will see an array of oriented lines in varying positions on the screen and you have to decide whether a target (an oddly oriented line) is present or absent. Please press the button either labelled "present" or "absent" as soon as you have made your decision. The experiment is divided into blocks of trials with breaks in between. The experiment takes approximately 50 minutes to complete.

Risks and Benefits: These tests are not painful, nor dangerous, in any way. There are no direct benefits to you for participation in this part of the study.

Confidentiality: The scientific information obtained from these experiments may be published in scientific papers, but your name will not appear in any public document, nor will the results be published in a form which would make it possible for you to be identified.

Right to refuse or withdraw: You may refuse to participate without any penalty. You may change your mind about being in the study and quit after the study has started, and if you feel, for any reason uncomfortable, the study will be discontinued.

Questions: After the experiment you will be fully de-briefed about the nature of the experiment and you will be given the chance to ask any questions. If you would like a copy of your results, please ask the researcher. Furthermore, we welcome the opportunity to answer any questions you may have about any aspect of the study or your participation in it after the event. You can contact either the experimenter directly (k.l.ball@durham.ac.uk) or Dr. Schenk (thomas.schenk@durham.ac.uk).

Appendix C: Consent form for TMS – Study E.

Cognitive Neuroscience Research Unit
Wolfson Research institute, University of Durham, Queen's Campus
University Boulevard, Thornaby, Stockton-on-Tees, TS17 6BH
Tel: 0191 334 0430. Fax: 0191 334 0452. Email: amanda.ellison@durham.ac.uk

Subject Questionnaire: If you agree to take part in this study, please answer the following questions. The information you provide is for screening purposes only and will be kept completely confidential.

Have you ever suffered from any neurological or psychiatric conditions? YES/NO
If YES please give details (nature of condition, duration, current medication, etc).

Have you ever suffered from epilepsy, febrile convulsions in infancy or had recurrent fainting spells? YES/NO

Does anyone in your immediate or distant family suffer from epilepsy? YES/NO
If YES please state your relationship to the affected family member.

Have you ever undergone a neurosurgical procedure (including eye surgery)? YES/NO
If YES please give details.

Do you currently have any of the following fitted to your body? YES/NO

i) Heart pacemaker
ii) Cochlear implant
iii) Medication pump
iv) Surgical clips

Are you currently taking any un-prescribed or prescribed medication including anti-malarials? If YES please give details. YES/NO

Are you left or right handed? LEFT/RIGHT

Subject Consent: I (please give full name in CAPITALS) ____________________________ confirm that I have read the letter of invitation and have completed the above questionnaire. I confirm that I am not taking recreational drugs and have not participated in a TMS experiment already today and feel well rested. The nature, purpose, and possible consequence of the procedures involved have been explained. I understand that I may withdraw from the study at any time.

Signature__________________________ Date______________________________

Please note: All data arising from this study will be held and used in accordance with the Data Protection Act (1984). The results of the study will not be made available in a way which could reveal the identity of individuals.

Appendix D: Search times in PPC localisation – Study E.

Table 17. Mean Search Times (ms) in the PPC Localisation Task in the Sham Condition (no TMS) and TMS to PPC Condition. Search Times are given for the PPC Site that showed the Greatest Slowing in Search Times Relative to the Sham Condition as this was the PPC Site Selected.

Participant	Sham RT (ms)	PPC RT (ms)	Difference (ms)
2	753	983	230
3	557	702	145
4	567	769	202
5	547	702	155
6	778	886	108
7	736	913	177
8	801	884	83
9	595	758	163
10	897	1136	239
11	676	1123	447
12	1074	1258	184

Note. PPC hunting was not done for participant 1 as the location was already known as the participant had previously completed the same PPC localisation task in another experiment.

Appendix E. Search times as a function of session – Study D.

Participants completed three sessions of trials on different days in Study D. In order to evaluate the effect of learning across the sessions, the average search times to trials for each priming condition have been analysed as a function of session. A repeated measures ANOVA with the factor Session (1, 2, 3) revealed significant main effects of Session for both Egocentric searches, $F(2,56) = 38.40$; $p < .025$, and Allocentric searches, $F(2,56) = 20.73$, $p < .025$. It can be seen from Figure 34 that search times decreased over the course of the three sessions: for egocentric searches the overall reduction in search times was 119.57 ms ($SD = 94.7$) and for allocentric searches it was 101.89 ms ($SD = 111.6$). There was no significant difference in the reduction in search times between the two frames of reference, $t(28) = 1.56$; $p = .130$.

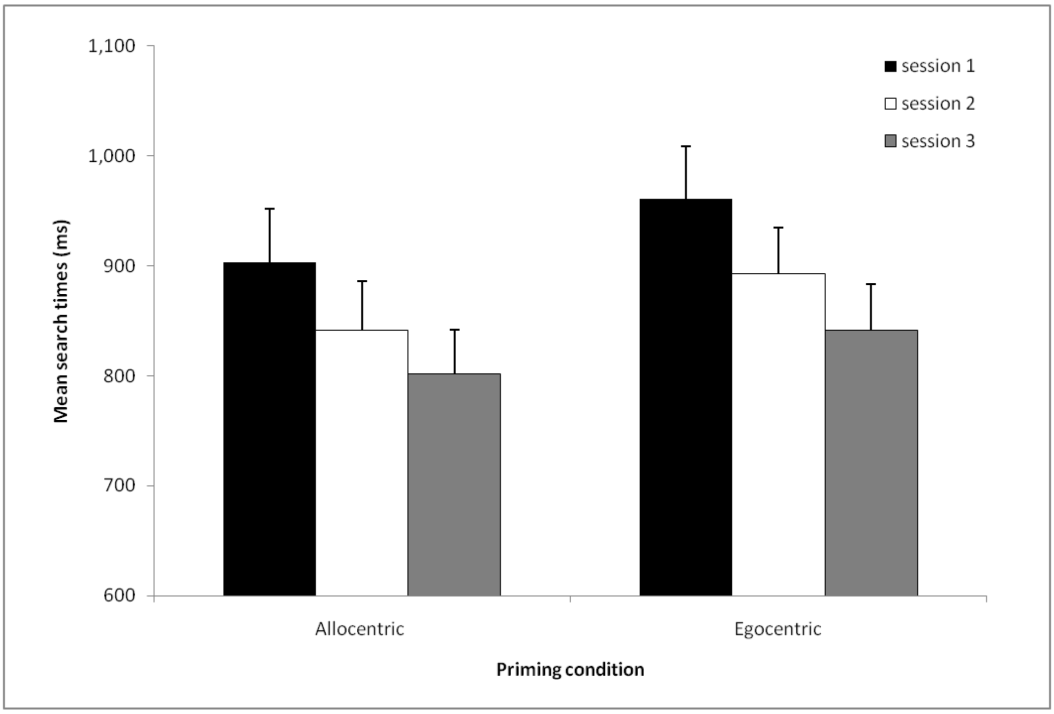

Figure 34. Mean search times (ms) to trials in allocentric and egocentric searches broken down by session in Study D. Error bars represent the standard error (SE).