Comparing the effect of temporal delay on the availability of egocentric and allocentric information in visual search.

Keira Ball[a], Yan Birch[a], Alison Lane[a], Amanda Ellison[a], and Thomas Schenk[b]

[a] Department of Psychology, Durham University, UK

[b] Klinische Neuropsychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany

Running header: Delay in spatial priming

Correspondence should be addressed to:

Keira Ball
Cognitive Neuroscience Research Unit,
Wolfson Research Institute,
Durham University,
Queen’s Campus,
University Boulevard,
Stockton on Tees, TS17 6BH.
Phone: +44 191 33 404 47
Fax: 0191 334 0006
Email: k.l.ball@durham.ac.uk

Abstract

Frames of reference play a central role in perceiving an object's location and reaching to pick that object up. It is thought that the ventral stream, believed to subserve vision for perception, utilises allocentric coding, while the dorsal stream, argued to be responsible for vision for action, primarily uses an egocentric reference frame. We have previously shown that egocentric representations can survive a delay; however, it is possible that in comparison to allocentric information, egocentric information decays more rapidly. Here we directly compare the effect of delay on the availability of egocentric and allocentric representations. We used spatial priming in visual search and repeated the location of the target relative to either a landmark in the search array (allocentric condition) or the observer's body (egocentric condition). Three inter-trial intervals created minimum delays between two consecutive trials of 2, 4, or 8 seconds. In both conditions, search times to primed locations were faster than search times to un-primed locations. In the egocentric condition the effects were driven by a reduction in search times when egocentric information was repeated, an effect that was observed at all three delays. In the allocentric condition while search times did not change when the allocentric information was repeated, search times to un-primed target locations became slower. We conclude that egocentric representations are not as transient as previously thought but instead this information is still available, and can influence behaviour, after lengthy periods of delay. We also discuss the possible origins of the differences between allocentric and egocentric priming effects.

Keywords

egocentric coding; allocentric coding; spatial memory; visual search; location priming, delay

1. Introduction

Describing the location of an object relative to myself (the pen is in front of me) uses an egocentric frame of reference, whereas defining the pen's location relative to another item in the visual array (the pen is to the left of the stapler) uses an allocentric framework [1] ; [2]. The distinction between allocentric and egocentric coding has long been an important one but it has reached new prominence with its incorporation in the perception-action model [3] ; [4]. Ungerleider and Mishkin [5] proposed the existence of two anatomically separate visual processing pathways in the human brain, namely the ventral stream and the dorsal stream. Milner and Goodale [6] went on to argue that the ventral stream was responsible for perceptual functions (vision for perception) and the dorsal stream was responsible for guiding motor actions (vision for action). Owing to the different nature of the outputs of the ventral and dorsal streams it is thought that they rely on different frames of reference. Judgements of object attributes are made in relation to other objects in the visual scene, suggesting that vision for perception uses an allocentric frame of reference [7] ; [4]. Conversely, in order to be able to reach out and grasp an object an accurate visual representation of how the location of the object corresponds to your location is required. As such it is argued that visuomotor performance depends on the use of egocentric representations [8]; [9]; [10] ; [11]. This current study assesses the claim that egocentric coding leads to very short-lived representations and that these representations are less persistent than those used in allocentric coding.

The assumption that egocentric representations are short lasting has been used to explain observations that memory-based actions (i.e. actions where the visual target is removed prior to the motor response being initiated) are typically less accurate than immediate actions (where the target is still in view when the motor response is started, [12]; [13]; [14] ; [11]. To explain this difference in delayed and non-delayed action it is argued that when there is a delay between target presentation and initiating a motor response towards it, as egocentric representations are unable to survive the delay period, the motor system is forced to rely on less accurate allocentric representations about the target location, which are presumably stored in the ventral stream. Introducing a delay differentially affects the motor performance of patients with dorsal and ventral stream damage: delay leads to an improvement in the visuomotor performance of patients with optic ataxia [15]; [16] ; [17] and a decline in the visuomotor performance of patients with visual agnosia [18] ; [19]. It is argued that the delay forces the motor system to rely on information from the ventral stream, meaning that in the case of a damaged dorsal stream (i.e. optic ataxia) performance will improve, while in the case of a damaged ventral stream (visual form agnosia) performance will get worse [4]. However, see also Hesse and Schenk [20] who report that in visual agnosia patient D.F. the decline in her visuomotor performance when a delay is introduced is dependent on the availability of visual feedback and environmental cues.

The explanation that dorsal representations have a limited duration is supported by the contrasting effects of visual illusions on perceptual and motor performance. Early studies suggested that visual illusions do not affect visuomotor acts [21] ; [22] and such findings were used to support the notion that allocentric information is used for perception but not for action. These findings were later extended to show that memory-based visuomotor responses were vulnerable to the effect of illusions [23] ; [24], thus supporting the assumption that memory-based actions were based on allocentric rather than egocentric information. This was taken as an indirect piece of evidence for the transient nature of egocentric information. However, these findings have proven quite controversial ([25]; for a review see Ref. [26]) and can no longer be taken as reliable evidence for the perception-action model and the claim that egocentric information is short-lasting. Indeed a number of studies have demonstrated that egocentric representations can survive delays of several seconds; for example, Fiehler et al. [27] observed memory for gaze centred information over three delay periods (5, 8, 12 s) and found that error patterns were consistent across the three intervals, and Chieffi et al. [28] found that after a 30 s delay egocentric coding of target location relative to the hand was still possible, although these movements were more erroneous than those made after a three second delay. Likewise, evidence of both arm and eye centred coding after delays has been reported [29] ; [30].

While the area of memory-based visuomotor performance has received a great amount of attention there has been less interest in the underlying assumption of the perception-action model that egocentric representations are highly transient. One might expect that the transient nature of egocentric cues should affect not just visuomotor tasks but also perceptual tasks. Therefore, when addressing the relative persistence of egocentric and allocentric coding it seems important to use a paradigm where the required spatial code is directly determined by the condition of the experiment. As such, we have previously used a perceptual task to investigate the persistence of egocentric information, with spatial priming in visual search being chosen as the appropriate method to investigate this issue. Not only does spatial priming allow egocentric and allocentric versions of the same task to be used, but being a perceptual task only visual information is carried over from one trial to the next.

By presenting a target in the same location across trials we inferred through a reduction in search times whether participants still had access to the target location information from the preceding trial [31] ; [32]. Using a feature search task we observed that search times decreased when the location of the target relative to a ‘landmark’ in the display (allocentric priming) was repeated and when the location of the target relative to the observer (egocentric priming) was repeated across trials [33]. In two subsequent studies, both of which employed the same conjunction search paradigm used here, we investigated the nature of the egocentric frame of reference further. We found that the priming effects were selectively observed when the location of the target was repeated with respect to the observer's body but not when its position relative to the fixation point, and thus eye position, was repeated, suggesting that the target location was coded in body-centred coordinates [34]. We went on to provide stronger evidence of body-centred coding: when participants moved to a different location between trials significant priming effects were still observed [35]. This last study allowed us to rule out the influence of any uncontrolled allocentric cues within the room on the participant's performance as the participant's movement invalidated these cues.

While both our observation that egocentric priming is surprisingly robust and the reports of other researchers that egocentric representations can survive delays (for example, [29]; [28]; [27] ; [30]) suggest that egocentric representations are not as transient as presumed by the perception-action model [3] ; [4], there remains the possibility that egocentric representations are less persistent and decay more rapidly at longer delays than their allocentric counterparts. We address this possibility in the current study by comparing the effect of delay on the availability of allocentric and egocentric information.

2. Method

Here we investigated the influence of three inter-trial intervals on visuospatial priming and compared the effects for allocentric and egocentric reference cues. The aim of this experiment was to examine whether egocentric information decays more rapidly than allocentric information.

2.1. Participants

42 naïve participants (7 male) took part in this experiment (age range 18–37 years, *M* = 21.10 years, *SD* = 3.9, 38 right handers). Participants were randomly assigned to one of two groups: Egocentric or Allocentric. There was no difference in the average age of

participants in the two groups (Egocentric: 21.6 years; Allocentric: 20.6 years; $p = 0.753$, Mann-Whitney U). Prior to testing ethical approval was granted from the Psychology Research Ethics Committee at Durham University. Participants gave informed consent and received course credit for taking part. All participants had corrected or corrected-to-normal visual acuity.

2.2. Stimuli

At the start of each trial a letter (randomly chosen from a set of five) was presented and participants had to report its identity. For each participant the smallest font size they could read when foveating was established prior to the experimental trials. The font sizes used varied between 8 and 16, corresponding to visual angles of 0.2° vertically and horizontally, and 0.7° vertically and horizontally (12 participants used font size 8, 15 used font size 10, 11 used font size 12, 2 used font size 14, and 2 used font size 16). This part of the trial ensured that participants looked at the fixation cross at the beginning of each trial and that their gaze did not linger at the location of the previous target. Participants were then presented with a visual search array consisting of red and green lines on black backgrounds. The target was always a green backward slash (oriented at −20° from vertical) and distractors were red backward slashes and green forward slashes (oriented at 20° from vertical). In target present displays six red backslashes and six green forward slashes were presented along with the green target, and in target absent displays the target was replaced with a green forward slash. In all search arrays two green distractors were placed next to each other and acted as a landmark in the allocentric priming condition.

There were two priming conditions: Egocentric and Allocentric. To induce position-priming sequences of trials were designed whereby a given target position, defined in either an allocentric or egocentric frame of reference, was used four times within a given sequence. These four trials were termed primed trials. In the egocentric priming condition the target maintained the same position relative to the observer’s body but it occupied different positions relative to both the landmark (two green distractors placed close together) and the fixation cross that preceded the presentation of the search array (Fig. 1Ai). In the allocentric priming condition the location of the target was maintained relative to the landmark but at different positions relative to both the observer’s body and the fixation cross (Fig. 1Aii). The allocentric anchor was present in all search arrays although it provided no information about the location of the target in the egocentric condition. The average distance between the location of the target and the location of the anchor was not different in the two priming conditions in either vertical or horizontal distance (y distance: egocentric = 2.23° visual angle, allocentric = 2.20°; $p = 0.738$, Wilcoxon Signed Ranks test; x distance: egocentric 2.25°, allocentric = 2.12°, $p = 0.189$).

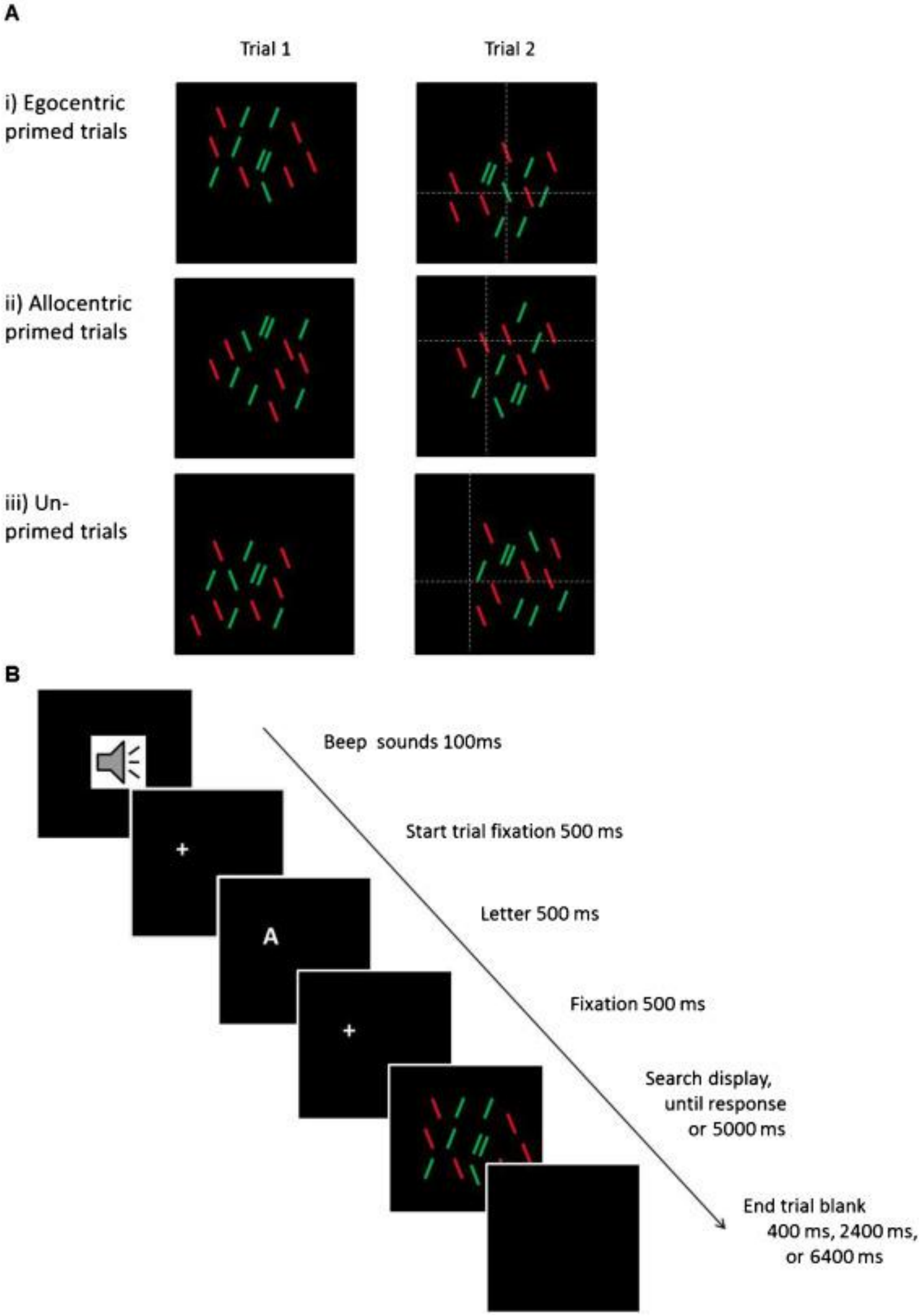

Fig 1

A. Schematic of stimuli for the three types of present trials. The target stimulus is a green backslash and the allocentric landmark is two green distractors close together. The position of the fixation cross varied from trial to trial. The intersection of the two dashed lines on the second trial indicates the absolute position of the target in the first trial (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article). i) Egocentric primed trials: when the egocentric position was repeated the target occupied the same absolute position relative to the observers' body, but it had no constant relationship with the allocentric landmark; therefore, the egocentric frame of reference used here is the participant's body.

ii) Allocentric primed trials: in trials 1 and 2 the target is to the left of the allocentric landmark but it occupies different positions relative to the observer.

iii) Un-primed trials: the target occupies a different position relative to the allocentric landmark and the observer, thus, no position priming is possible.

B. The sequence and timing of each trial.

Interspersed within these four "primed" trials there were two other types of trial: four trials where the target was not present in the array (target absent trials); and three trials where the target was present but not in the primed location (un-primed trials). In these un-primed trials the target appeared at a random location relative to the allocentric landmark, the observer, and the fixation cross (Fig. 1Aiii). The first trial in a new priming sequence (i.e. the trial in which the new to be repeated location was first introduced) was also classified as an un-primed trial, meaning that both primed sequences and un-primed sequences consisted of four trials. Thus, each sequence consisted of 11 trials, with the target stimulus present in seven of these (64%). The order of these 11 trials within a sequence was randomised. Participants completed 30 sequences of trials across two testing sessions with a new priming position, either allocentric or egocentric, being used for each sequence.

The stimuli were presented onto a blank screen using an Epson EMP-74 projector and observed from a distance of 3 m. 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. The fixation cross appeared at a random location across trials within the confines of the whole stimulus array. The luminance of the black background was 6.7 cd per square metre (cd/m^2) and the stimuli lines were 10.6 cd/m^2.

2.3. Procedure

Three delay conditions were used (10 sequences for each delay condition): short, medium and long. While the length of the delay was the same within a sequence of trials, the delays were randomised across sequences. A beep sounded for 100 ms at the start of each trial to alert participants that the next trial was starting. A fixation cross was then presented at a random location for 500 ms, and this was replaced, in the same location, with a letter which participants had to verbally report (presentation duration 500 ms). The fixation cross was then re-presented for 500 ms, meaning that there was a 1000 ms interval between the presentation of the letter and the search array, giving sufficient time for participants to verbally report the letter. The search display was then presented. Participants had to decide whether the target was present or not and make a key press response accordingly (Serial Response Box, Psychology Software Tools, Inc). Participants responded using their dominant hand and pressed the left most button when the target was present and the adjacent button when the target was absent. The search array remained on screen until either participants made their button press response or 5000 ms had elapsed and no response was made. A blank screen was then 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 (short), 4000 ms (medium), and 8000 ms (long). The trial procedure is shown in Fig. 1B. Participants were free to make eye movements throughout the trial. They were instructed to respond as fast but as accurately as possible and they were not given any feedback about whether they had responded correctly.

3. Results

3.1. Data analysis

Analysis is concerned with the time that participants took to decide whether the target was present or absent and it was measured from the onset of the search array. The mean search times for each participant were taken and used to calculate the mean for the two groups of participants. The data were tested for normality using the Shapiro-Wilk statistic and were normal unless otherwise stated (data violating this assumption was normalised using the log function, and when this could not be applied the appropriate non-parametric statistic was selected). Inferential statistics used a significance level of $p < 0.05$, except when a Bonferonni correction was applied to adjust the alpha-level for multiple comparisons.

The accuracy of letter reporting was 99.8% across all participants, indicating that participants fixated correctly at the beginning of each trial. Trials where the participant failed to report the letter correctly were not included in the analysis. Also excluded from analysis were incorrect button press responses (i.e. where the participant responded that the target was present when it was absent, and vice versa, 4.1% of trials) and outliers (responses with reaction times more than two standard deviations above or below the mean, 4.3% of correct trials). Participants were highly accurate in responding to the visual search stimuli (all target present trials: 95.4% correct; absent trials: 96.5% correct). Participants were marginally more accurate in the allocentric priming condition (all trials: 97.0% correct) than in the egocentric condition (95.0% correct), although this was not statistically significant, $U(40) = 147.5$, $Z = 1.84$, $p = 0.066$ (data not normally distributed).

Overall, search times to target absent trials ($M = 992.24$, $SE = 32.6$) were slower than those to primed trials ($M = 743.39$, $SE = 20.0$; $t(41) = 9.54$, $p < 0.001$) and un-primed trials ($M = 805.89$, $SE = 19.5$; $t(41) = 8.27$, $p < 0.001$).[1] Responses to primed trials were faster than those to un-primed trials, $t(41) = 9.27$, $p < 0.001$. This was observed in all delay conditions in both groups of participants (Table 1).

Table 1. Mean search times (ms) to absent, primed, and un-primed trials.

	Group 1: Egocentric			Group 2: Allocentric		
	Absent	Primed	Un-primed	Absent	Primed	Un-Primed
Short Delay						
Search time (ms)	950.56	730.00	787.33	944.48	692.80	767.04
Standard error	36.3	25.8	28.0	52.0	30.4	28.4
Medium Delay						
Search time (ms)	983.04	808.84	834.51	1000.6	715.12	801.34
Standard error	35.7	32.3	27.0	54.4	28.5	31.43
Long Delay						
Search time (ms)	1031.54	800.09	848.34	1043.21	718.48	796.78
Standard error	43.4	30.0	33.7	57.8	26.5	24.4

Primed trials represent the average of trials 2-4 in primed sequences. Un-primed trials represent the average of trials 1-4 in un-primed sequences.

3.2. Priming effects: comparing primed and un-primed trials

Search times to the four present trials of primed and un-primed sequences are shown in Fig. 2 for the Egocentric and Allocentric groups. Priming effects represent the difference in search times to primed trials and un-primed trials (i.e. trial 2 of a primed sequence minus trial 2 of an un-primed sequence). For each group three priming effects were computed (primed/un-primed comparison at trial 2, trial 3, and trial 4). The location of the target in the first present trial of the primed sequences is as unpredictable as the location of the target in the first present trial of the un-primed sequences; therefore, the priming effect at that point is 0. A negative number denotes that the un-primed trial was slower than the primed trial.

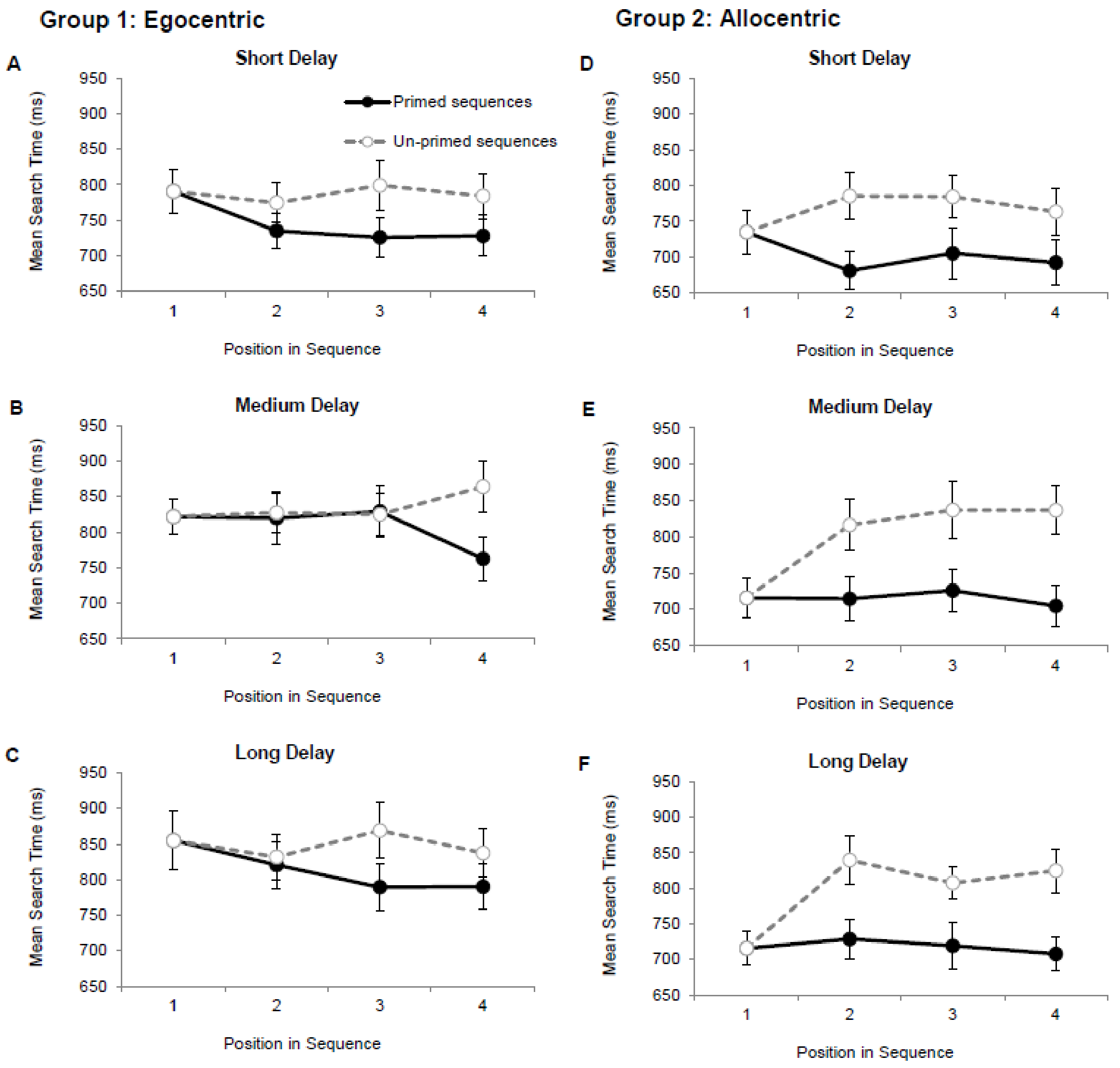

Figure 2. Mean search times to present trials in primed (solid line) and un-primed sequences (dashed line) for the Egocentric group (A-C) and the Allocentric group (D-F). Error bars represent the within-subjects' standard error of the mean.
Top: Short delay (minimum delay between two consecutive search displays of 2000 ms);
Middle: Medium delay (minimum delay between consecutive search displays of 4000 ms);
Bottom: Long delay (minimum delay between consecutive search displays of 8000 ms).

A mixed factor ANOVA with the between group factor of Group (Egocentric, Allocentric) and the within factors of Delay (Short, Medium, Long) and Priming Effect (Trial 2, Trial 3, Trial 4) was performed. The analysis revealed a significant main effect of Group, *F*(1,40) = 14.38; *p* = 0.001. The average priming effect in the Egocentric group was −45.70 ms (*SD* = 35.4), indicating that un-primed trials were slower than the primed trials in this group. The average priming effect in the Allocentric group was −101.70 ms (*SD* = 57.6), again suggesting that search times to un-primed trials were slower than those to primed trials. Moreover, it appears that the magnitude of the priming effect in the allocentric group was twice as big as that in the egocentric group. The two groups (egocentric versus allocentric group) are now analysed separately. The only other significant result was the interaction between Delay and Priming Effect, *F*(4,160) = 2.65; *p* = 0.035.

3.2.1. Egocentric group: priming effects

For the egocentric group a repeated measures ANOVA with the factors Delay (Short, Medium, Long) and Priming Effect (Trial 2, Trial 3, Trial 4) revealed a significant main effect of Priming Effect, *F*(2,40) = 4.27; *p* = 0.021 such that the priming effect increased across the course of a sequence (Trial 2: *M* = −19.55, *SE* = 9.2; Trial 3: *M* = −49.43, *SE* = 12.6; Trial 4: *M* = −68.14, *SE* = 14.7). This suggests that the priming effects were cumulative in that the more repetitions of a target location the greater the difference, and in this case, the speeding between search times to primed trials and un-primed trials. The interaction between Priming Effect and Delay was also significant, *F*(4,80) = 3.39; *p* = 0.013. The main effect of Delay was not statistically significant (*p* = 0.533).

For each delay condition, the average priming effect was calculated and compared to zero using one sampled *t*-tests. The average priming effect was significantly different from zero in the Short Delay condition, *t*(20) = −4.11; *p* = 0.001 (*M* = −56.18, *SE* = 13.7); marginally non-significant when adjusted for multiple comparisons (the critical *p* value is 0.017) in the Medium Delay condition, *t*(20) = −2.58; *p* = 0.018 (*M* = −34.90, *SE* = 13.5), and statistically significant in the Long Delay condition, *t*(20) = −3.58; *p* = 0.002 (*M* = −46.03, *SE* = 12.8).

3.2.2. Allocentric group: priming effects

The same analysis for the allocentric group (repeated measures ANOVA with the factors Delay and Priming Effect) was performed. The analysis did not reveal any significant main effects or interactions (main effect of Delay: $p = 0.246$; main effect of Priming Effect; $p = 0.528$; Interaction: $p = 0.490$), thus suggesting that priming effects in this condition are both constant across the trial sequence and unaffected by the length of the delay between trials.

As before, the average priming effect for each delay condition was calculated and compared to 0. At all three delays the priming effects were statistically significant: Short Delay: $t(20) = -4.58$; $p = 0.001$ ($M = -84.92$, $SE = 18.5$); Medium Delay: $t(20) = -7.58$; $p = 0.001$ ($M = -114.75$, $SE = 15.1$); Long Delay: $t(20) = -7.07$; $p = 0.001$ ($M = -105.42$, $SE = 14.9$). Therefore, for allocentric sequences search times were slower to un-primed trials than primed trials at all three delays.

However, on inspection of Fig. 2 it would appear that the consistent priming effects reported above for the allocentric group are driven largely by changes in search times to un-primed trials and less by changes in search times to primed trials. Thus, it would seem that search times are not benefitting (i.e. becoming faster) when the allocentric information is repeated. Conversely, it is suggested that the priming effects observed in the egocentric group are driven largely by a reduction in search times to primed trials, with search times to un-primed trials remaining mostly constant. This therefore suggests that when egocentric information regarding a target location is repeated, search times become faster. We conducted further tests to explore this potential difference in the origin of the “priming” effects in the allocentric and egocentric groups. To do this, we divided the data set into four subsets: allocentric un-primed sequences; allocentric primed sequences; egocentric un-primed sequences; and egocentric primed sequences, and we carried out separate repeated measures

ANOVAs for each of those subsets with each ANOVA using the factors of Delay (Short, Medium, Long) and Repetition (trials 1–4 of a sequence).

3.2.3. Allocentric group: un-primed sequences

The analysis revealed a significant main effect of Repetition for un-primed trials in the Allocentric group, $F(3,60) = 19.12$; $p = 0.001$. Search times became slower between the first and last trial of un-primed sequences (Trial 1: $M = 722.05$, $SE = 25.5$; Trial 2: $M = 813.71$, $SE = 29.6$; Trial 3: $M = 809.58$, $SE = 28.4$; Trial 4: $M = 808.20$, $SE = 29.8$). The effect of Delay was also significant, $F(2,40) = 3.40$; $p = 0.043$, as was the interaction between Delay and Repetition, $F(6,120) = 2.33$; $p = 0.037$.

3.2.4. Allocentric group: primed sequences

The analysis revealed a non-significant main effect of Repetition ($p = 0.280$), a non-significant main effect of Delay ($p = 0.409$), and a non-significant interaction ($p = 0.051$) for primed trials in the Allocentric group.

3.2.5. Egocentric group: un-primed sequences

The analysis revealed a non-significant main effect of Repetition for un-primed trials in the Egocentric group ($p = 0.587$). The effect of Delay was significant, $F(2,40) = 8.06$; $p = 0.001$, while the interaction was not ($p = 0.352$).

3.2.6. Egocentric group: primed sequences

The analysis revealed a significant main effect of Repetition for primed trials, $F(3,60) = 8.11$; $p = 0.001$. Search times became faster between the first and last trial of primed sequences (Trial 1: $M = 822.53$, $SE = 30.4$; Trial 2: $M = 791.92$, $SE = 28.5$; Trial 3: $M = 781.62$, $SE = 29.8$; Trial 4: $M = 760.39$, $SE = 26.6$). The effect of Delay was also significant, $F(2,40) = 11.23$; $p = 0.001$, while the interaction was not ($p = 0.085$).

The analyses presented in Sections 3.2.3–3.2.6 demonstrate that repetition is a significant factor in both Allocentric and Egocentric conditions but for different aspects of the experiment and therefore presumably for different reasons. Repetition was a significant factor for Allocentric un-primed sequences but not for Allocentric primed sequences, while the reverse was true for the Egocentric condition. From the analysis in Section 3.2, significant priming effects (faster search times to primed trials relative to un-primed trials) were observed in both the Allocentric and Egocentric groups and it appeared that the priming effects were greater in the allocentric condition. However, it is now clear that the effects in the allocentric group are driven by a change in search times to un-primed trials, in that search times to un-primed trials became slower as opposed to search times becoming faster when allocentric information was repeated. Conversely, in the egocentric group, our data suggest that the priming effects are driven by search times decreasing when egocentric target location information is repeated, thus reflecting a "*true"* priming effect in this condition.

3.3. Cumulative priming

The final analysis involves calculating the difference between search times to the first and fourth trials of a sequence to provide a measure for the degree of change across the sequence. This is termed cumulative priming and a positive number indicates that search times decreased. These differences for each delay condition are shown in Table 2 with the average difference across the three delay conditions shown in Fig. 3. It can clearly be seen that there are differences in the change in search times across sequences according to Group (Egocentric, Allocentric) and Sequence Type (Primed, Un-primed). For primed sequences, cumulative priming effects were significantly greater in the egocentric condition ($M = 62.15$, $SE = 16.1$) compared to the allocentric condition ($M = 20.50$, $SE = 11.7$, $t(40) = 2.09$; $p = 0.043$, independent-samples *t*-test). When the egocentric position of a target was repeated search times decreased and this was observed in all three delay conditions. Moreover, there was no significant difference between cumulative priming across the three egocentric delay conditions (repeated measures ANOVA: $p = 0.986$, see also Table 2). For un-primed sequences there was again a significant difference between allocentric (*M* = −86.14, *SE* = 18.5) and egocentric sequences (*M* = −6.00, *SE* = 15.7, *t*(40) = 3.30; *p* = 0.002, independent-samples *t*-test): search times to allocentric un-primed sequences became slower across the course of a sequence, indicating a cost when target location is not repeated.

Table 2. Mean search time (ms) difference between trials 1 and 4 of a sequence, known as cumulative priming.

	Group 1: Egocentric	Group 2: Allocentric
Primed Sequences:		
Short Delay	62.40 (19.8) **	42.71 (17.8) *
Medium Delay	59.17 (24.1) **	11.12 (19.1)
Long Delay	64.87 (30.8) *	7.66 (11.5)
Average across all delays	62.15 (16.1)	20.50 (11.7)
Un-Primed Sequences:		
Short Delay	6.49 (27.2)	-28.40 (25.2)
Medium Delay	-42.09 (24.7)	-120.79 (25.2) **
Long Delay	17.63 (26.2)	-109.23 (24.4) **
Average across all delays	-6.00 (15.7)	-86.14 (18.5)

A positive number represents a speeding in search times. Standard error is presented in brackets.
**denotes statistically significant at *p* < .025
* denotes *p* < .05 but not statistically significant when correction for multiple comparisons is applied

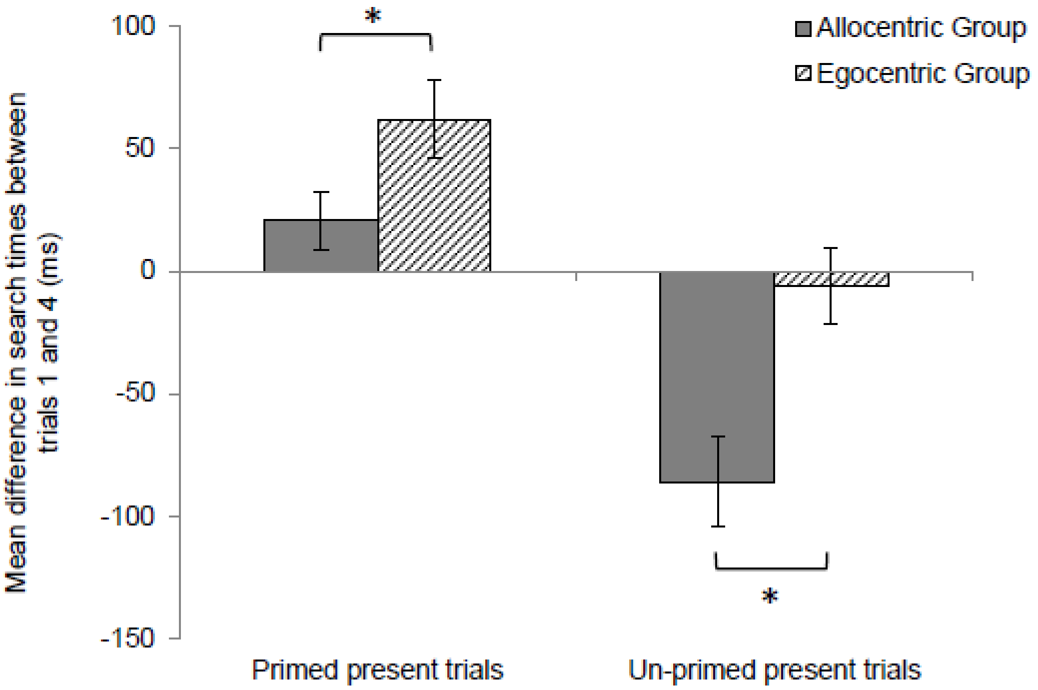

Figure 3. Mean difference in search times to the first and fourth present trial of primed and un-primed sequences for Egocentric and Allocentric groups. Error bars represent the within-subjects' standard error of the mean. * denotes *p* < .05.

4. Discussion

Here we evaluated egocentric and allocentric coding for target location in a visual search task and compared the effect of delay on the availability of these two types of information. We found significant egocentric cumulative priming at the short and medium delays (2000 ms and 4000 ms) and observed a reduction in search times at the longest delay condition where there was a minimum of 8000 ms between trials (although not statistically significant when *p* was adjusted for multiple comparisons). These cumulative egocentric priming effects represent the difference in search times to the first and fourth target present trials of a sequence; therefore, while the minimum amount of time that elapsed between two consecutive trials was 2000 ms, 4000 ms or 8000 ms, the actual time that the egocentric representations were influencing search behaviour was considerably longer than this. Additionally, interspersed within the egocentric primed trials there were absent trials and trials where the target was at an un-primed location. The egocentric cumulative priming effects were no different in the three delay conditions which suggests that the availability of the egocentric representations used in spatial priming are not as limited as previously thought and that they do not degrade substantially over prolonged periods of time.

Our findings suggest that egocentric information is still available and can influence behaviour after lengthy periods of delay. This is in line with observations made by other researchers (for example, [28]; [27]; [25] ; [8]). Taken together the findings challenge Milner and Goodale's [4] claim that egocentric representations do not survive delays and that such representations decay very quickly. Specifically, the observation of stable egocentric representations in our study seems to conflict with findings that visuomotor performance deteriorates when a delay is introduced between seeing an object and reaching for/pointing towards it [12] ; [13]. The perception-action model accounts for this decline in performance by stating that since egocentric representations in the dorsal stream are highly transient, less accurate allocentric representations in the ventral stream are used to complete a motor action following a delay. Thus, the model suggests that after a delay, owing to the short term nature of dorsal stream representations, there is a shift from using the dorsal stream to using the ventral stream [3]; [4] ; [24]. However, recently this account has been criticised by a number of studies. For example, it has been observed that dorsal stream areas are activated when participants complete a motor action after a delay and that the areas involved in delayed and immediate action overlap [36]; [37]; [38] ; [39]. Likewise, using transcranial magnetic stimulation, the anterior intraparietal sulcus (AIP) which is located in the dorsal stream has been found to be required in the completion of both immediate and delayed grasping [40]. Further, single unit recordings in monkeys find that many of the neurons in AIP are active during the delay period between seeing an object and making a corresponding hand movement to it [41]. Thus, there have been a number of demonstrations of the involvement of the dorsal stream in delayed action (for a review see Ref. [9]) which suggests that the visual information used for action-guidance, presumably egocentric in nature, is not as transient as was originally claimed. Furthermore, while the differential effects of visual illusions on delayed and immediate motor performance have been taken as evidence that the ventral stream is being used after a delay, it has also been found that the availability of visual feedback may instead explain the differences between immediate and delayed performance [25]. In the immediate condition visual feedback is typically available throughout, allowing on-line corrections to be made which reduce the apparent effects of the illusion; however, this information is not available in the delayed condition. Franz et al. [25] found that when the effect of visual feedback is controlled introducing a delay does not increase the visuomotor system’s susceptibility to a visual illusion. Likewise, Hesse and Schenk [20] observed that the availability of environmental cues is also a factor in determining how accurately an individual with visual agnosia could complete a delayed posting task: in the absence of environmental cues they observed that her performance was as accurate as that of control subjects, and thus challenging the claim that the ventral stream is necessary for carrying out delayed actions.

We have shown here that egocentric representations are not as transient as previously thought; however, we now need to compare their persistence with that of allocentric representations. In comparing search times to primed and un-primed trials, the difference between the two was significantly greater in the allocentric condition: in the allocentric condition search times were on average 101.70 ms slower to un-primed trials than primed trials, while in the egocentric condition this slowing was 45.70 ms. On the face of it, it would appear that egocentric priming is less effective than allocentric priming; however, an intriguing difference between the two conditions is highlighted in Fig. 3. It is clear that the egocentric priming effects are the result of search times becoming faster when the egocentric position of a target is repeated across a sequence of trials, while in this group search times to un-primed trials are unchanged. Conversely, for the allocentric group, while there appears to be little benefit to search times when the target location is repeated, there is a substantial search time cost on un-primed trials. Therefore, it appears that egocentric priming, in the truest meaning of the word, is more effective here than allocentric priming. However, it is necessary to consider potential explanations for the search time cost on un-primed allocentric trials. Since this finding was unexpected, we can at present only offer some speculative explanations.

First, it should be pointed out that this asymmetry between modest benefits compared to significant costs for attentional priming is not without precedence. In Posner's voluntary cueing task a similar difference is found for valid versus invalid conditions [42]. A response time advantage when targets appear in locations that have been previously cued (valid trials) and a response time cost when targets appear in a location different to the one that was cued (invalid trials) is an established phenomenon [43] ; [44]. The characteristic response-time slowing associated for attending to invalid target locations allows us to speculate that in the allocentric priming condition attention is being shifted to the primed locations, and that when this expectation is violated (i.e. when the target appears in an un-primed target location) attention has to be disengaged from the previous target location, resulting in the search time costs observed between primed and un-primed trials. Interestingly, this cost of violating a target location is not seen in the egocentric condition, suggesting that allocentric but not egocentric priming is driven by the voluntary allocation of spatial attention to primed locations.

This hypothesis that allocentric priming but not egocentric priming is supported by voluntary deployment of spatial attention is also supported by a comparison of the contradicting findings from Maljkovic and Nakayama [45] and Barrett et al. [46]. Maljkovic and Nakayama [45] reported that position priming was driven by an allocentric, and not egocentric, frame of reference. Conversely, Barrett et al. [46] found a reaction time advantage for targets presented in valid egocentric positions but not for targets presented in valid allocentric positions [46]. However, the method of capturing attention is likely to explain the differences between the two studies: in the former study, a feature singleton was defined as the target, presumably inducing goal directed and voluntary attention capture, while in the latter a change in visual salience resulted in a shift in reflexive attention [46]; [45]; [47] ; [48]. Therefore, it is possible that the distinction between allocentric and egocentric priming can be related to the distinction between voluntary and reflexive shifts of attention. Given our use of an implicit task here, coupled with the observations of consistent egocentric priming effects, it demonstrates the natural tendency of participants to exploit egocentric information. In line with this, there is evidence that allocentric and egocentric coding may rely on explicit and implicit mechanisms respectively; for example, it has consistently been reported that while implicit memory is intact in Schizophrenia patients their explicit memory function is limited [49]; [50] ; [51]. Of relevance here, Weniger and Irle [52] found that these patients were impaired on a navigation task reliant on allocentric coding on account that it required explicit memory processes, while the same patient group performed normally on an egocentric, and presumably implicit, version of the task. Thus, the literature speaks to allocentric coding being related to both voluntary attention capture and explicit memory processes while egocentric coding is more automatic and implicit. Given the research findings discussed above, the task we used here may have been biased towards the use of egocentric information, thus offering a potential explanation as to the superior priming effects observed in the egocentric condition relative to the allocentric condition. Therefore, the possibility remains that using an explicit task may be more suited to the exploitation of allocentric relationships, resulting in greater priming effects as opposed to the cost in search times we observed here.

However, the distinction between explicit versus implicit spatial cues is only one possible account for the different pattern of results found for allocentric versus egocentric priming. There are also perceptual factors that could account for the difference. These factors will be explored in the current paragraph. In our study, we employed a landmark consisting of two parallel tilted lines to provide a reference for the allocentric priming. In the allocentric condition the spatial relationship between the landmark and the target remained consistent, thereby potentially creating a new Gestalt, i.e. the impression that the landmark and the target combine to form a new visual object. Thus, in contrast to the Posner paradigm, the presence and validity of the priming cue itself may have changed the perceptual form of the target, thereby potentially inducing observers to adopt a new search template. This new template (i.e. in the case of allocentric priming) would correspond to the combination of the target and the landmark presented in a consistent spatial relationship. This new object presumably, being bigger and being quite distinct from all other items in the search display (new object consisting of three lines, distractors consisting of only one line), might appear more salient and adopting it as search template could potentially offer search benefits. However, in the context of our experiment such a search template based on the combination of the landmark and the target is highly unreliable and participants who adopted such a new search template will be forced to replace it with the original search template in half of the trials (i.e. the un-primed trials), thereby potentially creating considerable search-time increases for un-primed trials. Such effects have been observed before in studies looking at contextual cueing effects [53] ; [54]. Moreover, it is also known that forcing observers to adopt a new search template between trials without informing them, as we did here, results in a slowing in search performance [55]; [56] ; [57].

In addition to the target-landmark relationship being changeable on un-primed allocentric trials, the location of this target-landmark pairing was unpredictable in both the primed and un-primed allocentric searches. Conci et al. [58] observed that when relocations of a target are predictable, contextual cueing benefits can still be observed; however, when the target is relocated to an unpredictable location, similar to our experiment here, the benefits of contextual cueing are no longer seen. Furthermore, the past contents of the target's new location can influence responding to the current contents: when a target moved to a location that previously contained a distractor there was a search time cost [59] ; [60]. Given the nature of our search arrays and the relatively small search area, it is possible that the target-landmark pairing moved into a location that had previously been occupied by a distractor, resulting in extended search times. Thus taken together, there is good evidence in the literature that unreliable contextual cues can (for a number of reasons) induce substantial search costs. We therefore conclude that the semi-consistent, but unreliable, target-landmark pairing in the allocentric condition is responsible for the increased search times observed for un-primed trials in this condition.

In conclusion, on the basis that there seems to be a cost associated with violating a target position defined in an allocentric frame of reference, we conclude that egocentric priming, taking the true nature of priming to be a reduction in search times with repetition, is more effective than allocentric priming. This is consistent with findings from our previous studies: when both allocentric and egocentric information were repeated the priming effects were driven by egocentric information [33]. Moreover, as the egocentric priming effects in the longest delay condition were driven by information that was presented more than eight seconds before, it is clear that egocentric representations are not as transient as originally thought.

Acknowledgements

This work was supported by Animal Free Research UK. The authors acknowledge Stuart Flegg and Kirstie Mathie for the data collection.

---

[1] For this analysis and the data presented in Table 1, responses to primed trials represent the average search times to trials 2–4 in primed sequences. While the first trial of these sequences is classified as being part of primed sequences in later analysis, for the purposes of this analysis it is not classified as a primed trial as it is the first presentation of a target location. Un-primed trials represent the average of trials 1–4 in un-primed sequences.

References

[1]
N. Burgess, H.J. Spiers, E. Paleologou
Orientational manoeuvres in the dark: dissociating allocentric and egocentric influences on spatial memory. Cognition, 94 (2) (2004), pp. 149–166

[2]
G.D. Rains
Principles of Human Neuropsychology
McGraw-Hill Companies Inc., USA (2002)

[3]
A.D. Milner, M.A. Goodale
The Visual Brain in Action
(1st ed.)Oxford University Press Inc, Oxford (1995)

[4]
A.D. Milner, M.A. Goodale
The Visual Brain in Action
(2nd ed.)Oxford University Press Inc., Oxford (2006)

[5]
L.G. Ungerleider, M. Mishkin
Two cortical visual systems
D.J. Ingle, M.A. Goodale, R.J.W. Mansfield (Eds.), Analysis of Visual Behaviour, MIT Press, Cambridge, MA (1982), pp. 549–586

[6]
A.D. Milner, M.A. Goodale
Visual pathways to perception and action
T.P. Hicks, S. Molotchnikoff, T. Ono (Eds.), Progress in Brain Research, vol. 95, Elsevier, Amsterdam (1993), pp. 317–337

[7]
G. Galati, E. Lobel, G. Vallar, A. Berthoz, L. Pizzamiglio, D. Le Bihan
The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study
Exp. Brain Res., 133 (2000), pp. 156–164

[8]
G. Jager, A. Postma
On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence Neuropsychologia, 41 (4) (2003), pp. 504–515 Pii S0028-3932(02)00086-6

[9]
T. Schenk, R.D. McIntosh
Do we have independent visual streams for perception and action?
Cognit. Neurosci., 1 (2010), pp. 52–61

[10]
R.F. Wang, E.S. Spelke
Updating egocentric representations in human navigation
Cognition, 77 (3) (2000), pp. 215–250

[11]
D.A. Westwood, M. Heath, E.A. Roy
No evidence for accurate visuomotor memory: systematic and variable error in memory guided reaching J. Motor Behav., 35 (2) (2003), pp. 127–133

[12]
M.F. Bradshaw, S.J. Watt
A dissociation of perception and action in normal human observers: the effect of temporal-delay Neuropsychologia, 40 (11) (2002), pp. 1766–1778

[13]
D. Elliott, J. Madalena
The influence of premovement visual information on manual aiming Q. J. Exp. Psychol., 39A (1987), pp. 541–559

[14]
C. Hesse, V.H. Franz
Memory mechanisms in grasping Neuropsychologia, 47 (6) (2009), pp. 1532–1545

[15]
A.D. Milner, H.C. Dijkerman, L. Pisella, R.D. McIntosh, C. Tilikete, A. Vighetto, Y. Rossetti
Grasping the past: delay can improve visuomotor performance Curr. Biol., 11 (2001), pp. 1896–1901

[16]
A.D. Milner, Y. Paulignan, H.C. Dijkerman, F. Michel, M. Jeannerod
A paradoxical improvement in optic ataxia with delay: new evidence for two separate systems of localization Proc. R. Soc. Lond.: Biol. Sci., 266 (1999), pp. 2225–2230

[17]
N.J. Rice, M.G. Edwards, I. Schindler, T.D. Punt, R.D. McIntosh, G.W. Humphreys, A.D. Milner Delay abolishes the obstacle avoidance deficit in unilateral optic ataxia
Neuropsychologia, 46 (5) (2008), pp. 1549–1557

[18]
M.A. Goodale, L.S. Jakobson, J.M. Keillor
Differences in the visual control of pantomimed and natural grasping movements Neuropsychologia, 32 (10) (1994), pp. 1159–1178

[19]
S. Rossit, L. Szymanek, S. Butler, M. Harvey
Memory-guided saccade processing in visual form agnosia (patient D. F.) Exp. Brain Res., 200 (2010), pp. 109–116

[20]
C. Hesse, T. Schenk
Delayed action does not always require the ventral stream: a study on a patient with visual form agnosia Cortex, 54 (0) (2014), pp. 77–91

[21]
S. Aglioti, J.F.X. DeSouza, M.A. Goodale
Size-contrast illusions deceive the eye but not the hand Curr. Biol., 5 (6) (1995), pp. 679–685

[22]
A.M. Haffenden, M.A. Goodale
The effect of pictorial illusion on prehension and perception J. Cognit. Neurosci., 10 (1) (1998), pp. 122–136

[23]
Y. Hu, M.A. Goodale
Grasping after a delay shifts size-scaling from absolute to relative metrics J. Cognit. Neurosci., 12 (5) (2000), pp. 856–868

[24]
D.A. Westwood, M.A. Goodale
Perceptual illusion and the real-time control of action Spat. Vis., 16 (2003), pp. 243–254

[25]
V.H. Franz, C. Hesse, S. Kollath
Visual illusions, delayed grasping, and memory: no shift from dorsal to ventral control
Neuropsychologia, 47 (6) (2009), pp. 1518–1531

[26]
T. Schenk, V. Franz, N. Bruno
Vision-for-perception and vision-for-action: which model is compatible with the available psychophysical and neuropsychological data? Vis. Res., 51 (8) (2011), pp. 812–818

[27]
K. Fiehler, I. Schutz, D.Y.P. Henriques
Gaze-centered spatial updating of reach targets across different memory delays Vis. Res., 51 (8) (2011), pp. 890–897

[28]
S. Chieffi, D.A. Allport, M. Woodin
Hand-centred coding of target location in visuo-spatial working memory Neuropsychologia, 37 (4) (1999), pp. 495–502

[29]
P.A. Byrne, D.C. Cappadocia, J.D. Crawford
Interactions between gaze-centered and allocentric representations of reach target location in the presence of spatial updating Vis. Res., 50 (24) (2010), pp. 2661–2670

[30]
J. McIntyre, F. Stratta, F. Lacquaniti
Short-term memory for reaching to visual targets: psychophysical evidence for body-centered reference frames J. Neurosci., 18 (20) (1998), pp. 8423–8435

[31]
T. Geyer, H.J. Müller, J. Krummenacher
Cross-trial priming of element positions in visual pop-out search is dependent on stimulus arrangement J. Exp. Psychol. Hum. Percept. Perform., 33 (4) (2007), pp. 788–797

[32]
L. Huang, A.O. Holcombe, H. Pashler
Repetition priming in visual search: episodic retrieval, not feature priming Mem. Cognit., 32 (1) (2004), pp. 12–20

[33]
K. Ball, D. Smith, A. Ellison, T. Schenk
Both egocentric and allocentric cues support spatial priming in visual search Neuropsychologia, 47 (6) (2009), pp. 1585–1591

[34]
K. Ball, D. Smith, A. Ellison, T. Schenk
A body-centred frame of reference drives spatial priming in visual search Exp. Brain Res., 204 (4) (2010), pp. 585–594

[35]
K. Ball, A. Lane, A. Ellison, T. Schenk
Spatial priming in visual search: memory for body-centred information Exp. Brain Res., 212 (3) (2011), pp. 477–485

[36]
J.D. Connolly, R.A. Andersen, M.A. Goodale
fMRI evidence for a ‘parietal reach region' in the human brain Exp. Brain Res., 153 (2003), pp. 140–145

[37]
K. Fiehler, M.M. Bannert, M. Bischoff, C. Blecker, R. Stark, D. Vaitl, et al.
Working memory maintenance of grasp-target information in the human posterior parietal cortex Neuroimage, 54 (3) (2011), pp. 2401–2411

[38]
M. Himmelbach, M. Nau, I. Zundorf, M. Erb, M.T. Perenin, H.O. Karnath
Brain activation during immediate and delayed reaching in optic ataxia Neuropsychologia, 47 (6) (2009), pp. 1508–1517

[39]
A. Singhal, L. Kaufman, K. Valyear, J.C. Culham
fMRI reactivation of the human lateral occipital complex during delayed actions to remembered objects Vis. Cognit., 14 (2006), pp. 122–125

[40]
N. Cohen, E.S. Cross, E. Tunik, S.T. Grafton, J.C. Culham
Ventral and dorsal stream contributions to the online control of immediate and delayed grasping: a TMS approach Neuropsychologia, 47 (6) (2009), pp. 1553–1562

[41]
A. Murata, V. Gallese, M. Kaseda, H. Sakata
Parietal neurons related to memory-guided hand manipulation J. Neurophysiol., 75 (5) (1996), pp. 2180–2186

[42]
M.I. Posner, Y. Cohen Components of visual orienting H. Bouma, D. Bouwhuis (Eds.), Attention and Performance X: Control of Visual Processing, Erlbaum, Hillside, NJ (1984), pp. 531–556

[43]
M.I. Posner Orienting of attention Q. J. Exp. Psychol., 32 (February) (1980), pp. 3–25

[44]
M.I. Posner, C.R.R. Snyder, B.J. Davidson Attention and the detection of signals J. Exp. Psychol.–Gen., 109 (2) (1980), pp. 160–174

[45]
V. Maljkovic, K. Nakayama Priming of pop-out: II. The role of position Percept. Psychophys., 58 (7) (1996), pp. 977–991

[46]
D.J.K. Barrett, M.F. Bradshaw, D. Rose, J. Everatt, P.J. Simpson
Reflexive shifts of covert attention operate in an egocentric coordinate frame Perception, 30 (9) (2001), pp. 1083–1091

[47]
H. Pashler, J.C. Johnston, E. Ruthruff
Attention and performance Annu. Rev. Psychol., 52 (2001), pp. 629–651

[48]
R.W. Remington, J.C. Johnston, S. Yantis
Involuntary attentional capture by abrupt onsets Percept. Psychophys., 51 (3) (1992), pp. 279–290

[49]
L. Clare, P.J. McKenna, A.M. Mortimer, A.D. Baddeley
Memory in schizophrenia: what is impaired and what is preserved? Neuropsychologia, 31 (11) (1993), pp. 1225–1241

[50]
W. Perry, G.A. Light, H. Davis, D.L. Braff
Schizophrenia patients demonstrate a dissociation on declarative and non-declarative memory tests Schizophr. Res., 46 (2–3) (2000), pp. 167–174

[51]
S.R. Sponheim, V.R. Steele, K.A. McGuire
Verbal memory processes in schizophrenia patients and biological relatives of schizophrenia patients: intact implicit memory, impaired explicit recollection Schizophr. Res., 71 (2–3) (2004), pp. 339–348

[52]
G. Weniger, E. Irle
Allocentric memory impaired and egocentric memory intact as assessed by virtual reality in recent-onset schizophrenia Schizophr. Res., 101 (1–3) (2008), pp. 201–209

[53]
M.M. Chun, Y. Jiang
Contextual cueing: implicit learning and memory of visual context guides spatial attention Cognit. Psychol., 36 (1) (1998), pp. 28–71

[54]
I.R. Olson, M.M. Chun
Perceptual constraints on implicit learning of spatial context Vis. Cognit., 9 (3) (2002), pp. 273–302

[55]
W. Schneider, R.M. Shiffrin
Controlled and automatic human information processing: I. Detection, search, and attention
Psychol. Rev., 84 (1) (1977), pp. 1–66

[56]
T.J. Vickery, L.-W. King, Y. Jiang
Setting up the target template in visual search J. Vis., 5 (1) (2005), pp. 81–92

[57]
J.M. Wolfe, T.S. Horowitz, N. Kenner, M. Hyle, N. Vasan
How fast can you change your mind? The speed of top-down guidance in visual search
Vis. Res., 44 (12) (2004), pp. 1411–1426

[58]
M. Conci, L. Sun, H.J. Müller
Contextual remapping in visual search after predictable target-location changes
Psychol. Res., 75 (4) (2011), pp. 279–289

[59]
T. Makovski, Y.V. Jiang
Contextual cost: when a visual-search target is not where it should be Q. J. Exp. Psychol. (Hove), 63 (2) (2010), pp. 216–225
[60]
Y. Yang, E.C. Merrill
Response cost to repeated displays-when previous distractors become targets
Q. J. Exp. Psychol. (Hove), 68 (4) (2015), pp. 625–634