Both egocentric and allocentric cues support spatial priming in visual search

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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, A. D., & Goodale, M. A. (1995). The visual brain in action (1st ed.). Oxford: Oxford University Press; Milner, A. D., & Goodale, M. A. (2006). The visual brain in action (2nd ed.). Oxford: Oxford University Press Inc.]. The dorsal stream codes spatial information egocentrically, that is, relative to the observer. Egocentric representations are argued to be highly transient; therefore, it might be expected that egocentric information cannot be used for spatial memory tasks, even when the visual information only needs to be retained for a few seconds. Here, by applying a spatial priming paradigm to a visual search task, we investigated whether short-term spatial memory can use egocentric information. Spatial priming manifests itself in speeded detection times for a target when that target appears in the same location it previously appeared in. Target locations can be defined in either egocentric 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, or if both are. Our results show that both allocentric and egocentric cues were used in spatial priming, and that egocentric cues were in fact more effective than allocentric cues for short-term priming. We conclude that egocentric information can persist for several seconds; a conclusion which is at odds with the assumption of the perception–action model that egocentric representations are highly transient.

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1. Introduction

The locations of objects in a visual environment can be defined using different frames of reference. Egocentric frames of reference (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. Conversely, allocentric frames of reference (object-based metrics) consider spatial relations between objects, and rely on the external environment to define space. That is, by using landmarks [Burgess, Spiers, & Paleologou, 2004]. Milner and Goodale (1993) argue that visuomotor control relies on representations which are centred on the individual: 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. Furthermore, Milner and Goodale (1993) argue that owing to the fact that the position of our head, body, and eyes relative to external objects constantly change, the dorsal stream does not rely on stored representations. They use this assumption to explain the complementary effects of temporal delays on the visuomotor performance of patients with either dorsal or ventral stream damage (Goodale, Jakobson, & Keil, 1994; Milner et al., 2001; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999).

Supporting the view that the dorsal stream cannot store spatial information, Westwood, Heath, and Roy (2001) found greater pointing errors when the target was occluded for 500 ms before movement was cued compared to when the movement was cued immediately, thereby suggesting very limited availability of dorsal stream representations. Additionally Westwood and Goodale (2003) observed that although visual illusions do not affect motor performance when the action is executed immediately (Aglioti, DeSouza, & Goodale, 1995), visual illusions have a significant effect on visuomotor performance already after delays of 2.5 s. This suggests that after a delay it is the ventral rather than the dorsal stream, which provides the visual information for the control of the movements. It is also suggested that 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 movement; therefore, suggesting that egocentric representations have a short time span (Westwood, Heath, & Roy, 2003). Given that the relevant information in visuomotor control is egocentric in origin, and that egocentric information has been associated with dorsal stream structures, one might therefore expect that egocentric information cannot be stored for more than 2 s,
and that tasks, which depend on visual memory, have to rely on allocentric representations.

The research into topographical memory has not been conclusive about whether egocentric representations can be stored; for example, while some have shown that changing the egocentric information between the learning phase and the testing phase causes less disruption than changing the allocentric information (Burgess et al., 2004; Simons & Wang, 1998; Wang & Simons, 1999), others report that recognition performance of object location is affected by egocentric changes (Christou & Buelthoff, 1999; Diwadkar & McNamara, 1997; Finlay, Motes, & Kozhevnikov, 2007; Shelton & McNamara, 2004). However, in most of these studies participants are required to report whether the location of an object has changed relative to other objects or landmarks in the scene, thus by its very nature the task prompts participants to employ allocentric information. Furthermore, generally these studies used long delays (7–13 s). Therefore, they cannot be used to address the question of whether egocentric information might be useful for short delays of a few seconds, a question which is of obvious interest in the context of Milner and Goodale’s perception and action model since they used the dorsal stream’s inability to store information, even for more than 2 s, to explain the significant effects of such short delays on visuomotor performance in optic ataxia, visual form agnosia, and studies using visual illusions.

To address this question, there are three conditions which must be met in order to accurately assess the duration and use of egocentric spatial information. Firstly, spatial memory must be tested over very short time spans. Secondly, performance in an egocentric condition must be compared directly with that in an allocentric condition. To allow a direct comparison between these two conditions the same behavioural task must be used. Since in Milner and Goodale’s model allocentric information is associated with perceptual tasks while egocentric information is associated with visuomotor tasks, there is always a risk that using either a perceptual or a visuomotor task might provide a bias against the use of egocentric or allocentric information, respectively. In our study we decided to use a perceptual task to provide a stronger test of the hypothesis that egocentric information is unavailable after a delay. Since a perceptual task might bias against the use of egocentric information any evidence of its use after a delay has to be taken even more seriously. Furthermore using a perceptual task also allows us to address another interesting question, namely whether Milner and Goodale’s thesis that egocentric information is not relevant for typical perceptual tasks is correct. Finally, participants should not be prompted towards using one type of spatial information, so no instructions about how the target is coded should be provided.

An experimental paradigm, which fulfils these criteria, is priming in visual search. A standard visual search task requires the observer to decide whether a specified item, the target, is present in the display or not; the time taken to make this judgement is known as the search time and provides an index of search efficiency (Wolfe, 1998). Priming in visual search refers to the influence that memory processes can have from one trial to the next or within the same trial (Shore & Klein, 2001). Between-trial memory, known as trial-to-trial priming, operates over a time scale in the order of seconds to minutes. In trial-to-trial priming experience of a stimulus can influence future encounters with that same stimulus, specifically, repetition of a feature can facilitate the processing and speed of detection of that feature. It is likely that this repetition priming results from a memory representation of the first trial being stored and which is retrieved when that same trial is presented a second time, leading to more efficient processing of that stimulus. Trial-to-trial priming has been shown for target colour (Hilstrom, 2000; Huang, Holcombe, & Pashler, 2004; Maljkovic & Nakayama, 1994) and target location (Kristjansson, Vuilleumier, Malhotra, Husain, & Driver, 2005; Kumada & Humphreys, 2002; Maljkovic & Nakayama, 1996).

Although it is clear that spatial position can be primed, it is not clear whether the memorized position that underlies the priming effect is coded relative to the observer (i.e. the egocentric position) or relative to other items in the search array (i.e. the allocentric position). Past studies did not address this question and typically if in priming trial the position remained the same relative to other items on the screen, it was also presented at the same position on the screen relative to the observer. Maljkovic and Nakayama (1996) attempted to address this issue 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 bigger when egocentric information was added, it remained unclear whether this effect would be statistically significant.

The aim of the current study was to investigate, using a visual search task, priming of target location when both allocentric and egocentric information are available, and to directly compare this with allocentric and egocentric priming. If egocentric representations cannot be stored, as suggested by the perception–action model, egocentric priming will not be observed and there should be no or little difference between priming in the allocentric condition and priming in the combined allocentric–egocentric condition. However, if egocentric representations can be stored, egocentric priming will be observed and this will have implications for the perception–action model.

2. Method

2.1. Participants

30 naive participants from the University of Durham took part in this experiment and received course credit. Ethical approval was obtained from the Psychology Research Ethics Committee at Durham University and participants gave informed consent. Participants all had normal or corrected-to-normal visual acuity.

2.2. Stimuli

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. The purpose of this part of the trial was to ensure that participants returned to the centre of the screen at the start of each trial. To obtain the ideal font size, a staircase procedure was used for each participant to determine 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 to 0.5°, respectively). We had already established in a pilot experiment (12 participants) that for letters of such a small font size, accuracy of letter identification dropped below 50% when participants had to fixate on any position other than the position at which the letter was presented.

During the second part of a trial a search array was presented, consisting of white lines on black backgrounds. The defining feature of the target line was its orientation: distractors were oriented at 20° from vertical and the target was oriented at ~20° from vertical (see Fig. 1A). Each visual search array consisted of 12 lines: in target present trials there were 11 distractors and 1 target, and in target absent trials there were 12 distractors. In all search arrays, two distractors were placed close together and acted as a landmark for the allocentric priming condition. The stimuli were projected onto a blank wall and were observed from a distance of 3 m. The search arrays measured approximately 9° both horizontally and vertically. These were placed onto a black background so the whole stimulus display measured 33° horizontally and 27° vertically.

There were 3 types of priming conditions: allocentric, egocentric, and combined (i.e. combining allocentric and egocentric information, see Fig. 1A). In the allocentric priming condition the location of the target was positioned relative to the landmark at 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. In the combined priming condition, the target occupied the same location relative to the observer and had the same relationship with the landmark.
2.3. Procedure

At the beginning of each trial a fixation cross was presented at the centre of the screen for 1000 ms. The fixation cross was then replaced with a letter (randomly chosen from a set of 5), which was presented for 500 ms. Participants had to report the letter to the experimenter. The presentation of this letter ensured that participants re-fixated in the centre of the display before each trial and could not linger at the location of the previous target. Following the presentation of the letter, the central fixation cross was represented for 200 ms. The search display was then presented and remained on screen until participants made their key-press response. The task of the participants was to decide whether the target stimulus (a line slanted to the left) was present. Participants were encouraged to respond accurately but also as rapidly as possible. The response type and time were measured by the computer. Once participants had pressed a response key, a blank screen was presented for 500 ms and the next trial was initiated. There was a minimum of 2200 ms between two consecutive search displays. The trial sequence is illustrated in Fig. 1B.

The target stimulus was present in 80% of trials. To induce position-priming we designed sequences of trials where a given target position was used 6 times within a given sequence. Interspersed within a sequence there were also 2 control trials (the target stimulus was present but at a new position) and 2 absent trials (the target stimulus was not present), thus, each sequence consisted of 10 trials. 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. 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, we ensured that the same priming condition was never used twice in a row.

3. Results

All analyses are concerned with participants’ reaction times to make a target present or target absent decision. Incorrect answers and outliers (responses more than two standard deviations above

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**Fig. 1.** Illustrations of the priming conditions and trial sequence. (A) Schematic of stimuli for the three priming conditions. (i) Allocentric priming condition: in trial 1 and trial 2 the target stimulus is to the lower left of 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 allo-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. (B) The sequence and timing of each trial.
or below the mean) were removed. All data were tested for normality using the Shapiro–Wilk statistic; the data were normal unless otherwise stated.

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 found to be 99.3% 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.

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. Search times to target absent trials \( (M = 594.73, \text{ S.D.} = 71.6) \) were significantly slower than those to target present trials \( (M = 497.17, \text{ S.D.} = 56.1) \), \( t(29) = 10.11; p < .05 \). Search times to primed trials (where the target was presented at the same position as in a previous trial in the trial sequence) were faster than those to control trials (where the target was present but not at the given position for that sequence, \( M = 541.7, \text{ S.D.} = 67.4 \)), \( t(29) = 12.26; p < .05 \). For this analysis, and only for this analysis, the first present trial of each target sequence was classed as a control trial. This speeding for priming trials relative to control trials is an indirect measure of priming and was observed for all three priming conditions (Table 1).

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Allocentric</th>
<th>Egocentric</th>
<th>Combined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Present</td>
<td>506.1 (59.4)</td>
<td>505.6 (62.2)</td>
<td>479.8 (52.8)</td>
</tr>
<tr>
<td>Absent</td>
<td>593.7 (74.5)</td>
<td>602.0 (78.0)</td>
<td>588.5 (69.0)</td>
</tr>
<tr>
<td>Control</td>
<td>545.8 (70.7)</td>
<td>547.8 (73.2)</td>
<td>531.5 (66.3)</td>
</tr>
</tbody>
</table>

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

#### 3.1. Immediate priming effects

Fig. 2 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 or control trials). The first of these
trials is the first presentation of a target position. A 2 × 3 repeated measures ANOVA with the factors Repetition (first present trial and second present trial) and Priming Condition (allocentric, egocentric, and combined) revealed a significant main effect of Repetition, such that search times were faster on the second presentation of a target position, F(1, 29) = 8.04, p < .05; 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 tests (2-tailed t-tests) revealed that this interaction was driven by significantly greater priming for the egocentric and combined conditions compared to the allocentric condition (egocentric vs. allocentric: t(29) = 4.00, p < .05; combined vs. allocentric: t(29) = 3.71, p < .05). There was no difference between the egocentric and combined conditions (p = .460). Fig. 2 illustrates this interaction.

3.2. Cumulative priming effects

Within each sequence of trials, the target stimulus was at a given position 6 times. Fig. 3 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 × 3 repeated measures ANOVA with the factors Sequence (1st, 2nd, 3rd, 4th, 5th, and 6th presentation) and Priming Condition (allocentric, egocentric, and combined). The ANOVA revealed a significant main effect of Sequence, F(5, 145) = 51.82, p < .05; a significant main effect of Priming Condition, F(2, 58) = 20.88, p < .05; and a significant Priming Condition by Sequence interaction, F(10, 290) = 4.07, p < .05. Fig. 3 shows that search times decreased between the 1st present trial and the 6th present trial of a sequence. Post hoc tests revealed the main effect of Sequence was significant for the allocentric condition, F(5, 145) = 5.78, p < .05; the egocentric condition, F(5, 145) = 23.68, p < .05; and the combined condition, F(5, 145) = 25.62, p < .05. Thus, there was a significant cumulative priming effect for all three priming conditions.

On the significant main effect of priming condition, post hoc tests (2-tailed t-tests) showed that participants were faster responding in the combined condition than in both the allocentric condition, t(29) = 5.11, p < .05, and the egocentric condition, t(29) = 5.95, p < .05. There was no difference between search times to the allocentric and egocentric conditions (p = .485).

Finally, the interaction between priming condition and sequence. The effect of cumulative priming was significantly greater for the egocentric condition (44.2 ms reduction), the 1st and 6th present trial 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 < .05, t(29) = 2.95, p < .05, respectively. There was no significant difference between the magnitude of cumulative priming for the egocentric condition and combined condition (p = .616).

4. Discussion

The aim of this experiment was to investigate location priming for targets defined in allocentric, egocentric, and combined allocentric–egocentric coordinates. Contrary to the predictions made by the perception–action model, priming was observed for all three conditions. Surprisingly, we observed that egocentric information not only makes a contribution to the combined priming effect but that it seems to be more effective than the allocentric information: priming in the combined allocentric–egocentric condition was significantly greater than for that of the allocentric only condition. It is clear from our findings that egocentric information does contribute towards the priming effect. Furthermore, given that a minimum delay of 2200 ms separated trials in our experiment, and that the cumulative priming effect observed built up over 6 present trials 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 1 or 2 s.

At first glance, our results 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. The current study did include an egocentric only priming condition, and therefore we can provide 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. We did not monitor eye movements and therefore we can neither confirm nor reject this possibility. 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 (Fig. 2). 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 (Sclaf & 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 ours (Carrasco, Evert, Chang, & Katz, 1995; Carrasco, McLean, Katz, & Frieder, 1998; Viviani & Swenson, 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. We 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 subjects in the egocentric condition possibly could also have used allocentric landmarks. However, we
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 our experiment was relatively short. However, we deliberately chose a short delay 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 noticed that 2200 ms was the minimum delay. In some cases the delay between subsequent presentations may have been longer and in this context is also interesting that we observed a cumulative priming effect that occurred over a number of subsequent trials, thereby spanning a much longer time-interval. However, we still think that it would be very interesting to conduct further experiments with varying delay-intervals to plot the timecourse 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 the response time 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 our experiment a longer response time also meant a longer presentation time for the search display. This might explain why the target location provided at the first presentation of the egocentric condition might have been more memorable. We cannot rule out this possibility and thus while we cannot claim that egocentric priming is more effective than allocentric priming, we can maintain that egocentric priming is effective. 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 response times and accuracy rates are comparable for the two conditions and we still observed a significantly greater priming effect for the combined condition, presumably reflecting the added benefit of egocentric spatial information.

While our findings suggest that egocentric information can be used for location priming we do not know which particular egocentric frame of reference was used. In our 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. 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. 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 us to establish which of the different potential egocentric reference frames is most effective in driving location priming during visual search.

What are the implications of our findings for the perception–action model? Milner and Goodale (1993, 1995, 2006) argued that egocentric visual information in the dorsal stream is used to guide actions. However, as this information changes with every movement of the observer, they therefore assumed that such egocentric representations in the dorsal stream are not stored. Contrary to this assumption, our findings suggest that egocentric information can persist for more than 2 s. While we cannot directly show that the egocentric information which was used in our experiment derived from the dorsal stream, it has been shown in an earlier study that ventral stream damage selectively affects allocentric coding but not egocentric coding (Schenk, 2006). Furthermore, research into the neural correlates of spatial coding suggests that different mechanisms are involved in making allocentric and egocentric judgements. The posterior parietal cortex, thus dorsal stream areas, has been associated with egocentric representations (Committeri et al., 2004; Galati et al., 2000), as has the precuneus (Zaehle et al., 2007), an area which is involved in the control of visually guided hand movements and has been linked with optic ataxia (Karnath & Perenin, 2005). Therefore, it is tempting to conclude that the egocentric information is derived from dorsal stream structures.

This conclusion raises an interesting question. If egocentric visual representations can persist for several seconds they should be available to the motor system. In this case, how can we explain the degrading effects of visual delays on visuomotor performance (Bradshaw & Watt, 2002; Elliott & Madalena, 1987; Westwood et al., 2003)? One explanation for this degradation of performance is that the internal representation of a visual scene or 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.

In conclusion, our findings suggest that both egocentric and allocentric information are used in spatial priming during visual search tasks. Given that such priming effects are driven by information which has been provided (in our experiment) more than 2 s before, the findings seem to suggest that egocentric information can persist for more than 2 s. This conclusion is at odds with the assumption of the perception–action model that egocentric representations are of a highly transient nature. Our findings also suggest that contrary to the assumption in 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.

References


