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## The effects of landmarks on the performance of delayed and real-time pointing movements

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**Abstract** Converging lines of evidence suggest that the presence of non-target landmarks affects the performance of delayed target-directed movements (e.g., Diedrichsen et al. 2004; Sheth and Shimojo 2004). In the present experiment, we examined the effects of non-target landmarks on the accuracy and precision of delayed and immediate target-directed pointing movements. In our experiment, the landmarks were present just prior to and during the presentation of the target; they were never present during the execution of the movement. Absolute errors were significantly reduced when the landmarks were available during target presentation for both delayed and immediate action conditions. In contrast, the presence of landmarks improved the precision of delayed but not immediate movements (as indexed by the variable error). The locus of this “landmark benefit” appears to be in the encoding of target position since landmarks were never available after target offset. We suggest that, when available, information provided by landmarks is used to improve the accuracy of the estimation of target location. Since the targets were presented for only 100 ms, it is apparent that the spatial information available from landmarks can be quite rapidly used to estimate target position. Further, with respect to the precision of movements, we suggest that the presence of landmarks serves to improve the stability of the estimation of target position. This particular reliance on landmark information becomes more critical as the movement is delayed.

**Keywords** Frames of reference · Visuomotor control · Landmarks · Pointing · Spatial localization

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### Introduction

A wealth of neuropsychological, neurophysiological, and behavioural evidence supports the notion of two dissociable visual streams arising from early visual areas in the primate cerebral cortex: a ventral ‘perception’ stream projecting to inferotemporal cortex and a dorsal ‘action’ stream projecting to the posterior parietal cortex (Goodale & Milner, 1992; Milner & Goodale, 1995). Both streams process information about the structure of objects and about their spatial locations, but they transform this information into a quite different output. The visuomotor systems of the dorsal stream, which mediate the control of highly skilled actions, must compute the absolute metrics of target objects in ego-centric reference frames centered on the actor. In contrast, perceptual processing in the ventral stream, which allows us to recognize objects and their causal relations, must be able to recognize a particular object regardless of its absolute size and its momentary orientation and position with respect to the observer. This fundamental difference between the types of processing in the two streams helps to explain why actions are rarely susceptible to pictorial illusions, which by definition affect perception.

In most cases target-directed actions unfold in real time. We typically do not direct movements to targets after they have disappeared from view. Indeed, it has been suggested that in cases when delayed actions are made towards remembered targets, they are mediated not by the dorsal stream (at least by itself), but rather by information that was initially garnered by perceptual mechanisms in the ventral stream. Thus, while immediate actions are immune to the effects of pictorial illusions, delayed actions are not. That is, if a target is briefly flashed within an illusory display and a delay is inserted before the cue to move is presented, the subsequent movement becomes subject to the influence of the illusion (for review, see Goodale et al. 2004). It is this kind of evidence that has been used to argue that

delayed actions make use of earlier perceptual processing of the visual array. Thus, delayed grasping movements fall victim to size-contrast illusions and other perceptual phenomena of this kind (e.g., Westwood & Goodale 2003; Rossetti 1998 for a review). By the same token, delayed saccades and manual aiming movements have been shown to be affected by the relative position of a frame surrounding a previously presented target, suggesting that scene-based (allocentric) frames of reference are used to program movements to remembered targets (e.g., Wong and Mack 1981; Bridgeman et al. 1981, 1997). The notion of an interaction between egocentric and allocentric coding of target position has been put forward in a number of other studies. For example, Gentilucci et al. (1996) used the Müller-Lyer illusion to examine the systems underlying visual perception and motor action. They required subjects to point to the distant apex of Müller-Lyer figures after a 0 or 5 sec delay. They found that the influence of the illusion on pointing movements increased as a function of delay length. The authors suggested that information about a target scene is represented in parallel in both egocentric and allocentric frameworks. They also speculated that when use of the egocentric representation is inefficient, as is the case when movements are made to remembered targets or in the absence of visual feedback, interaction between allocentric and egocentric representations increases, and both contribute to movement planning. Such interaction between two different representational systems has also been found in other experiments (e.g., Hu and Goodale, 2000; Carrozzo et al. 2002; Gentilucci et al. 1994).

While there is a good deal of evidence to suggest that delayed aiming movements make use of scene-based information in movement programming, rather less work has examined whether or not the provision of landmark information actually improves performance (i.e., the accuracy and precision) of delayed movements. Although a few studies have investigated this question, the results have been inconsistent, with some studies showing a clear improvement in accuracy as a result of providing contextual cues and others finding no accuracy benefit of such cues (e.g., Conti and Beaubaton 1980; Krigolson et al. 2004; Blouin et al. 1993; Toni et al. 1996). In addition, results from these studies are hard to reconcile as some have presented the contextual cues throughout the movement planning and execution phase, while others have selectively provided such cues at target presentation only.

In a recent study investigating which frames of reference are used for delayed pointing movements, Diedrichsen et al. (2004) demonstrated that the movement endpoints of delayed pointing movements were distorted when participants pointed towards the remembered locations of targets that had been presented alongside non-target landmarks. The target was presented (alone or together with landmarks) for 1,000 ms after which the display was masked for a brief time. Upon disappearance of the mask the landmarks were re-presented (or

not re-presented, depending on the experiment) and participants pointed to the remembered target location. Even if the landmarks were not presented during the movement execution, the fact that landmarks had been visible when the target was presented led to a distortion of movement endpoints towards the location of the nearest landmark. This finding fits well with another study in which visual distractors presented in a target scene were shown to influence hand trajectories suggesting a competition between target and distractor for motor output (Chieffi et al. 2001). Moreover, the interesting aspect of Diedrichsen et al.'s (2004) result is that the distortion of endpoints does not appear to be dependent on a process that matches the conditions at encoding with the conditions at the time the movement is made, because landmarks were only available during the target presentation period. Although Diedrichsen et al. (2004) concluded that scene-based (allocentric) information plays an important role in the encoding of target position for delayed actions, they did not explore whether or not immediate actions are similarly affected by the presence of landmarks during the encoding phase. Hence, to date, it is unknown whether or not the presence of non-target landmarks also affects the encoding of target position for immediate (i.e., real time) actions. Moreover, although Diedrichsen et al. (2004) observed distortions in the distribution of movement endpoints when landmarks had been presented during the encoding phase, there was no evidence that performance actually improved with the introduction of such cues. Thus, in the present study, we sought to determine whether or not landmarks could improve performance—and whether or not such improvement was more evident in delayed, compared to real-time movements.

Other recent experiments have shown that when a frame, originally presented around a target, was re-presented after a delay, but in a different position, participants' estimates of target location shifted with the frame (Sheth and Shimojo 2004). Similar results have also been found recently in another experiment (Lemay et al. 2004). Such results show that delayed actions are influenced by contextual cues, and suggest that non-target landmarks are incorporated into a spatial map that is used to guide delayed actions initiated when direct vision of the target is removed. Although the results of Sheth and Shimojo (2004) provide some insights into how target location is coded in memory, they do not speak to whether or not such allocentric coding has a role to play in the programming of real-time actions (i.e., actions that are made immediately upon presentation of a target). Thus, an important aim of the present study was to determine the effects of landmarks on the performance of real time as well as delayed pointing movements.

Participants made delayed or immediate pointing movements towards targets that were presented either alone, or in the presence other landmark objects. If it is indeed the case that delayed actions are programmed

using contextual information, whereas immediate actions are programmed using information only about the target, we expected that the presence of the landmarks would have different effects on the two kinds of actions. More specifically, we predicted that the accuracy and precision of delayed but not immediate actions might be improved by the presence of landmarks.

## Methods

Eleven healthy right-handed participants gave their informed consent and took part in the experiment, which was conducted in accordance with local ethical guidelines.

### Experimental design and procedure

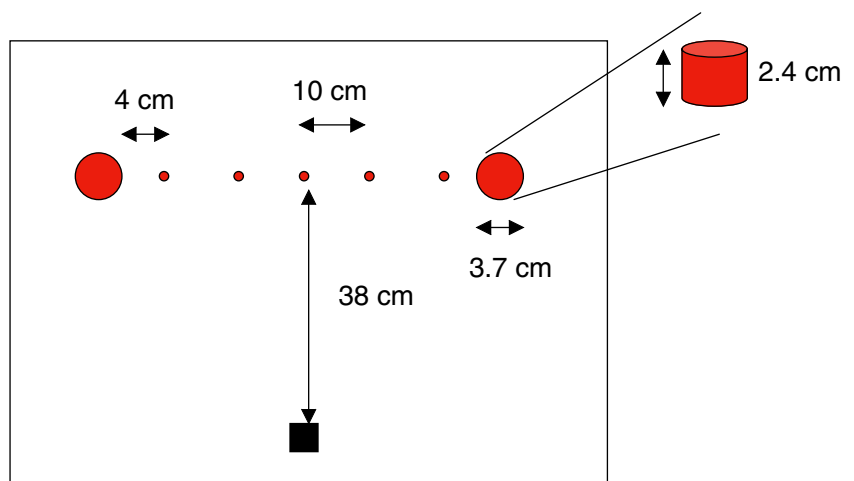
There were three main factors in the experiment: delay, presence of landmarks, and target position. Specifically, the movement could be made either immediately upon presentation of the target (immediate condition) or 2,000 ms after target offset (delay condition). In addition, the target was presented either in the presence of two non-target landmarks or in the absence of these landmarks. Lastly, the target could be presented in one of five different positions, which varied randomly from trial to trial.

The entire experiment was conducted in a completely dark room. During the experiment participants wore liquid crystal goggles and sat at a table upon which the target board was mounted. The target board consisted of a wooden board with LEDs lodged in holes drilled in a line (holes were spaced at 10 cm apart) between two Plexiglas cylinders (height = 2.4 cm, diameter = 3.7 cm) placed on the board as in Fig. 1. The board was covered with black speaker cloth to prevent excessive illumination of the target area when the LEDs were switched on. This setup ensured that illuminated LEDs

appeared as flat red circular targets, and that the landmarks (the Plexiglas cylinders) were not visible unless illuminated.

In the immediate action condition, participants were required to place their right index finger on a start pad, which consisted of a Velcro square. Once this initial position had been assumed participants signaled to the experimenter with a verbal “yes” to confirm that they were ready to begin and the experimental trial was initiated. In the landmarks-present condition, the liquid crystal goggles then opened and participants saw a completely dark environment except for two softly illuminated Plexiglas cylinders (colored red) situated 24 cm left and right of a point 38 cm directly in front of the subject. Great care was taken to ensure that the light from the cylinders did not illuminate the surrounding workspace. Three independent observers were asked to observe the experimental workspace and report if they detected a change in what they could see when the landmarks were illuminated and when they were switched off. None of the three observers were able to see any more of the experimental workspace containing the targets when the landmarks were illuminated as compared to when they were switched off. In this way, any effects of the landmarks would be due merely to their presence and not the possibility that they improved the ability of participants to see the display. The cylinders remained visible for 1,000 ms after which one of five possible red LEDs situated in a line intersecting the Plexiglas cylinders flashed on for 100 ms. At the same time the LED target flashed on, a beep signaled to the subject to move their right index finger as quickly and accurately as possible to the target location. After the 100-ms target flash, the goggles closed, ensuring that visual information was only available to participants during part of the programming phase of their movement. In the immediate action, landmarks-absent condition, the same sequence of events occurred except that the Plexiglas cylinders were never visible and the target LED flashed on in a completely dark environment.

**Fig. 1** The targets (*small circles*) and landmark objects (*larger circles*). *Black square* is the start pad. In each trial, participants pointed to one of the five targets, either immediately or after a 2,000-ms delay. Targets were presented either alone, or in the presence of the landmarks



In the delayed action condition, participants were again exposed to the environment for 1,000 ms (either with or without the landmarks) and to a target flash of 100 ms. In delayed action, however, after the target flash, the goggles closed and there was a 2,000-ms delay before the beep signaled participants to move their right index finger as quickly and accurately as possible to where they remembered the target location to be. Since participants were exposed to the experimental workspace for 1,000 ms before the target flash and then 100 ms during the target flash, viewing time of the target scene was absolutely identical in the immediate action and the delayed action conditions.

Immediate action, landmarks-present and landmarks-absent conditions and delayed action landmarks-present and landmarks-absent conditions were run in separate blocks and the order of blocks was varied pseudo-randomly across participants. Each block consisted of 20 trials to each of the five possible movement targets, randomly interleaved. Hence in total there were 400 trials (100 in each block). Participants were given 20 practice trials to familiarize them with the experimental conditions prior to the experiment proper and were also given a 5-min break between blocks. In addition, after every few trials, the experimenter turned on a bright lamp to prevent participants from becoming dark-adapted.

#### Data collection and dependent measures

An infrared emitting diode was attached to the top of each participant's right index finger to allow the recording of kinematic data by an OPTOTRAK<sup>TM</sup> optoelectronic movement recording system. The x, y, z position data was sampled at 200 Hz and stored on a computer for offline analysis. Measurements of reaction time (RT), movement time (MT), and the endpoint position of the right index finger, were calculated. The onset and the end of the movement were defined as the time when the resultant velocity of the index finger exceeded or fell below (respectively) 20 mm/s for five consecutive samples. RT was defined as the time interval between the onset of the beep and the beginning of the movement, and MT was defined as the time between the beginning and the end of the movement. Participants were instructed to make smooth movements and not to make secondary movements once their finger had landed at its initial resting place and they were largely successful at following this instruction.

## Results

One participant, for whom many data points were missing, was excluded from the analysis. Dependent variables (end-point errors, RT, and MT) from the remaining 10 participants were then subjected to standard inferential statistical analysis.

#### End-point errors

To quantify participants' performance, we calculated the constant error (CE), the variable error (VE), and the absolute error (AE) in the x (left–right) and y (near–far) dimensions. The constant error (CE) is a measure of the average signed difference between the target position and the endpoint of a movement. The variable error (VE) is the variability of movement endpoints around the average endpoint. Finally, the absolute error (AE) is the absolute value of the CE and represents the amount by which the target was missed, regardless of the direction in which it was missed. For all error analyses, a 2 (delayed or immediate) x 2 (landmarks or no landmarks) x 5 (targets) repeated measures ANOVA was conducted.

#### Constant errors

##### *Main effects of the delay*

As can be seen in Fig. 2, movements made in the immediate action condition produced significantly smaller CEs in the y dimension than those made in the delayed action condition ( $F_{1,9} = 18.091$ ,  $P = 0.002$ ). There was no such effect of the delay factor on the CE in the x dimension ( $F_{1,9} = 0.152$ ,  $P = 0.706$ ). See Fig. 2 caption for explanation of the figure.

##### *Main effects of the landmarks*

Although, in general, the presence of the landmarks improved the accuracy in the y dimension, this effect failed to reach statistical significance ( $F_{1,9} = 4.07$ ,  $P = 0.074$ ). There were no effects of the landmarks or trends towards effects for CEs in the x dimension ( $F_{1,9} = 0.64$ ,  $P = 0.445$ ).

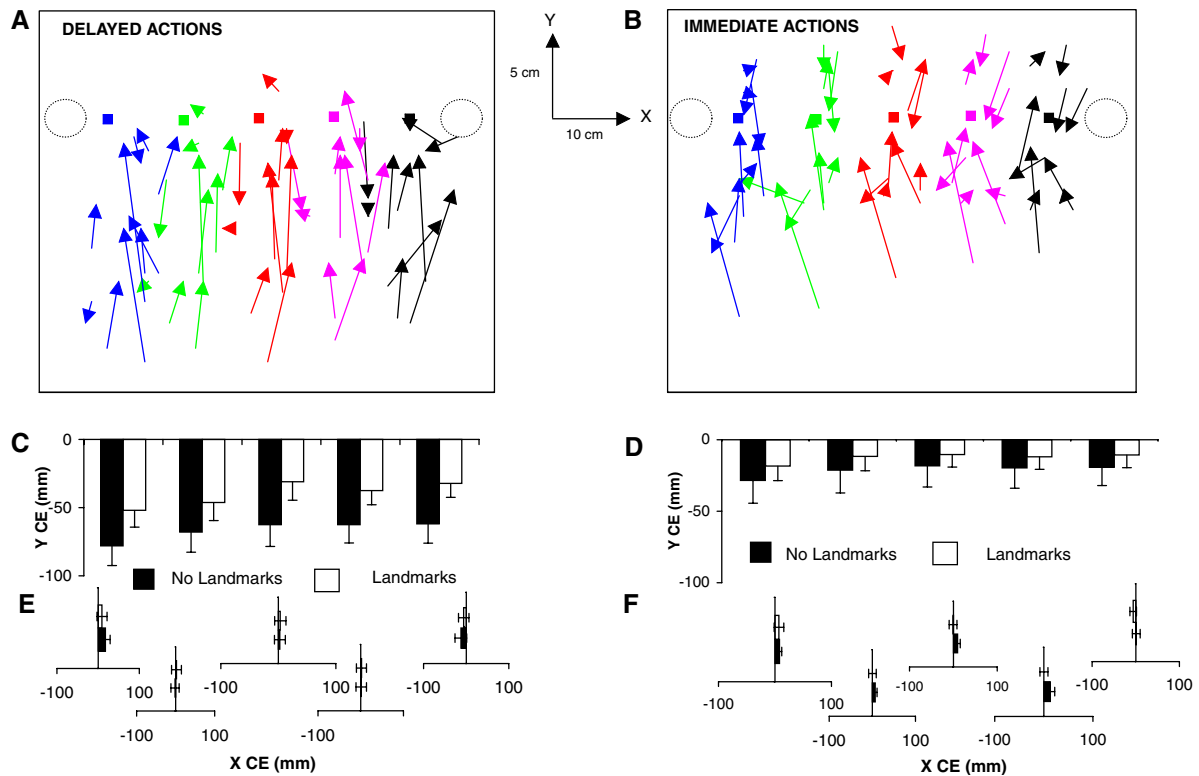
##### *Main effects of target position*

There was no significant main effect of target position on the CEs in the y or x dimensions ( $F_{4,36} = 3.604$ ,  $P = 0.058$ ;  $F_{4,36} = 3.276$ ,  $P = 0.082$  respectively). In general, the CE in the y dimension was slightly greater for targets in left hemisphere.

##### *Interactions between the factors*

There were no significant landmarks x target interactions for CE in the y or x dimensions ( $F_{1,9} = 0.609$ ,  $P = 0.658$ ,  $F_{1,9} = 0.391$ ,  $P = 0.814$  respectively). There were also no significant delay x target interactions for CEs in the y or x dimensions ( $P = 0.136$  and  $P = 0.221$  respectively). This was also true for delay x landmark interactions in both the y and x dimensions ( $P = 0.176$  and  $P = 0.140$  respectively). Finally, there were no delay x landmark x target interactions for CEs in the y or x dimensions ( $P = 0.659$  and  $P = 0.133$  respectively).





**Fig. 2 a, b** Shifts in end-points in delayed and immediate pointing—movements to different targets are shown in *different colours*. *Filled squares* represent the target positions and the *dashed circles* represent the approximate position of the landmarks (when they were present). *Origin of each arrow* is the mean end-point of the movement for each subject in the landmarks-absent condition and the arrow head is the mean endpoint for each subject in the landmarks-present condition. Note that immediate movements are significantly more accurate than delayed movements. **c, d** The constant error in the *y* dimension in the landmarks-present and landmarks-absent condition for delayed and immediate pointing. Note that there is no significant difference between landmarks-present and landmarks-absent conditions. **e, f** The constant error in the *x* dimension for delayed and immediate pointing. Note that there are no significant effects of landmarks on the *x* constant error. *Error bars in bar graphs* are SE in the mean

#### Variable errors

##### *Main effects of the delay*

As Fig. 3 shows, there was a significant main effect of delay on the VE in the *y* dimension ( $F_{1,9}=7.366$ ,  $P=0.024$ ), which was manifested as a significant reduction in precision of movements in the delayed condition compared to the immediate condition. In contrast, there was no effect of delay on the VE in the *x* dimension (mean variable error in *x* dimension in delay =  $22.5 \pm 2.5$  mm; mean variable error in *x* dimension in immediate condition =  $19.3 \pm 10.6$  mm;  $F_{1,9}=0.889$ ,  $P=0.370$ ).

##### *Main effects of the landmarks*

Movements in the landmarks-present condition were significantly more precise in the *y* dimension than those

in the landmarks-absent condition ( $F_{1,9}=10.532$ ,  $P=0.01$ ). Although the same pattern of effects on the VE in the *x* dimension was observed, the effect of landmarks was not significant (mean variable error in *x* dimension in landmarks-absent condition =  $24.3 \pm 11.6$  mm; mean variable error in *x* dimension in landmarks-present condition =  $17.5 \pm 3.9$  mm;  $F_{1,9}=4.59$ ,  $P=0.06$ ).

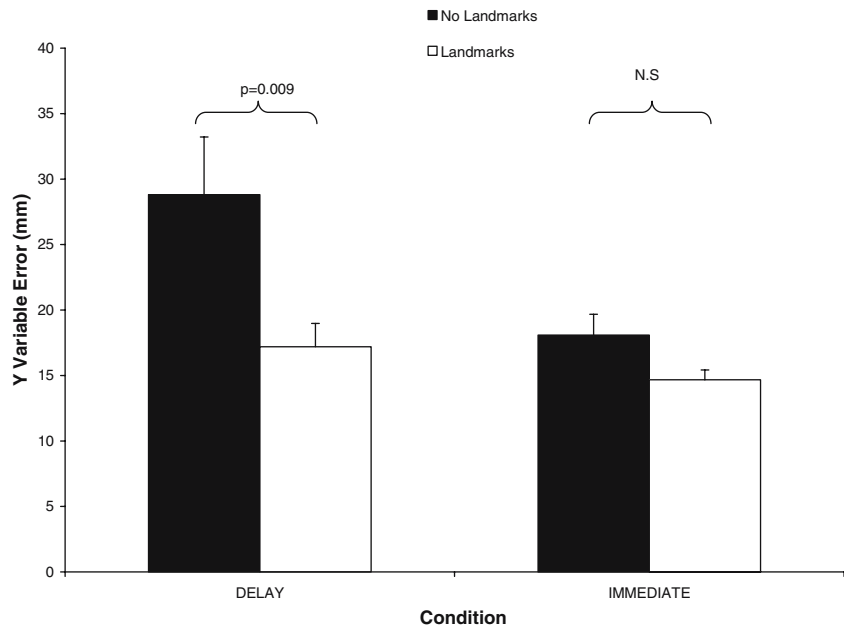
##### *Main effects of target position*

There were no significant effects of target position on VE in either the *y* or *x* dimensions ( $P=0.820$  and  $P=0.121$  respectively).

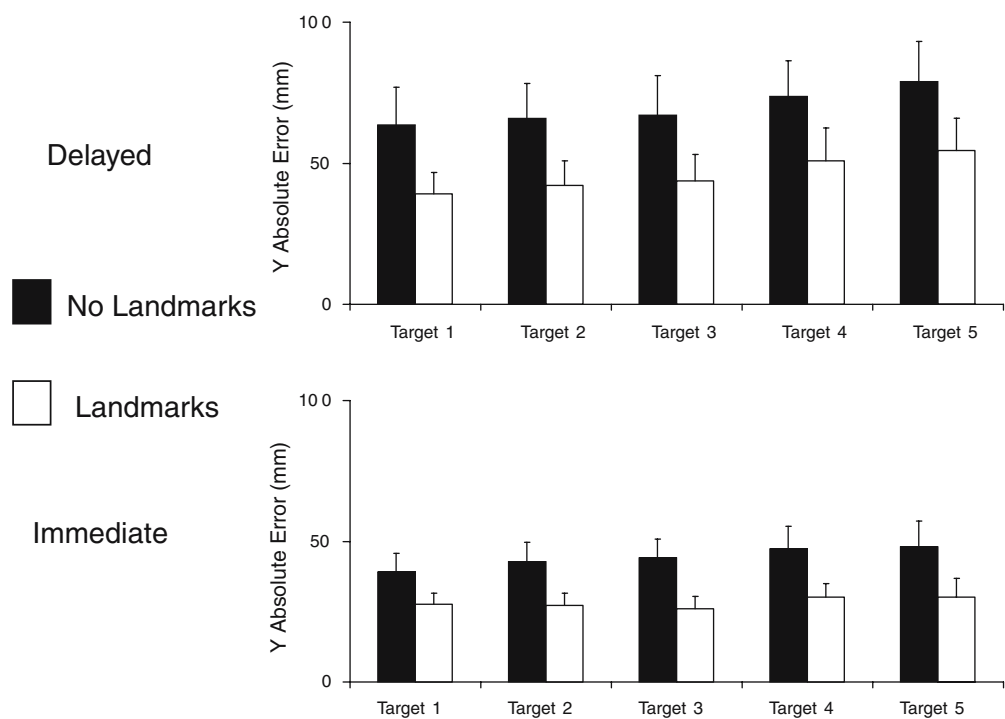
##### *Interactions between the factors*

As Fig. 3 shows, there was a significant delay  $\times$  landmark interaction for the VE in the *y* dimension but not in the *x* dimension ( $F_{4,36}=7.94$ ,  $P=0.02$  and  $F_{4,36}=0.651$ ,  $P=0.440$  respectively). Follow-up tests showed that the landmarks significantly improved the precision of movements in the *y* dimension in the delay condition ( $P=0.009$ ), but not in the immediate condition ( $P=0.062$ ). Clearly, since the magnitude of VE in the *y* and *x* dimensions was similar when the landmarks were absent, the lack of a delay  $\times$  landmarks interaction for this dependent variable cannot be attributed to a floor effect in which the VE in the *x* dimension was already so low (in the landmarks-absent condition) that the landmarks could not have helped to improve performance. In addition, the

**Fig. 3** The effects of the landmarks on the variable error for delayed and immediate pointing. Note that the landmarks helped to reduce variable error significantly in delayed actions but not in immediate actions. *Error bars in graphs are SE in the mean*



**Fig. 4** The effects of landmarks on the absolute error for delayed and immediate pointing movements. Note that the landmarks significantly improved accuracy for both delayed and immediate movements. *Error bars in graphs are SE in the mean*



VE (in the y dimension) of delayed movements in the landmarks-present condition was not significantly different from the VE of the immediate movements in either the landmarks-present or the landmarks-absent conditions ( $P=0.698$  and  $P=0.261$  respectively). In short, the presence of landmarks improved precision only in the delayed movement condition.

**Absolute errors**

*Main effects of the delay*

As Fig. 4 illustrates, the AEs of movements in both the y and x dimensions, were significantly larger in the delay condition than in the immediate action condition

( $F_{1,9}=7.039$ ,  $P=0.026$ ,  $F_{1,9}=9.924$ ,  $P=0.012$  respectively).

#### *Main effects of the landmarks*

As can be seen in Fig. 4, movements made in the landmarks-present condition were significantly more accurate in the y dimension than those made in the landmarks-absent condition ( $F_{1,9}=8.586$ ,  $P=0.017$ ). In contrast there were no effects of the landmarks on the AE in the x dimension ( $F_{1,9}=0.211$ ,  $P=0.657$ ).

#### *Main effects of target position*

There were no significant main effects of target position for AEs in either the y or the x dimensions ( $F_{4,36}=2.658$ ,  $P=0.109$  and  $F_{4,36}=1.278$ ,  $P=0.297$  respectively).

#### *Interactions between the factors*

For AEs in the y dimension there were no significant delay x landmarks interactions ( $P=0.496$ ), delay x target position interactions ( $P=0.079$ ), landmark x target position interactions ( $P=0.896$ ), or delay x landmarks x target position interactions ( $P=0.538$ ). For AEs in the x dimension, there were no delay x landmarks interactions ( $P=0.350$ ), delay x target position interactions ( $P=0.360$ ), or delay x landmarks x target position interactions ( $P=0.262$ ). There was, however, a significant landmark x target position interaction for the AE in the x dimension ( $P=0.011$ ). Follow-up tests confirmed that only movements towards the outer target in right hemisphere were affected by the presence of the landmarks. Specifically, the landmarks served to increase the AE of movements towards this target and this effect was nearly significant ( $P=0.052$ ).

#### Reaction time

##### *Main effects of the delay*

A  $2 \times 2 \times 5$  repeated measures ANOVA showed that there was a significant main effect of the delay on RT ( $F_{1,9}=26.474$ ,  $P=0.001$ ). In particular RT in the immediate action condition was significantly longer than RT in the delayed action condition (mean RT in immediate =  $317.5 \pm 0.07$  ms; mean RT in delayed =  $247.9 \pm 0.05$  ms).

##### *Main effects of the landmarks*

There were no significant effects of the landmarks on RT (mean RT in landmarks-present condition =  $287.6 \pm 0.04$  ms; mean RT in landmarks-absent condition =  $277.8 \pm 0.07$  ms,  $P=0.418$ ).

#### *Main effects of target position*

There was a significant main effect of target position on RT ( $F_{1,9}=6.848$ ,  $P<0.0001$ ). Corrected follow-up *t* tests showed that RTs of movements towards the outer most target in left hemisphere were significantly longer than RTs of movements towards the middle target ( $P=0.003$ ) and the target closest to the central target in right hemisphere ( $P=0.001$ ).

#### *Interactions between the factors*

There were no significant delay x landmark interactions for RT ( $P=0.878$ ). There was, however, a significant delay x target position interaction ( $P=0.015$ ). Follow-up of *t* tests revealed that for each target, RTs for immediate movements were longer than RTs for delayed movements (all tests  $P<0.02$ ). There were no other significant interactions between any of the factors with respect to RT.

Importantly, there are no differences in RT between the landmarks-present and landmarks-absent condition and hence, RT effects cannot explain the spatial accuracy advantage due to the landmarks.

#### Movement time

##### *Main effect of the delay*

A  $2 \times 2 \times 5$  repeated measures ANOVA showed that there was no significant main effect of the delay on MT (mean delayed MT =  $733.7 \pm 0.17$  ms; mean immediate MT =  $738.4 \pm 0.18$  ms,  $P=0.823$ ).

##### *Main effects of the landmarks*

There were no significant main effects of the landmarks on MT (mean landmarks-present MT =  $746.9 \pm 0.19$  ms; mean landmarks-absent MT =  $725.2 \pm 0.16$  ms,  $P=0.377$ ).

##### *Main effects of target position*

There was a significant main effect of target position on the MT ( $F_{4,36}=21.547$ ,  $P<0.0001$ ). Bonferroni-corrected pairwise comparisons showed that movements to the furthest target in left hemisphere took significantly longer than movements to all other targets (all tests  $P<0.05$ ). In addition, movements to the second furthest target in left hemisphere took significantly longer than movements to the middle target ( $P=0.040$ ) and the target closest to the middle target in right hemisphere ( $P=0.008$ ). Finally, there were no differences in MT between any of the targets in right hemisphere.

### *Interactions between the factors*

There were no interactions between any of the factors for MT (all tests,  $P > 0.1$ ).

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## **Discussion**

The present experiment investigated the effects of extra-target landmarks on the performance of target-directed pointing movements, both when these movements were made immediately upon target presentation, and when they were made after a delay of 2,000 ms following target offset. The absolute-error measurements showed that movements made towards targets that were presented together with non-target landmarks were significantly more accurate than those made towards targets that were presented alone. The pattern of results was similar for the constant errors, with movements undershooting the targets less in landmarks-present conditions; however this result was not statistically significant. Since, the target was only ever presented for a very brief time (i.e., 100 ms), it appears that spatial information about landmarks can be used very rapidly to help in the estimation and encoding of target position. Importantly, the landmarks significantly improved the precision of the movements only in the delayed condition.

The pattern of absolute errors strongly suggests that the availability of non-target landmarks during the target presentation phase aided in the estimation of the true location of the target. In other words, the presence of landmarks improved accuracy for both immediate and delayed movements. However, a different story emerged with the variable error. Here the landmarks were more useful in the delayed rather than the immediate movement conditions. That is, landmarks improved the precision of delayed but not immediate aiming movements. The precision of movements reflects to some extent the stability of the representation of a target from trial to trial. It is possible that the presence of landmarks can somehow increase that stability, particularly when movements are delayed. Importantly, the advantage afforded by the landmarks is not dependent on the landmarks being re-presented at the time of the movement. Simply providing landmarks just before and during target presentation aids performance, suggesting that it is the encoding of target position that is improved via the use of non-target landmarks. The fact that the presence of landmarks appears to be more useful for improving precision in delayed than immediate actions may again reflect the contribution that the presence of other visual stimuli might make to the computation of target position. Although vergence has been shown to be one of the most important cues in a reaching task (particularly for distance), such information is quite transient and might not survive a delay, particularly if the eyes move. Indeed, the use of this information presumably depends on the tight coupling between eye and

limb movements (Goodale et al. 1986; Neggers and Bekkering 2000)—a coupling that was likely to be weakened in delay.

These results confirm previous suggestions that non-target landmarks have an influence on movements directed at remembered targets in their vicinity (Sheth and Shimojo 2004; Diedrichsen et al. 2004; Lemay et al. 2004; Carrozzo et al. 2002; Krigolson et al. 2004; Gentilucci et al. 1996; Bridgeman et al. 1997). They extend these results by demonstrating that immediate movements also benefit from the presence of contextual cues available during the target presentation phase. Indeed, an important aspect of both the present study and the earlier one by Diedrichsen et al. 2004 was the selective presentation of landmarks during target encoding. In contrast to other recent studies (e.g., Lemay et al. 2004; Krigolson et al. 2004), this manipulation allowed us to infer that the landmark advantage must be at least partially due to the encoding of the stimulus array. That is not to say that additional benefit would not be observed if the landmarks were present during movement execution, but to stress that at least part of the effect of landmarks occurs early on in the initial encoding of target position.

The fact that RTs were longer for immediate than for delayed actions is consistent with results from other studies and probably reflects the fact that, in this condition, the target was visible for part of the programming phase (e.g., Diedrichsen et al. 2004). Critically however, there were no differences in RT between the landmarks-present and the landmarks-absent conditions suggesting that RT effects did not contribute to the main findings of this study. In addition, the fact that RTs and MTs were longest to the furthest target in contralateral hemispace is consistent with previous reports on the speed and efficiency of movements directed to contralateral versus ipsilateral hemispace (e.g., Fisk and Goodale 1985; Prablanc et al. 1979).

Contrary to Diedrichsen et al. (2004), we did not observe a spatial distortion effect (i.e., a significant bias in the direction of the landmarks) in which movement endpoints were significantly shifted towards the nearest landmark. The reason that we did not see a significant shift of movement endpoints towards the nearest landmark could be a direct result of the type of presentation used. In the experiment by Diedrichsen et al. (1997) the landmark(s) and the target were presented simultaneously. As such, it is possible that movements to both target and landmarks were automatically planned and that interference took place causing movements to be shifted somewhere between the actual target position and the position of the nearest landmark. That is, neuronal population vectors constructed for movements to both the target and the landmark might mutually interfere with one another to produce a “centered” movement (e.g., Tipper et al. 1992). In our experiment, however, care was taken to avoid this situation by presenting the landmarks for 1,000 ms prior to the presentation of the target. As such there was no confusion



over landmarks and targets. In fact, the landmarks represented a stable environment with respect to which participants could base their coding of target position. Nevertheless, our results do provide support for Diedrichsen et al.'s (1997) suggestion that effects of landmarks are not entirely dependent on a matching process that compares the allocentric location of targets during initial encoding and movement execution.

Sheth and Shimojo (2004) suggested that allocentric encoding could dominate when landmarks are available, and even suppress the use of egocentric information. In their experiment, when non-target landmarks were present during encoding but were absent during movement execution, performance was actually worse than when landmarks were never available (i.e., when only egocentric information was available). Contrary to this, we found that the presence of landmarks during encoding always improved performance, even though the landmarks were not present during movement execution. Thus, in the landmarks-absent condition, in which only egocentric coding of target position was possible, participants' accuracy was extremely poor as compared to their performance in the landmarks-present condition. This was also true for the precision of delayed but not immediate actions. All this suggests that when spatial information from landmarks is available, it can actually supplement whatever egocentric information about target location might be present (e.g., information from vergence). In short, in our paradigm, in which stable and reliable landmarks were used, we did not find evidence for a suppression of egocentric coding by the presence of landmarks (which would be considered a source of allocentric information by Sheth and Shimojo 2004). One reason why Sheth and Shimojo (2004) may have found evidence for such suppression relates to the unreliability of landmarks in their task as compared to ours. Such unreliability may have led to participants not using allocentric cues to encode target position and instead relying on egocentric encoding of target position. If this were true, and given the results of Sheth and Shimojo (2004) showing that a pure egocentric condition yielded better performance than a condition in which extrinsic cues were available and then withdrawn, one can infer that the presence of the landmarks actually hampered the formation and/or the use of an egocentric representation. This type of argument could account for their findings but it seems to depend on the question of whether or not subjects can ignore the presence of landmarks. In any case, neither our results, nor those of Sheth and Shimojo, can conclusively confirm or disconfirm this possibility. At this point, the differences in reliability of landmarks in both experiments cannot be ruled out as a contributor to the seemingly different results from the two studies. Moreover, there were substantial differences in the two experiments with respect to the nature of the task, the visual array, the arrangement of experimental trials, and the landmark manipulations that were employed. Any one or all of these differences could

account for the discrepancies in the findings of the two studies.

Although the presence of landmarks during encoding improved the precision of movements in delayed but not immediate actions, there was nonetheless a clear 'landmark' benefit for accuracy in the immediate condition. Even though both the location of the landmarks and the location of the target could be combined in programming the movement, the relative weighting of the two sources of information might differ as a function of the time course of the task. The fact that there was a clear beneficial effect of the landmarks on the accuracy of immediate actions might appear to be at odds with a number of conceptions of how movements are coded in the dorsal 'action' system, which is thought to use predominantly egocentric coding (e.g., Cohen and Andersen 2002; Goodale et al. 2004; Rossetti 1998; Goodale and Haffenden 1998). However, it should be noted that most experimental paradigms that have examined the role of the dorsal stream in computing target location have presented targets in isolation, and have not considered the possibility that visuomotor mechanisms in the dorsal stream might also process other visual stimuli in the array. In fact, recent evidence from both neurological patients and normal observers suggests that the location of potential obstacles or other contextual information in the workspace is probably processed by dorsal-stream mechanisms (Schindler et al. 2004; Coello et al. 2003; Haffenden and Goodale 2000; Bruno 2001). It is not yet clear whether the locations of such obstacles are computed within egocentric or allocentric frames of reference (or some complex combination of both). In fact, the same problem arises in the context of landmarks, which in the present study, for example, were clearly not obstacles. Part of the difficulty here is the lack of a useful operational definition of what is meant by allocentric coding—and when in the process of planning a target-directed action, allocentric information is brought to bear. Ultimately, of course, an action must unfold within an egocentric frame of reference. But if allocentric cues are indeed used, how are they incorporated into the final programming of the action? The answer to this question will require careful experimental investigation, not only with behavioural studies, but also with neuroimaging and single-unit work in monkeys. In fact, it is not clear whether the improvement of performance in immediate actions conferred by non-target stimuli is entirely a dorsal-stream function or whether it also reflects processing in other visual pathways such as the ventral stream. It is entirely possible that the increased weighting given to landmarks as movements are delayed (as indicated by the improvement in precision) could reflect the increased contribution of ventral-stream representations to the programming of target-directed actions. But again, even here, the movement must eventually incorporate whatever information the brain has about landmarks into an egocentric coordinate system. These are all issues that need to be carefully considered in future work on frames of reference for action.

In sum, we have demonstrated that the presence of non-target landmarks in a visual scene containing a target helps to improve participants' ability to localize the target in pointing. Although this effect appears to be greater for delayed actions than for immediate actions with respect to the precision of movements, there is a clear beneficial effect of the landmarks on the accuracy of both delayed and immediate actions. The locus of this landmarks-advantage appears to be in the target-encoding phase since, unlike most previous studies, we did not re-present the landmarks at the time of the movement. We suggest that, when available, information about the location of non-target stimuli can be combined with information about the location of the target, and thus serve to improve the accuracy of the movement. With respect to movement precision, we also suggest that the relative weighting given to spatial information derived from landmarks is dependent upon the time course of the movement task, with relatively more weighting being given to the landmark as movements are delayed. These results challenge previous suggestions that only delayed actions are subject to the influence of contextual cues, but are consistent with several recent studies suggesting that the mechanisms involved in real-time movement may be capable of processing information about multiple objects in a scene.

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## References

- Blouin J, Bard C, Teasdale N, Paillard J, Fleury M, Forget R, Lamarre Y (1993) Reference systems for coding spatial information in normal subjects and a deafferented patient. *Exp Brain Res* 93(2):324–331
- Bridgeman B, Kirch M, Sperling A (1981) Segregation of cognitive and motor aspects of visual function using induced motion. *Percept Psychophys* 29(4):336–342
- Bridgeman B, Peery S, Anand S (1997) Interaction of cognitive and sensorimotor maps of visual space. *Percept Psychophys* 59(3):456–469
- Bruno N (2001) When does action resist visual illusions? *Trends Cogn Sci* 1;5(9):379–382
- Chieffi S, Ricci M, Carlomagno S (2001) Influence of visual distractors on movement trajectory. *Cortex* 37(3):389–405
- Coello Y, Richaud S, Magne P, Rossetti Y (2003) Vision for spatial perception and vision for action: a dissociation between the left-right and near-far dimensions. *Neuropsychologia* 41(5):622–633
- Cohen YE, Andersen RA (2002) A common reference frame for movement plans in the posterior parietal cortex. *Nat Rev Neurosci* 3(7):553–562
- Diedrichsen J, Werner S, Schmidt T, Trommershauser J (2004) Immediate spatial distortions of pointing movements induced by visual landmarks. *Percept Psychophys* 66(1):89–103
- Fisk JD, Goodale MA (1985) The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Exp Brain Res* 60(1):159–178
- Gentilucci M, Negrotti A (1994) Dissociation between perception and visuomotor transformation during reproduction of remembered distances. *J Neurophysiol* 72(4):2026–2030
- Gentilucci M, Chieffi S, Deprati E, Saetti MC, Toni I (1996) Visual illusion and action. *Neuropsychologia*. 34(5):369–376
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15(1):20–25
- Goodale MA, Pelisson D, Prablanc C (1986) Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* 24–30;320(6064):748–750
- Goodale MA, Westwood DA, Milner AD (2004) Two distinct modes of control for object-directed action. *Prog Brain Res* 144:131–144
- Haffenden AM, Goodale MA (2000) Independent effects of pictorial displays on perception and action. *Vis Res* 40(10–12):1597–1607
- Hu Y, Goodale MA (2000) Grasping after a delay shifts size-scaling from absolute to relative metrics. *J Cogn Neurosci* 12(5):856–868
- Krigolson O, Heath M (2004) Background visual cues and memory-guided reaching. *Hum Mov Sci* 23(6):861–877
- Lemay M, Bertram CP, Stelmach GE (2004) Pointing to an allocentric and egocentric remembered target. *Motor Control* 8(1):16–32
- Milner AD, Goodale MA (1995) *The visual brain in action*. Oxford University Press, Oxford
- Neggers SF, Bekkering H (2000) Ocular gaze is anchored to the target of an ongoing pointing movement. *J Neurophysiol* 83(2):639–651
- Prablanc C, Echallier JF, Komilis E, Jeannerod M (1979) Optimal response of eye and hand motor systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand movements and their relationships when varying the amount of visual information. *Biol Cybern* 35(2):113–124
- Pratt J, Abrams RA (1994) Action-centered inhibition—effects of distractors on movement planning and execution. *Hum Mov Sci* 13(2):245–254
- Rossetti Y (1998) Implicit short-lived motor representations of space in brain damaged and healthy subjects. *Conscious Cogn* 7(3):520–558
- Schindler I, Rice NJ, McIntosh RD, Rossetti Y, Vighetto A, Milner AD (2004) Automatic avoidance of obstacles is a dorsal stream function: evidence from optic ataxia. *Nat Neurosci* 7(7):779–784
- Sheth BR, Shimojo S (2004) Extrinsic cues suppress the encoding of intrinsic cues. *J Cogn Neurosci* 16(2):339–350
- Tipper SP, Lortie C, Baylis GC (1992) Selective reaching—evidence for action-centered attention. *J Exp Psychol Hum Percept Perform* 18(4):891–905
- Toni I, Gentilucci M, Jeannerod M, Decety J (1996) Differential influence of the visual framework on end point accuracy and trajectory specification of arm movements. *Exp Brain Res* 111(3):447–454
- Westwood DA, Goodale MA (2003) Perceptual illusion and the real-time control of action. *Spat Vis* 16(3–4):243–254
- Wong E, Mack A (1981) Saccadic programming and perceived location. *Acta Psychol* 48(1–3):123–131