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The Use of Prescanning in the Parameterization of Sequential Pointing and Reaching Movements

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ABSTRACT. The accuracy of reaching movements is improved when active gaze can be used to fixate on targets. The advantage of free gaze has been attributed to the use of ocular proprioception or efference signals for on-line control. The time course of this process, however, is not established, and it is unclear how far in advance gaze can move and still be used to parameterize subsequent movements. In this experiment, we considered the advantage of prescanning targets for both pointing and reaching movements. The authors manipulated the visual information and examined the extent to which prescanning of targets could compensate for a reduction in on-line visual feedback. In comparison with a conventional reaching/pointing condition, the end-point error in pointing was reduced, the eye–hand lead decreased, and both the hand-closure time and the size of the maximum grip aperture in reaching were modulated when prescanning was allowed. These results indicate that briefly prescanning multiple targets just prior to the movement allows the refinement of subsequent hand movements that yields an improvement in accuracy. This study therefore provides additional evidence that the coordinate information arising from efference and/or ocular-proprioceptive signals can, for a limited period, be buffered and later used to generate a sequence of movements.

Keywords: Reach and grasp; visuo-motor control; sequential movement; motor planning

Active gaze is a vital component of many goal-directed movements. A simple demonstration of the advantage active gaze provides during reaching movements is that movement accuracy decreases when adults are required to fixate on one target while moving to a second target (Desmurget & Grafton, 2000; Fisk & Goodale, 1985; Prablanc, Eschallier, Komilis, & Jeannerod, 1979; Wilmut, Wann, & Brown, 2006). In everyday tasks, gaze is constantly shifting from one location to the next during the performance of complex movements. In naturalistic studies (e.g., observing a participant while he or she makes a cup of tea), the eye was found to shift well ahead of the hand, often moving to a new object before the hand has acquired the previous object (Hayhoe, 2000; Land & Hayhoe, 2001; Land, Mennie, & Rusted, 1999). On first consideration, this may seem to be a simple case of advance preparation. The eyes often fixate on the target before the preparation of limb movement begins (Carlton, 1981). This provides information about both the position of the target and, at later stages, the hand relative to the target (Elliott et al., 1993). But in tasks that have multiple or sequential targets, such as many everyday actions, the issue of how the eye guides the hand is problematic. In the case of a single target action, the generation of an eye movement towards a target produces an efference copy, and these signals can then be used in the generation of a hand movement towards the same target (Miall & Reckess, 2002; Prablanc et al., 1979). The eye landing on a target also gives rise to ocular-proprioceptive signals regarding the precise location of the target in headcentric coordinates, and these signals can then be used to direct a hand movement (Goodale, Pellision, & Prablanc, 1986). Finally, if the eye foveates the target ahead of the hand, it provides precise visual information regarding the final hand approach. In the case of multiple targets, however, if the eye jumps ahead to a second object (e.g., the mug) before the hand has acquired the first object (e.g., the kettle), then the initial retinal and extraretinal information regarding the kettle will be overwritten by information regarding the mug. Overwriting of information in this way becomes an issue when one uses efference copy or ocular-proprioception to aid the accurate guidance of the hand when the eye precedes the hand. In cases such as these, the efference or proprioceptive signals for Target 2 are generated prior to the completion of Movement 1. Therefore, some type of storage is required for the ocular proprioception to guide Movement 1, while at the same time buffering the efference signals to be used in the generation of the subsequent movement to Target 2.

There are two approaches to the problem of the eye moving so much earlier than the hand. Neggers and Bekkering (2000, 2001) proposed a gaze-anchoring theory, whereby the eyes remain fixed until the hand reaches the foveated object, at which point the eyes are released and can move to the next object. Wilkie and colleagues proposed a similar type of model for the control of steering, in which a point on the future path is fixated until the locomotor trajectory is established and only then is gaze switched to the next steering target (Wann & Wilkie, 2004; Wilkie, Wann, & Allison, in press).

A more flexible explanation, proposed by Land and Furneaux (1997), is the notion of a temporal buffer that can hold procedural information arising from eye-movement information and avoid overwriting by subsequent fixations. Land and Furneaux were alluding to the storage of motor-sequence information, such as that gleaned from music script. In our previous article, we extended the notion of a procedural buffer to the storage of efference and ocular-proprioceptive signals over a short duration (<500 ms), which would explain how this information is used to guide hand movements even when the eye has moved ahead to a new target (Wilmut et al., 2006).

In this study, we decided to push the proposal of a gaze-movement buffer to the next stage. In research settings, targets are often presented (illuminated) as a means to prompt movement initiation, and thus the precise target location is unknown before a hand movement is required. In natural life settings, targets or objects are normally present before and during a movement, and an actor will often briefly prescan the objects on a table before reaching for each in turn. It may seem obvious that this will proffer some advantage, but how does it lead to a refinement of subsequent movements? Some advantage may be gleaned at a general categorical level. For example, a prescanning actor would know s/he will be moving to the top left then the bottom right. This may lead to a faster movement initiation than if the actor is presented with unknown target locations that are illuminated as a signal to start. But one would not predict that categorical coding would lead to a refinement of the kinematics of the action. To result in a change to the approach kinematics, a reduction in deceleration time, or a refinement of the grasp response, the prescanning action would need to yield precise coordinate information for each of the targets. This could be accomplished by “storing” efferent commands or ocular- proprioception for each of the targets or by transforming these inputs into a set of hand coordinates. In either case, the buffering of coordinate information from an ocular prescan of multiple targets has not been previously demonstrated.

The majority of laboratory tasks that have focused on the advantage of eye movements to the later coordination of the hand have used aimed pointing movements. Reach-to-grasp movements, however, are more complex and require both a transport component and prehension component. A number of observations of the coordination of the eye and hand during prehension have shown that when sight of both the hand and object is not available during reaching, participants open their hand further, reach peak aperture sooner, and spend more time making final pick-up adjustments (Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Churchill, Hopkins, Ronnqvist, & Vogt, 2000; Jakobson & Goodale, 1991).

We presented participants with a pointing or reaching task to multiple targets. In one condition (prescan), we allowed participants to prescan the targets that were illuminated, in another condition (no scan) participants were required to maintain a central fixation while the targets were illuminated. In both cases, similar general categorical information was available, but precise ocular coordinate information was only gleaned in the prescan condition. In both conditions, gaze was free to move once the generation of a hand movement was prompted, and we examined tasks where the participant simply pointed to targets or grasped and transported target objects. In addition, we varied the number of sequential movements: participants were prompted for either a two-step movement (two targets for the pointing task or one pick-up and place movement for the reaching task) or a four-step movement (four targets for the pointing task or two pick-up and place movements for reaching task). Finally, we manipulated the time course of visual illumination of targets after movement initiation. In the target-on condition, the targets remained illuminated throughout the movement, whereas in the target-off condition they were extinguished as soon as movement initiation was cued. Our hypotheses for the combination of conditions were as follows:

1. Prescanning of targets would result in an improvement in movement accuracy for both pointing and reaching.
2. Due to storage limits, the prescan advantage would be less marked for longer movement sequences than for the targets that remained illuminated throughout.
3. The pre-scan advantage would reemerge for longer sequences when the target illumination was extinguished at onset, due to the errors arising in the generation of four sets of target coordinates from peripheral retinal information in the no prescan condition.

Method

Participants

A group of 10 right-handed adults were included in this study; this sample was an opportunistic sample of postgraduate students and research staff at the University of Reading (Reading, Berkshire, United Kingdom). The group included 5 female and 5 male participants, with a mean age of 29 years (age range: 18–36 years). All participants had normal or corrected vision. All participants were naive to the purpose of the experiment.

Apparatus

Participants sat at an 890 mm × 605 mm table, which stood 810 mm from the ground. The top of the table was made from clear Plexiglas (6 mm thick) with one satin surface, which provided a semiopaque tabletop. Underneath the table-top, an acrylic mirror (6 mm thick) lay at a 45^{o} angle facing away from the participant. A Hitachi CP-X328 projector (Tokyo, Japan), positioned 1,300 mm away from the mirror, projected an image onto the mirror which was then reflected onto the underside of the tabletop and was viewable from above. The scene image, driven by LabVIEW, consisted of six "place" locations, which lay on the midline of the participant, and eight "pick" locations, half of which lay to the right of midline and half of which lay to the left of midline. Targets were 25 mm in diameter and were separated by 30 mm See Figure 1 for an illustration of target locations and participant viewpoint. For reach movements, eight Perspex cylinders, measuring 25 mm in diameter and 42 mm in height, were placed at the pick locations, and a Perspex peg board with eight holes suitable for the Perspex cylinders (26 mm diameter) was laid over the place locations. In this manner, both the cylinders and the place locations could be discretely illuminated by the projected image. The positioning of the targets was such that the maximum amplitude of any one saccade was ~20^{o}. A Vicon 3D motion capture system (Oxford Metrics, United Kingdom) was used to track the movement of four reflective markers (6.5 mm in diameter) placed on the thumb, index finger, knuckle, and wrist of the dominant hand. The Vicon system ran at 120-Hz with a calibration residual error of less than 1% of the distance between each camera and the center of 3D space available to that camera (i.e., an effective spatial resolution of ~1 mm). Eye movements were recorded via a Panasonic digital camcorder (60 Hz; Seacaucus, NJ), which was placed 630 mm from the participant and synchronized with the Vicon motion capture system to provide frame-by frame registration of gaze position within Vicon at each 120-Hz sample frame. The start of Vicon and the video recording was triggered at the beginning and end of each trial by a ±5-v digital signal sent via a National Instruments data acquisition card (Austin, TX) controlled by the LabVIEW program.

Procedure

The experiment consisted of two main movement tasks: pointing and reaching. Each of these were considered under eight different conditions in a 2 × 2 × 2 design: (a) pre-scan, in which participants were allowed to fixate on targets prior to the generation of a hand movement, and no scan, in which participants were not allowed to fixate on targets prior to generating a hand movement; (b) The number of movements used to complete the task (either two or four); and (c) the “on” condition, in which the targets remained visible throughout the experiment, and the “off” condition, in which the targets were removed just prior to the start of the hand movement. Participants completed all trials for one movement task followed by all trials for the other movement task, and we counterbalanced the order of tasks across participants. Within each task, participants completed four blocks: no scan and two steps, no scan and four steps, prescan and two steps, and prescan and four steps. Target illumination (“on” vs. “off”) was randomized within each block. The order of blocks was counterbalanced across participants. Prior to each block, participants were given two practice trials. The sequence of events for each trial is shown schematically in Figure 1.

A white circle appeared at the bottom of the display, and participants were told to pinch their finger and thumb together on this point and wait until they heard an auditory tone, which was the signal to generate a hand movement. For the prescan condition, participants were allowed to direct their gaze where they wished throughout the whole trial, but they could not move their hand until they heard the auditory tone. For the no-scan condition, however, participants were instructed to remain fixated on the start point until they heard the auditory tone, after which, they could move both their hand and their eyes. Prior to the signal for the hand movement, the targets were illuminated in order with a 500-ms delay between each. For the four-step movements, the third target was illuminated in the hemispace opposite Target one (see Figure 1). The auditory tone for the hand movement start was provided 1,000 ms after the final target (2 or 4) in the sequence had been illuminated. After the auditory tone, the targets could either remain illuminated (the “on” condition) or the illumination could be turned off (the “off” condition). Across all trials, participants were instructed to move to the targets in the order in which they appeared. To aid in the sequencing of targets, pick-and-place pairs were color matched.

This sequence of events was the same for both movement tasks (i.e., pointing and reaching), apart from the presence of the Perspex cylinders and peg board and the instruction to move the illuminated cylinder to the corresponding illuminated hole in the reaching condition In the pointing condition, participants were instructed to point to target locations while making sure they touched the tabletop. In each block, participants completed 16 trials: 8 with the “on” condition and 8 with the “off” condition. Each movement type consisted of four blocks; thus, the participants completed a total of 128 trials. Target location was randomized for all trials, but the two pick locations in 4-step trials were always in opposite hemispaces and the place locations were always separated by at least one target.

Insert figure 1 here

Data Analysis

Trials were excluded if fixation was either not apparent directly before target presentation (in the prescan condition) or was not maintained until the tone was heard (in the no-scan condition). Trials in which we saw either a hand movement before the tone or an anticipatory hand movement (onset <100 ms) were also excluded. Participant responses met the requirements for inclusion for at least 75% of trials in each condition, and, on this basis, no participants were excluded from the group analysis. Participants were not directed as to how to prescan the display, therefore, prescan trials during which no prescanning eye movements occurred were excluded; this accounted for 1.4%–18.0% of trials within each movement task. Because all targets lay on the same horizontal plane, movement accuracy was calculated in the *x* and *y* plane using a planar vector length error. Eye movements were analyzed using the synchronized close up video image of the eye, and eye onset times were determined using a frame-by-frame analysis of the video data: When the eye departed from fixation and continued to move for two frames or more, we recorded onset time from the start of that movement. This method provided the onset times of eye movements but not the landing times. We filtered Vicon hand movement data with an optimized Woltring filter and used MatLab routines for analysis. Onset and landing times of the hand were determined from velocity curves. The time point at which velocity departed or returned to zero (<3% max) was identified and double-checked by eye. For each participant, both constant error (average of signed error values across trials) and variable error (standard deviation across signed error values) were calculated for each block of trials. Five independent variables were considered: movement task (pointing or reaching), scan (no scan or prescan), target illumination ("on" or "off"), step (the number of movements made, two or four), and movement (first movement, second movement, third movement, fourth movement). We used analysis of variance (ANOVA) to examine the data. Unless otherwise stated, pointing two-step movements (P2), pointing four-step movements (P4), reaching two-step movements (R2), and reaching four-step movements (R4) were all considered separately. Effect size (partial-eta squared, η^2, equivalent to r^2), which quantifies the magnitude of the observed effect independently of sample size, is reported for all significant results. Cohen (1992) reported a small effect size is indicated by $r = 0.10$ ($r^2 = 0.01$), a medium effect size is indicated by $r = 0.30$ ($r^2 = 0.09$), and a large effect size is indicated by $r = 0.50$ ($r^2 = 0.25$).

Results

The onset times for the first eye and hand movement were longer in the prescan condition than they were in the no-scan condition - P2, $F(1, 9) = 10.701$, $p < .01$, $\eta^2 = 0.543$; P4, $F(1, 9) = 433.193$, $p < .001$, $\eta^2 = 0.980$; R2, $F(1, 9) = 26.704$, $p < .001$, $\eta^2 = 0.748$; R4, $F(1, 9) = 265.819$, $p < .001$, $\eta^2 = 0.967$. This effect occurred because participants tended to dwell on the last viewed target before initiating a response. Once underway, the pattern of movement time was similar for all movement types. There was a main effect of the number of steps, whereby the first movement was longer than the proceeding movements, and this was found for all movement types: P2, $F(1, 9) = 10.783$, $p < .01$, $\eta^2 = 0.637$; P4, $F(3, 27) = 24.018$, $p < .001$, $\eta^2 = 0.637$; R2, $F(1, 9) = 18.389$, $p < .01$, $\eta^2 = 0.671$; R4, $F(3, 27) = 10.920$, $p < .001$, $\eta^2 = 0.548$. No effect of prescan or target illumination was found for movement time

Accuracy for Pointing Movements

Constant and variable error were calculated for the hand and were considered separately for pointing movements using a three-way ANOVA (Scan × Target Illumination × Step). Both constant and variable errors are depicted in Table 1. As might be expected, there was a main effect of target illumination. Constant error for both two- and four-step movements was greater when target illumination was extinguished at the start of the hand movement even when the participants were allowed to fixate on the targets prior to a movement: P2, $F(1, 9) = 46.616$, $p < .001$, $\eta^2 = 0.838$; P4, $F(1, 9) = 153.565$, $p < .001$, $\eta^2 = 0.945$. No differences were seen in variable error. When we considered the two- and four-step tasks separately for constant error, we found a main effect with prescanning improving accuracy for two-step movements: P2, $F(1, 9) = 27.758$, $p < .001$, $\eta^2 = 0.755$. No interaction was found between prescanning and target illumination, suggesting an accuracy advantage to prescanning even when targets remained illuminated and could be fixated during the movement. For the four-step movements, an interaction was found between the prescanning and illumination conditions - P4, $F(1, 9) = 41.462$, $p < .001$, $\eta^2 = 0.822$—but additional analyses of the "on" condition confirmed that there was still an effect of prescan even when targets remained illuminated: P4, $F(1, 9) = 12.489$, $p < .01$, $\eta^2 = 0.681$. No differences were seen in variable error in pointing.

Eye-Hand Lead for Pointing Movements

The extent to which the eye preceded the hand was calculated by subtracting the onset time of the eye towards a target from the onset time of the hand movement towards the same target, which resulted in two or four eye-hand lead times, one for each targets. The lead values can be found in Figure 2. An ANOVA (Scan × Target Illumination × Movement) for two- and four-step pointing movements found a main effect of prescanning: P2, $F(1, 9) = 13.631$, $p < .01$, $\eta^2 = 0.584$; P4, $F(1, 9) = 24.675$, $p < .001$, $\eta^2 = 0.733$. The effect of prescanning may have been solely due to the "off" condition, so we used additional analyses to examine the targets in the "on" condition alone (Scan × Movement). We found a main effect of prescanning: P2, $F(1, 9) = 15.407$, $p < .01$, $\eta^2 = 0.631$; P4, $F(1, 9) = 19.466$, $p < .01$, $\eta^2 = 0.684$. This suggests that prescanning allowed the hand movement to be initiated much more quickly after the eye movement had commenced (mean lead time for prescan = -30.7 ms). In conditions where prescanning was not allowed, the participants tended to wait until the eye had landed at the target before initiating a hand movement (mean lead time for no prescan = 105.9 ms).

Insert Table 1 here

Insert Figure 2 here

Accuracy and Grasp Aperture for Reaching Movements

When the target locations remained illuminated, the number of pick and place errors was extremely small (<1% of trials); however, when target illumination was extinguished at the start of the movement sequence, participants sometimes picked up the wrong cylinder or placed it in the incorrect hole (this was not totally unexpected). The movement time data confirms, however, that they did this just as quickly and efficiently as when they had when they selected the correct target. The rate of target selection error varied when illumination of targets was removed: when there were only two prescanned targets, <1.00% of pick and place movements were errors, this rose to an average of 8.75% for two targets when no prescan was allowed; and when there were four target locations, prescanning kept the average error rate down to 3.5%, whereas 45.8% of pick and place movements were at incorrect locations in the no-scan condition. This is not particularly surprising. The set of pick locations (and, similarly, place locations) were only vertically separated from one another by approximately 6^{o} of visual angle. When participants were required to fixate at the start location and four targets were illuminated in their peripheral field, they mislocalized some of them and made errors if the targets were extinguished at the start signal. Prescanning clearly compensates for this, but this does not demonstrate storage of precise spatial coordinates. For this reason, we do not report spatial endpoint errors for these movements because they would show a large effect of prescanning due to simple mislocalization if calculated relative to the cued target, or there would be no errors if calculated to the target object that was incorrectly selected. To look for evidence of spatial encoding, we compared the kinematics of reach-and-grasp actions to prescanned and unscanned targets. As the hand approaches an object, the distance between the finger and thumb is adjusted so that the optimal aperture is attained prior to the hand reaching the object. We calculated both the distance between the thumb and the pointing finger (i.e., size of maximum grip aperture [MGA], referred to MGAsize1 and MGAsize2 for Pick 1 and Pick 2, respectively) and the time needed to close the fingers from MGA onto the object for each pick movement. The time calculation was based on the time at which the hand reached Object 1 minus the time at which the closure of the finger and thumb started for Object 1 (MGAtime1), resulting in a positive duration. The same measure was calculated for Object 2 (MGAtime2). This provided an indication of the time required for the grasping movement to home in on the object, which we felt would reflect the acuity of the spatial localization; this temporal estimate is less prone to contamination from overall movement duration than is the time to MGA following movement initiation. These values can be found in Table 1. For MGAsize, an ANOVA (Scan × Target Illumination × Step) for the first and second movement separately found an interaction between scan and steps, $F(1, 9) = 32.891$, $p < .001$, $\eta^2 = 0.785$, and a main effect of scan, $F(1, 9) = 310.405$, $p < .001$, $\eta^2 = 0.972$, and step, $F(1, 9) = 10.965$, $p < .01$, $\eta^2 = 0.549$. For the second movement, we found only a main effect of scan, $F(1, 9) = 181.352$, $p < .001$, $\eta^2 = 0.953$. These results indicate that MGAsize was larger in the no-scan condition than it was in the prescan condition and that this difference across conditions was exacerbated in four-step movements. For MGAtime, an ANOVA (Scan × Target Illumination × Step) found no interaction and no main effects. When we analyzed two- and four-step movements separately (Scan × Target Illumination), we found a main effect of scan for both two- and four-step movements: R2, $F(1, 9) = 9.201$, $p < .05$, $\eta^2 = 0.506$; R4, $F(1, 9) = 15.393$, $p < .01$, $\eta^2 = 0.631$. These results indicate that participants in the no-scan condition not only attained a larger MGA (i.e., a larger distance between the finger and thumb), they also allowed a greater closure time to reach MGA than they did when they could prescan the locations. So although the objects to be picked up (the Perspex cylinders) always remained visible and had been picked up repeatedly, the ability to prescan the object locations enabled more efficient coding of the grasp aperture for pick and place movements.

Eye-Hand Lead for Reaching Movements

The extent to which the eye preceded the hand movement was calculated by subtracting the onset time of the eye to a target from the onset time of the hand movement toward the same target, which resulted in one or two pick lead times for the cylinder(s) and one or two place lead times for the hole(s) in the peg board. These values can be found in Figure 2. We analyzed the eye-hand lead times with pick and place times as an additional factor. An ANOVA (Scan × Target Illumination × action; pick vs. place) considering two- and four-step movements separately (and considering first and second pick–place movements in the 4-step movements separately) found a Scan × Action interaction for both the two- and four-step movements: R2, $F(1, 9) = 39.055$, $p < .0001$, $\eta^2 = 0.813$; R4, first pick–place movement, $F(1, 9) = 7.548$, $p < .05$, $\eta^2 = 0.456$; R4, second pick–place movement, $F(1, 9) = 5.512$, $p < .05$, $\eta^2 = 0.380$. From these statistics and from Figure 2, we can see that the change in eye-hand lead from pick to place movements is markedly different across the prescan and no-scan condition. In the prescan condition, the participants' eye and hand move in sync for the pick movements, but the eye moves ahead of the hand for the place movement. In the no-scan condition, the eye moves ahead of the hand for both the pick and the place movement.

Velocity Profile: Symmetry and Jerk

The proportion of each movement that was assigned to deceleration was calculated (duration of deceleration of movement ÷ total duration of movement); these values can be found in Table 1. For this variable, a main effect of step was seen for all movement types: P2, $F(1, 9) = 7.819$, $p < .05$, $\eta^2 = 0.465$; P4, $F(3, 27) = 15.805$, $p < .001$, $\eta^2 = 0.637$; R2, $F(1, 9) = 15.152$, $p < .01$, $\eta^2 = 0.627$; R4, $F(3, 27) = 6.719$, $p < .01$, $\eta^2 = 0.427$. Post hoc analysis showed that the place movements have a longer deceleration period than the pick movements ($p < .05$, Bonferroni corrected). Mean squared jerk was also calculated (see Table 1). For pointing movements, no difference was seen in the jerk of movements. In contrast, a main effect of step was seen for both two- and four-step reaching movements: R2, $F(1, 9) = 18.156$, $p < .01$, $\eta^2 = 0.669$; R4, $F(3, 27) = 18.542$, $p < .001$, $\eta^2 = 0.673$. Post hoc analysis showed that both of these differences were due to a lower degree of jerk in place movements than in pick movements. These observations relate to the subsequent interpretation of the results of prescanning.

Discussion

The aim of this study was to establish the advantage of advance gaze information, gleaned from a brief prescan, for the parameterization of multiple pointing and reaching movements. On a very coarse assessment, the pick and place errors for the very difficult four-step, “off” condition show a clear advantage of prescanning. In the no-scan condition, participants fixated on the start location, and four target locations were illuminated in their peripheral field - this illumination was then extinguished when they received the start signal. It is not surprising that the participants often picked up the wrong cylinder or made pointing errors in this condition. When the targets could be prescanned prior to the start of the movement, error was much smaller (4 mm when targets remained illuminated and 14 mm when the illumination was extinguished prior to the generation of a movement). In the context of the pick and place task, this does not demonstrate the storage of precise spatial information during the prescan - the information gleaned could have been categorical (e.g., move the second cylinder from the top to the bottom hole). But this argument does not hold for the pointing task, in which the range of possible locations was not displayed. We also confirmed that there was still an advantage to prescanning for pointing accuracy, even when the targets remained illuminated.

The advantage of prescanning was also reflected in the eye-hand lead for pointing, and participants appeared able to initiate a hand movement close to the initiation of the eye movement to the same target. Even if motor commands to eye and hand were issued synchronously, it might be anticipated that the eye might lead the hand by a small degree due to different premotor delays. If we consider the eye-hand lead in the prescan condition, it is unlikely that each target was foveated prior to initiation of the hand movement. Typically, the eye and hand had the same onset time, and in cases where the eye did move ahead of the hand, the difference between the two was less than the duration of a typical saccade (for saccades with amplitudes of ~20^{o}, a typical saccade will last 65 ms; Carpenter, 1988). We can speculate that ocular-proprioception gained during prescanning could have been used to remove the need to foveate the target prior to a hand movement. The pattern of results was different for pointing movements under the no-scan condition. The eye led the hand (57–80 ms for two-step movements and 144–158 ms for four-step movements), and it seems likely that the eye landed on the target prior to the onset of a movement in most trials. Whether the information gained during foveation of the target was actually used in the generation of the hand movement, however, is uncertain. A delay of 57–158 ms between the eye and hand may not be long enough for the effective use of ocular-proprioceptive feedback. There are inherent delays in the motor system. In general, cortical activity is seen 100–150 ms prior to the onset of a movement (Georgopoulos, 1995). The eye-hand lead delay durations could be taken as evidence of a feed-forward system for the control of fast accurate pointing movements (Miall & Reckess, 2002; Wilmut et al., 2006). Irrespective of the mechanism for parameterizing the hand trajectory in the no-scan condition, the evidence is clear that briefly prescanning the targets just prior to movement allows the use of a different control strategy, with a shorter eye-hand lead, that yields an improvement in accuracy.

As a performance measure for reaching, we looked at the maximum grasp aperture and closure time needed to reach maximum grasp aperture. Both of these measures supported the case that prescan information improves the accuracy of the action. A simple interpretation of this would be that the prescan allowed clearer identification of object size, but the same objects were picked up and placed repeatedly in all trials. The differential advantage afforded by prescanning in the grasp task would seem to be more related to the precise location information that it provided. There was an interesting interaction when we considered eye-hand lead for reaching movements. The results for the pick-up movements were equivalent to those for pointing; after prescanning, movements had an eye-hand lead approaching 0 ms, showing that the eye did not fixate the target prior to movement onset. In the no-scan condition, however, the trend was for eye-hand lead times that would allow foveation of the target prior to movement onset (saccade initiated 119–188 ms before the hand in two-step movements and 93–288 ms before the hand in four-step movements; see Figure 2). Following each pick-up movement, there was a placement movement, for which the eye moved ahead of the hand and most likely foveated the target prior to movement onset. This occurred irrespectively of whether a prescan had taken place. Our estimate of jerk for both phases of movement confirmed that the place movements were smoother, and we might hypothesize that they were under on-line visual control. This suggests the information held following a prescan may be of sufficient specificity for fast targeted movements such as pointing or grasping, but not for movements that require very precise end-point accuracy and velocity control, such as placing a cylinder in a hole of almost the same diameter.

The changes observed in eye-hand lead from the pre-scan condition to the no-scan condition could be explained by a more rapid initiation of the hand movement (due to more precise information regarding target position) or a later eye movement (due to interference from the prescan with the initial eye movement) in the prescan condition. But any such interference would only pertain to the first eye movement and would not account for the eye-hand lead differences across scan conditions in subsequent movements. Consequently, the consistent finding of shorter eye-hand lead times in the prescan condition for every movement suggests a robust finding rather than an artifact of the conditions.

The advantage gained by prescanning target location implies that information regarding target location gained during the generation of an eye movement (efference information) and during foveation (ocular-proprioceptive information) can be held in temporary register and used at a later time. Land and Furneaux (1997) proposed a temporal buffer for the storage of information gained through vision in complex tasks, such as sight reading music. Wilmut et al. (2006) also discuss the idea of buffering efference signals and ocular-proprioceptive information for up to 120–200 ms. The current study extends previous findings by showing that a putative buffer can hold information for up to four complex prehensile movements when targets are prescanned. If we calculate the duration from the onset of the first prescanning eye movement (when the first set of efference signals would be generated) until the onset of the first hand movement, the results suggest that information can be buffered for up to 1.1 s (1,146 ms) in two-step movements and up to 2.6 s (2,610 ms) in the four-step movements. The former seems plausible, the latter is quite surprising. This maximum buffer size is significantly longer than that suggested by Land and Furneaux (1997), who suggested a buffer up to 1.4 s for sight reading music. Whatever the precise duration, the ability to buffer precise spatial information for up to 4 sequential movements in parallel occurring 1–2 s after the scan period shows a remarkable capacity within the visuo-motor system.

REFERENCES

Berthier, N., Clifton, R. K., Gullapalli, V., McCall, D. D., & Robin, D. J. (1996). Visual information and object size in the control of reaching. *Journal of Motor Behavior, 28,* 187–197.

Carlton, L. G. (1981). Visual information: The control of aiming movements. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 33,* 87–93.

Carpenter, R. H. S. (1988). *Movements of the eyes* (2nd ed.). London: Pion Limited.

Churchill, A., Hopkins, B., Ronnqvist, L., & Vogt, S. (2000). The role of visual information about hand position and environmental context in reaching and grasping. *Experimental Brain Research, 134,* 81–89.

Cohen, J. (1992). A power primer. *Psychological Bulletin, 112,* 155–159.

Desmurget, M., & Grafton, S. (2000). Forward modelling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences, 4,* 423–431.

Elliott, D., Roy, E. A., Goodman, D., Carson, R. G., Chua, R., & Maraj, B. K. V. (1993). Asymmetries in the perception and control of manual aiming movements. *Canadian Journal of Experimental Psychology, 47,* 570–589.

Fisk, J. D., & Goodale, M. A. (1985). The organisation of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental Brain Research, 60,* 159–178.

Georgopoulos, A. P. (1995). Current issues in directional motor control. *Trends in Neuroscience, 18,* 506–510.

Goodale, M. A., Pellision, D., & Prablanc, C. (1986, April 24). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature, 320,* 748–750.

Hayhoe, M. (2000). Vision using routines: A functional account of vision. *Visual Cognition, 7,* 43–64.

Jakobson, L. S., & Goodale, M. A. (1991). Factors influencing higher order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research, 102*, 519–530.

Land, M. F., & Furneaux, S. (1997). The knowledge base of the oculomotor system. *Philosophical Transactions of the Royal Society of London, Series B, 352,* 1231–1239.

Land, M. F., & Hayhoe, M. (2001). In what ways do eye movement contribute to everyday activities? *Vision Research, 41,* 3559–3565.

Land, M. F., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily life. *Perception, 28,* 1311–1328.

Miall, R. C., & Reckess, G. Z. (2002). The cerebellum and the timing of eye and hand tracking. *Brain and Cognition, 48,* 212–226.

Neggers, S. F. W., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology*, *83*, 639–651.

Neggers, S. F. W., & Bekkering, H. (2001). Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. *Journal of Neurophysiology, 86,* 961–970.

Prablanc, C., Eschallier, J. F., 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 relationship when varying the amount of visual information. *Biological Cybernetics, 35,* 113–124.

Wann, J. P., & Wilkie, R. M. (2004). How do we control high speed steering? In L. M. Vaina, S. A. Beardsley, & S. K. Rushton (Eds.), *Optic flow and beyond* (Vol. 324). New York: Springer.

Wilkie, R. M., Wann, J. P., & Allison, R. (in press). Active gaze, visual look-ahead and locomotor control. *Journal of experimental psychology: Human perception and performance*

Wilmut, K., Wann, J. P., & Brown, J. H. (2006). How active gaze informs the hand in sequential pointing movements. *Experimental Brain Research, 175,* 654–666.

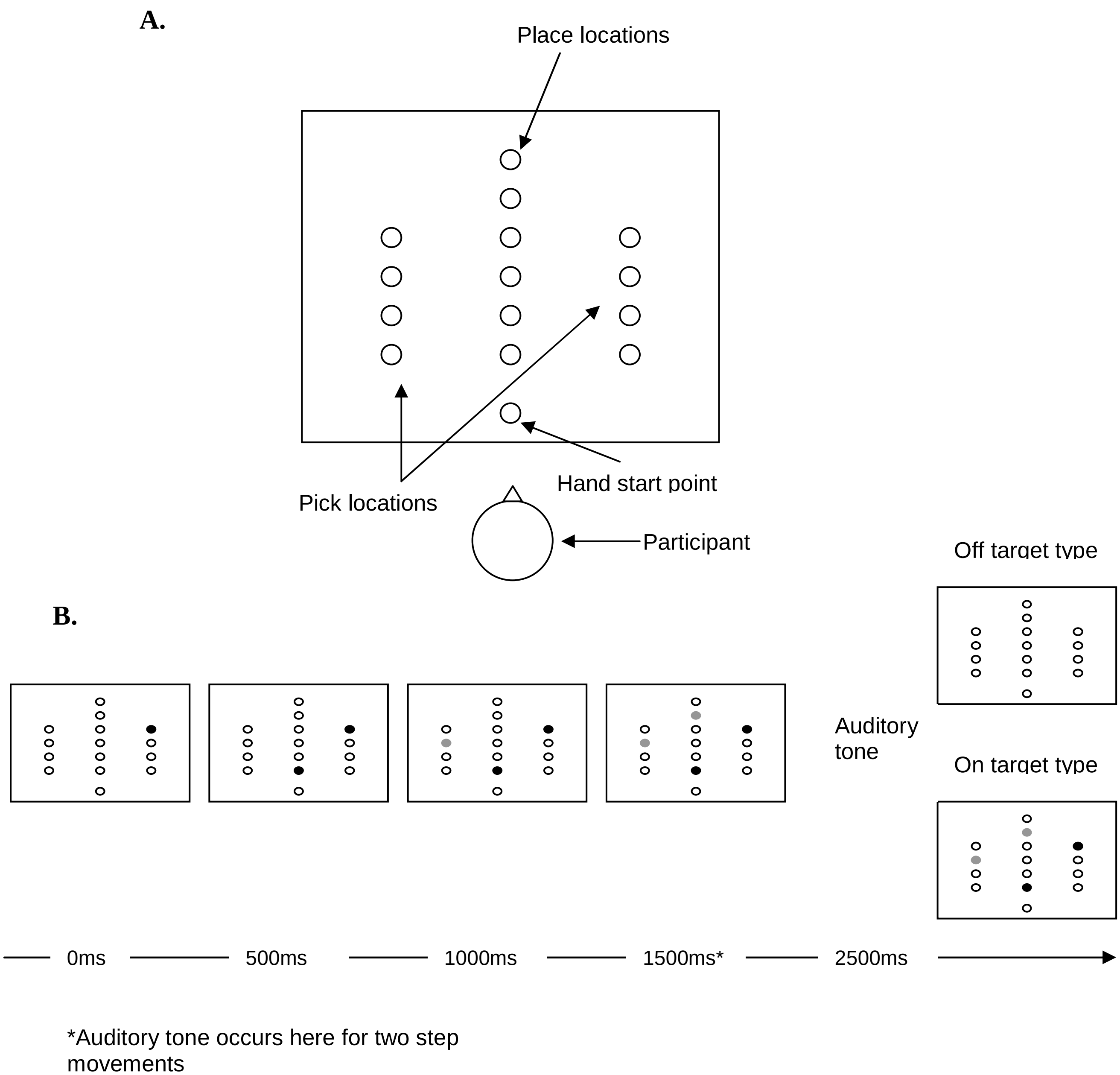

Figure 1. A. Schematic illustration of pick and place target locations, including the view point of the participant. B. An illustration of the sequence of events. The sequence of events was the same for pointing and reaching movements and for pre-scan and no scan.

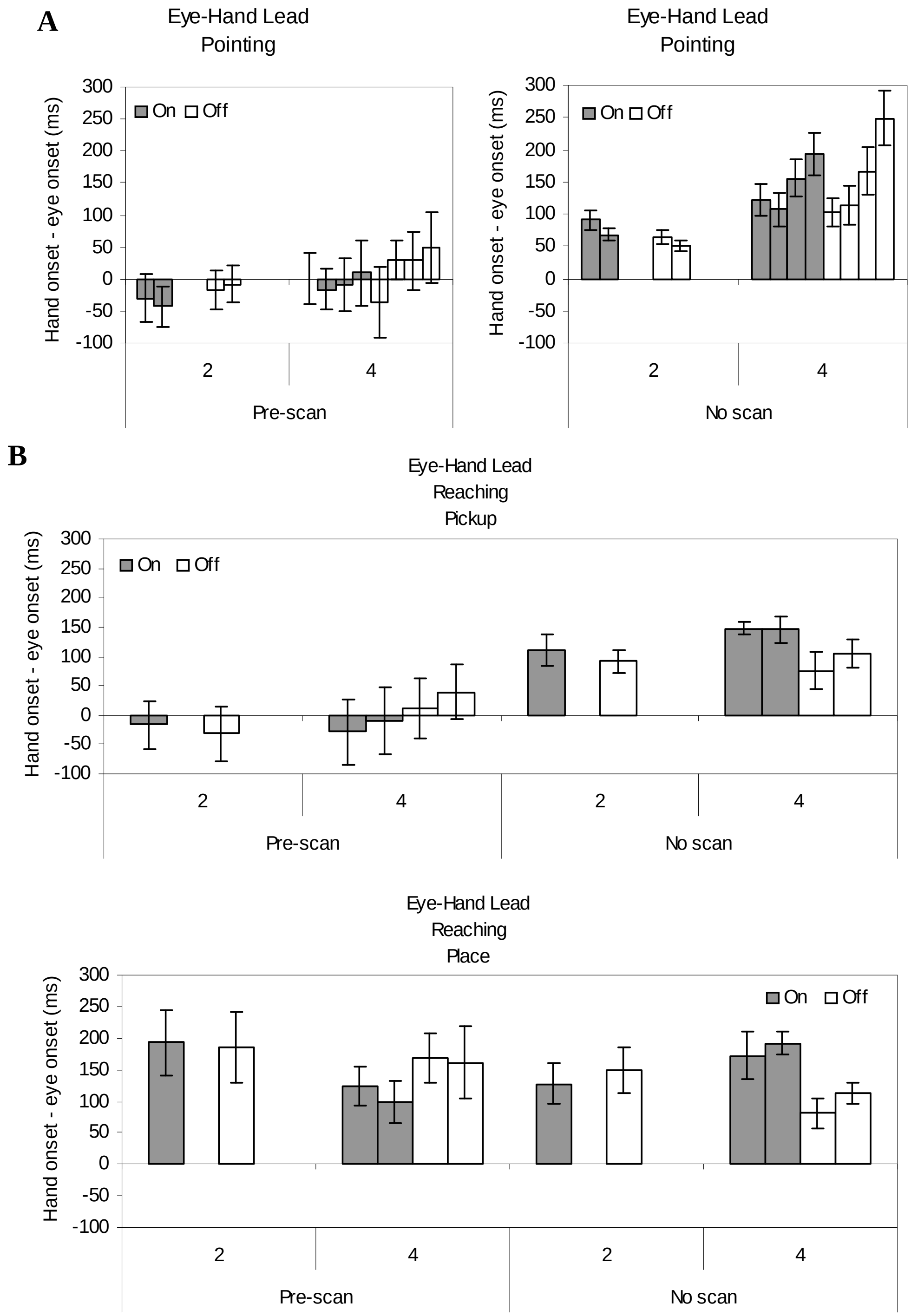

Figure 2. A. Graphs showing Eye-Hand Lead times for pointing movements for pre-scan and no-pre scan conditions. B. Graphs showing Eye-Hand Lead times for reaching movements, with pick and place movements separated. In both graphs grey bars represent On target types and white bars represent Off target types, the first bar of each shade represents the first movement and each bar thereafter represents a subsequent movement. Error bars show standard error across participants.

		On				Off			
		Mov 1	**Mov 2**	**Mov 3**	**Mov 4**	**Mov 1**	**Mov 2**	**Mov 3**	**Mov 4**
Accuracy of pointing movements (mm)									
P	2	7.70 (4.43)	8.13 (5.21)	-	-	15.31 (5.40)	19.11 (7.41)	-	-
Scan	4	11.46 (5.66)	8.84 (4.37)	13.24 (5.75)	11.81 (3.31)	22.98 (12.94)	21.53 (7.90)	25.59 (9.21)	21.80 (8.61)
P	2	11.24 (6.08)	10.94 (8.45)	-	-	21.66 (6.50)	20.71 (8.46)	-	-
No	4	16.97 (5.45)	15.98 (5.53)	16.42 (6.38)	16.40 (6.42)	37.23 (11.45)	32.97 (11.30)	39.16 (11.00)	36.88 (12.67)
Jerk (s/m^{-3})									
P	2	1348 (864)	1081 (887)	-	-	1283 (830)	988 (608)	-	-
Scan	4	1393 (1048)	1495 (1496)	1348 (1261)	1352 (1228)	1618 (1397)	1195 (1074)	1343 (1337)	1185 (1220)
P	2	1681 (1312)	1584 (1558)	-	-	1359 (795)	115 (737)	-	-
No	4	1152 (842)	1198 (1075)	1170 (1020)	1235 (1280)	1142 (838)	1197 (1213)	1125 (1308)	1292 (1492)
R	2	1318 (613)	768 (476)	-	-	1407 (854)	727 (3990)	-	-
Scan	4	1293 (557)	704 (361)	1156 (514)	770 (516)	1204 (498)	604 (304)	929 (487)	608 (243)
R	2	1376 (1004)	670 (352)	-	-	1316 (979)	650 (394)	-	-
No	4	1273 (658)	760 (360)	1442 (715)	792 (533)	1115 (500)	755 (386)	1064 (554)	581 (289)
Deceleration period (proportion)									
P	2	0.59 (0.04)	0.63 (0.05)	-	-	0.61 (0.04)	0.66 (0.04)	-	-
Scan	4	0.60 (0.02)	0.64 (0.33)	0.59 (0.03)	0.63 (0.02)	0.60 (0.06)	0.65 (0.03)	0.59 (0.03)	0.62 (0.04)
P	2	0.60 (0.05)	0.63 (0.02)	-	-	0.59 (0.05)	0.64 (0.06)	-	-
No	4	0.59 (0.05)	0.62 (0.03)	0.58 (0.04)	0.61 (0.02)	0.61 (0.06)	0.63 (0.05)	0.59 (0.04)	0.62 (0.04)
R	2	0.57 (0.04)	0.64 (0.04)	-	-	0.58 (0.05)	0.63 (0.04)	-	-
Scan	4	0.58 (0.03)	0.62 (0.03)	0.56 (0.07)	0.62 (0.07)	0.57 (0.04)	0.61 (0.04)	0.55 (0.04)	0.60 (0.05)
R	2	0.57 (0.07)	0.63 (0.02)	-	-	0.58 (0.05)	0.64 (0.05)	-	-
No	4	0.56 (0.05)	0.62 (0.03)	0.58 (0.04)	0.62 (0.05)	0.56 (0.06)	0.62 (0.05)	0.56 (0.03)	0.62 (0.06)
Maximum grip aperture (mm)									
		On				Off			
		MGAsize1	MGAsize2			MGAsize1	MGAsize2		
R	2	44.8 (3.74)	-			46.9 (3.99)	-		
Scan	4	44.1 (3.67)	42.9 (3.67)			45.0 (2.52)	42.5 (4.30)		
R	2	58.4 (3.91)	-			60.8 (3.93)	-		
No	4	74.5 (7.50)	71.6 (7.56)			71.6 (6.47)	72.7 (8.07)		
Closure time from maximum grip aperture (ms)									
		On				Off			
		MGAtime1	MGAtime2			MGAtime1	MGAtime2		
R	2	476 (52)	-			482 (64)	-		
Scan	4	467 (67)	440 (43)			467 (37)	438 (40)		
R	2	533 (108)	-			548 (83)	-		
No	4	537 (56)	508 (35)			516 (63)	495 (75)		

Table 1. Constant and variable error for pointing movements, variable error can be found in brackets. Time to peak aperture, size of peak aperture, jerk and the proportion of the movement which is the deceleration phase (deceleration phase) are given for all reaching movement types and for 2 and 4 step movements. Values are given for pointing movements (P) and reaching movements (R) and for pre-scan conditions (scan) and no pre-scan conditions (no). Standard deviation is given in brackets**.**