Multiple spatial representations interact to increase reach accuracy when coordinating a saccade with a reach

Yuriria Vazquez¹, Laura Federici², Bijan Pesaran¹

¹Center for Neural Science
New York University
New York, NY USA

²Department of Pharmacy and Biotechnology
Piazza di Porta San Donato 2
University of Bologna
Bologna, Italy

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Abstract

Reaching is an essential behavior that allows primates to interact with the environment. Precise reaching to visual targets depends on our ability to localize and foveate the target. Despite this, how the saccade system contributes to improvements in reach accuracy remains poorly understood. To assess spatial contributions of eye movements to reach accuracy, we performed a series of behavioral psychophysics experiments in non-human primates (M. mulatta). We found that a coordinated saccade with a reach to a remembered target location increases reach
Look-reaching accuracy without target foveation. The improvement in reach accuracy was similar to that obtained when the subject had visual information about the current target’s location in the visual periphery and executed the reach while maintaining central fixation. Moreover, we found that the increase in reach accuracy elicited by a coordinated movement involved a spatial coupling mechanism between the saccade and reach movements. We observed significant correlations between the saccade and reach errors for coordinated movements. In contrast, when the eye and arm movements were made to targets in different spatial locations, the magnitude of the error, and the degree of correlation between the saccade and reach direction was determined by the spatial location of the eye and the hand targets. Hence, we propose that coordinated movements improve reach accuracy without target foveation, due to spatial coupling between the reach and saccade systems. Spatial coupling could arise from a neural mechanism for coordinated visual behavior that involves interacting spatial representations.

News and Noteworthy

How visual spatial representations guiding reach movements involve coordinated saccadic eye movements is unknown. Temporal coupling between the reach and saccade system during coordinated movements improves reach performance. However, the role of spatial coupling is unclear. Using behavioral psychophysics, we found that spatial coupling increases reach accuracy in addition to temporal coupling and visual acuity. These results suggest that a spatial mechanism to couple the reach and saccade systems increases the accuracy of coordinated movements.

Keywords: reach, saccade, accuracy, eye-hand coordination, visual-motor

Running title: Spatial coupling during coordinated eye-arm movements
Introduction

Reaching and grasping are natural and essential behaviors that allow primates to interact with the world. Accurate reaching to visually-presented targets often depends on target foveation. Typically, the eyes foveate the target before the hand arrives (Abrams et al. 1990; Helsen et al. 2000), allowing foveal visual information about the target to guide the reach. Reaching to peripheral targets during central fixation leads to inaccurate reaches (Prablanc et al. 1979). Thus, humans and non-human primates tend to coordinate eye and arm movements to foveate targets and reach accurately (Biguer et al. 1982; Iriki et al. 2001; Johansson et al. 2001; Land and Hayhoe 2001; Shepherd and Platt 2006). However, in humans, coordinated movements of the eyes and arms performed in absolute darkness without target foveation also lead to more accurate pointing dynamics (Bock 1986; Enright 1995; Henriques et al. 1998; Ren et al. 2006; Schütz et al. 2013). This suggests that in addition to visual target information, accurate reaching depends on coordinating a saccade with a reach.

Coordinating a saccade with a reach recruits spatial and temporal mechanisms. Several lines of evidence demonstrate temporal coupling between the reach and the saccade systems during coordinated eye-arm movements (Fisk and Goodale 1985; Neggers and Bekkering 2000; Dean et al. 2011; Hagan et al. 2012). However, some forms of temporal coupling do not necessarily involve spatial coupling. A shared signal to initiate both movements, for example, can result in temporal coupling without spatial coupling (Dean et al. 2012). Behavioral evidence for spatial coupling during eye-hand coordination is also relatively mixed (van Donkelaar 1997; Sailer et al. 2000). Spatial coupling in the form of an influence of the saccadic eye movement amplitude on the coupled reach movement has been reported (van Donkelaar 1997). Evidence of spatial coupling through correlations between the eye and the hand errors has, however, been ambiguous (Sailer et al. 2000; Kattoulas et al. 2008). Coordinated reach accuracy may involve
coupling between spatial representations of the target within the saccade and the reach system. If so, reach accuracy should be modulated by the degree of spatial coupling between the saccade and the reach systems. Alternatively, coordinated reach accuracy may not rely on a spatial interaction between the saccade and the reach system. If so, reach accuracy should be independent of the degree of spatial coupling between the saccade and the reach system. However, it remains unclear whether the spatial metrics of saccadic and reach movements are coupled during coordinated eye-hand behavior, whether coupling reflects a common spatial representation guiding both motor plans, and/or whether coupling contributes to improved coordinated reach accuracy.

To better understand the spatial mechanisms of coordinated reach accuracy, we performed behavioral psychophysics in non-human primates. The macaque monkey is the most frequently studied non-human primate model used to understand the neuronal basis of reach and saccade movements, (Andersen et al. 1985; Cui and Andersen 2007; Crawford et al. 2011; Konen et al. 2013), due to the similarity between behavior and movement kinematics with humans (Roy et al. 2000). The macaque monkey also offers practical advantages for studying eye-hand coordination. Extensive training can stabilize saccade and reach performance, multiple visual-motor tasks can be interleaved and many trials can be collected across the different tasks. We therefore investigated spatial coupling by training two monkeys in a set of visual-motor tasks including a novel task that spatially dissociates reach and saccade movements while maintaining their temporal coupling. We tested whether the magnitude of the movement errors, as well as the degree of correlation between the saccade and the reach direction was related to the spatial properties of the eye and the hand targets. The results support the hypothesis that coordinated movements improve reach accuracy in the absence of target foveation due to spatial coupling between the reach and saccade systems.
Methods

Experimental preparation

Two male rhesus monkeys (*Macaca Mulatta*) participated in the experiments (Monkey 1, 7.5 kg, 12 years old; Monkey 2, 11.2 kg, 8 years old). Monkeys were kept on a 12 h/12 h light/dark cycle. All experimental testing was completed during the light cycle under controlled-water access. Each animal was implanted with head-fixation hardware under isoflurane inhalant anesthesia and received buprenorphine and rimadyl analgesia for 72 hours after the surgical procedure. Head-fixation hardware was necessary to restrain the head during behavioral training and recording. All surgical and animal care procedures were approved by the New York University Animal Care and Use Committee and were performed in accordance with National Institutes of Health guidelines.

Behavioral Tasks

We trained two monkeys to perform six tasks involving a reach in which we manipulated visual target information and oculomotor behavior (Fig. 1): delay saccade-touch (DST), delay-reach-and-fixate (DRF), delay-reach-and-saccade (DRS), dissociated-delay-reach-and-saccade (DRSd), memory-reach-and-fixate (MRF), memory-reach-and-saccade (MRS), and dissociated-memory-reach-and-saccade (MRSd). Reaches were made with either the left arm (Monkey 1) or right arm (Monkey 2) on a touch-sensitive screen (ELO Touch Systems, CA). Eye position was monitored with an open-source video-based eye-tracker (Zimmermann et al. 2016). Visual stimuli were presented on an LCD display (Dell Computers, TX) placed behind the touchscreen. All visual stimuli displayed on the screen were isoluminant confirmed with a spot spectroradiometer (Photo Research PR 650). The testing room was otherwise maintained in complete darkness to limit the use of visual landmarks.
Monkeys were seated in a chair in front of the touch screen. The head was fixed. To begin each trial, each monkey placed his hands on two touch sensors located at waist height. When both of the touch sensors detected a touch, a yellow visual target (2° square) was illuminated at the center of the screen. The monkey had 1.0 s to reach and touch the yellow central square. Each monkey then maintained fixation and touch for a baseline period of (0.5-0.8 s). A spatial cue was presented in the form of one or two targets at random locations on a circle eccentricity 11° (Fig. 1). After a variable-duration instructed delay (0.7-1.0 s), the central visual target changed color from yellow to gray, instructing the monkey to reach or saccade to the peripheral target location. Monkeys were required to keep touch and fixation on the central yellow square from the beginning of the trial until the go cue.

Saccade reaction times were required to be within 0.05-0.5 s of the Go cue. Reach reaction times were required to be within 0.1-1.0 s of the Go cue. After acquiring the cued location, subjects maintained touch and fixation for 0.2-0.3 s. Each trial ended with the delivery of a fluid reward. The inter-trial interval was 0.3-0.7 s at which time the central visual target was re-illuminated for the next trial.

The color of the spatial cue served as the effector cue. Red instructed a saccade while maintaining central touch in single effector trials (Fig. 1A). Green instructed a reach while maintaining central fixation in single effector trials (Fig. 1B, D). Yellow instructed a coordinated reach and saccade in double effector trials (Fig. 1C, E). Single effector movement and double effector coordinated movement trials involved a spatial cue with one target. In the case of double effector trials with dissociated movements a pair of spatial cues with two targets, a green target for the reach and a red target for the saccade was presented (Fig 1F-G). For the
dissociation tasks, the reach and saccade targets were separated by at least $5^\circ$ of visual angle. The location of spatial cue was randomized trial-by-trial.

On delay trials the spatial cue was illuminated throughout the instructed delay period. On memory trials the spatial cue was illuminated for 0.3 s before being extinguished for the remainder of the instructed delay period. On memory trials, the spatial cue was re-illuminated for 0.1-0.15 s after the target was acquired.

The central visual target was a square, $2^\circ$ on a side. Touch and fixation was maintained within an acceptance window $2^\circ \times 2^\circ$. All tasks used the same windows, except for the hand tolerance window in the memory dissociation task, which was $3^\circ \times 3^\circ$.

Calibration data sets were collected at the beginning of each recording session. Touch position was calibrated using 100 trials of delay-reach (DR) task performed by a human subject seated with head position in the same location as the animal subject. The DR task is similar in nature to the DRF task (Fig. 1B), except that the human subject was free to look at the target, thus the touch endpoints were as precise as possible. After calibrating touch position, the monkey then performed 100 trials of a delay-saccade-and-touch task (Fig 1A, DST). These trials were used, offline, to calibrate fixation position.

For each recording session, each monkey performed a maximum of 1000 trials. Blocks of 100 trials of single-effector and double-effector task trials were randomly interleaved. Within each block of single effector trials, the saccade-and-touch task and the reach-and-fixate task (Fig. 1A-B, D) were randomly interleaved trial-by-trial in equal proportions. Within each block of double effector trials, the coordinated-reach-and-saccade task (Fig. 1C, E) and the dissociated-
reach-and-saccade (Fig. 1F-G) task were randomly interleaved trial-by-trial in equal proportions. Within each block, trials with a visual-delay and a memory-delay were randomly interleaved for all tasks trial-by-trial in equal proportions.

Data collection

The task was controlled using custom-code Labview code running on real-time platform (National Instruments, PXI-1031). Behavioral data were digitized (12 bits at 10 kHz; National Instruments, TX) and continuously recorded to disk for further analysis (custom C and Matlab code). Gaze calibration was performed using an initial offset and gain calibration for online control and later offline using a linear transformation. Fixation and touch position were calibrated offline by fitting a center and slope parameters using a linear regression applied to calibration data sets. Calibration parameters were used to transform the acquired gaze/reach endpoints into target position coordinates. Only successful trials with endpoints located within 3 standard deviations of the mean location were used for calibration. From the linear transformation, a slope and an intercept (center) were obtained and used to calibrate the rest of the trials. In M1, we collected a total of 8481 trials involving a reach (DRS=1558, MRS=1360, DRF=1154, MRF=1070, DRSd=914, MRSd=2425 trials) and 6356 trials involving a saccade (DRS=1572, MRS=1372, DRSd=944, MRSd=2468 trials). In M2, we collected a total of 5860 trials involving a reach (DRS=1284, MRS=1309, DRF=1028, MRF=998, DRSd=702, MRSd=1823 trials), and 5180 trials involving a saccade (DRS=1292, MRS=1325, DRSd=713, MRSd=1850 trials).

Data analysis

We analyzed data from sessions in which the eye tracking was stable and did not require recalibration. Trials in which movement endpoints were more than $20^\circ$ from the center of the screen were discarded. Trials in which the magnitude of the movement error differed from the
mean error by more than 3 standard deviations were discarded. All data were analyzed using custom Matlab code (The Mathworks, MA).

We quantified movement accuracy by calculating:

1) The **absolute magnitude of the error** (Fig. 2A-B): The magnitude of the distance between the target coordinates and the effector (hand/eye) endpoints coordinates:

\[
\text{error magnitude} = \sqrt{(\text{Effector Position } X - \text{Target Position } X)^2 + (\text{Effector Position } Y - \text{Target Position } Y)^2}
\]

2) The **angle of the reach error**: The angle formed between the target and the reach movement vector (Fig. 2B), calculated as the absolute difference between the reach and target angles.

\[
\begin{align*}
\text{Target Angle} & = \text{ArcTan}\left(\frac{\text{Target Position } Y}{\text{Target Position } X}\right) \\
\text{Hand Angle} & = \text{ArcTan}\left(\frac{\text{Hand Position } Y}{\text{Hand Position } X}\right) \\
\text{Angle error} & = | (\text{Hand Angle} - \text{Target Angle}) |
\end{align*}
\]

3) The **angle of the saccade error**: Analogous to the angle of the reach error on trials involving a saccade.

4) The **amplitude of the error**: The difference between the length of the effector vector and the length of the target vector. The length for the target/effector vector was calculated as the distance between the fixation touch-center, and the target/effector endpoint coordinates, respectively. For example:

\[
\text{Amplitude effector} = \\
\sqrt{(\text{Hand Position } X - \text{Center Position } X)^2 + (\text{Hand Position } Y - \text{Center Position } Y)^2}
\]

Thus, the amplitude of the error was computed as
Amplitude error = Amplitude effector − Amplitude target

Positive amplitudes indicate the subject was overshooting, whereas negative amplitudes indicate undershooting (Fig. 2C).

The same accuracy measures were used to analyze the dissociation task, except that we analyzed the errors as a function of the saccade and reach target locations. We divided target locations on the circle into 4 quadrants, 0-90°, 90-180°, 180-270°, 270-360°. We computed the reach error and saccade error for each of the 16 possible combinations of gaze and arm quadrants.

We also calculated:

5) The external angle of the effector: The angle formed between the target and the gaze shift/arm movement, with the target as a center (Fig. 2D). We first calculated the vector difference: \( \overrightarrow{D}(Dx, Dy) \), between the target and the effector (hand/gaze). We then calculated the angle:

\[
\text{Angle} = \text{sign}(Dy) \times \text{Arccos}(Dx)/\|D\|
\]

Here, Sign refers to the Matlab function that for each element returns a 1 if the element is greater than zero, 0 if it equals zero and -1 if it is less than zero. Angle, provides values between \([-180° \text{ and } 180°]\). For all values less than zero, we added 360°, shifting the output so that all angles lie within 0 - 360°.

We computed the correlations between the saccade and reach error using Pearson correlation coefficient.

We computed the circular correlation between the gaze angle error and the reach angle error using circ_corrcc from the Circular Statistics Toolbox for Matlab (Berens 2009).
Statistical analysis

We compared the means of the magnitude and amplitude of the errors using a one-way ANOVA test. We corrected for multiple comparisons using the Tukey-Kramer test ($p \leq 0.05$). For all statistics we took random samples within each population, to achieve the same number of samples across populations.

Mean angle error was compared using a Watson-Williams multi-sample test for equal means. The test is similar to running a one-way ANOVA test but for circular data. We used the toolbox for circular statistics in Matlab (Berens 2009).

Errors as a function of the saccade and reach targets in the dissociation trials were compared using a two-way ANOVA.

Statistical significance of the correlations between the saccade and reach error was assessed using a Student's t-distribution for a transformation of the correlation, assuming the errors are distributed normally.
Results

We investigated how reach accuracy depends on visual and oculomotor information about the target derived from 1 - the visual periphery, 2 - the fovea following target foveation, and 3 - a coordinated saccade without target foveation. A coordinated saccade involves spatial and temporal coupling to the reach. We first examined reach accuracy when the saccade is coordinated with the reach in space and time. We then examined reach accuracy when dissociating the saccade from the reach in space and maintaining coupling in time.

Contributions due to a coordinated saccade

To investigate reach accuracy due to a coordinated saccade, we compared reach accuracy during four tasks involving a spatial cue with a single target (Fig. 1B-E). In the delay-reach-and-saccade (DRS) task the reach is performed to the target with a coordinated saccade. Information is present from three sources: the visual periphery, the fovea following target foveation, and a coordinated saccade. In the memory-reach-and-saccade (MRS) task the reach is made with a coordinated saccade to a remembered target location. For this task, target information at the fovea is removed but remembered information from the visual periphery is used to coordinate a saccade with the reach. In the delay-reach-and-fixate (DRF) task the reach is made to the target while maintaining central fixation. Here, peripheral visual information about the target is present, but there is no coordinated saccade or target foveation. Finally, in the memory-reach-and-fixate (MRF) task the reach is performed to a remembered target location. There is no foveal target information and no coordinated saccade.

Figure 3A depicts the mean reach endpoints with respect to target location. Both monkeys showed a similar pattern across tasks. When a reach and saccade were performed to a visible target (DRS, yellow lines), the reach endpoints landed very near the target locations. When reaches were performed without target foveation but with a coordinated saccade (MRS,
orange lines), the reach endpoints were less accurate. Interestingly, when a reach was performed with peripheral vision of the target but without a coordinated saccade, reach endpoints were also less accurate (DRF, light green). As expected, the least accurate reaches were observed when reaches were made without target foveation and without a coordinated saccade (MRF, dark green).

We quantified reach accuracy across the four tasks by measuring the absolute magnitude, amplitude and angle, of the reach error trial-by-trial. The mean magnitude of the reach error differed significantly across tasks for both monkeys (Fig. 3B; $M_1$: $p=0.001$, $F$-value=377.11, $n=1070$, Tukey-Kramer corrected $p=0.001$; $M_2$: $p=0.001$, $F$-value=153.33, $n=988$, Tukey-Kramer corrected, all comparisons $p \leq 0.001$, except for the MRS versus the DRF task, $p=0.9074$). Smaller reach errors occurred when a coordinated saccade was performed and the target was visible (mean ± s.t.d. DRS, $M_1=0.94±0.01$ cm; $M_2=0.83±0.01$ cm). Meanwhile, the largest errors were observed when each monkey maintained fixation and made a reach to a remembered target location (MRF, $M_1=2.00±0.03$ cm; $M_2=1.44±0.02$ cm). Interestingly, the reach error elicited when making a reach with a coordinated saccade to a remembered target location was similar to ($M_2$: $p=0.9074$) or smaller than ($M_1$: $p=0.001$) the reach error elicited when making a reach to a visible peripheral target while maintaining fixation (MRS $M_1=1.37±0.01$ cm; $M_2=1.07±0.01$ cm; DRF $M_1=1.79±0.02$ cm; $M_2=1.09±0.02$ cm).

We obtained similar results when we quantified reach accuracy by the angle formed between the target location and the reach endpoint. Figure 3C presents the mean reach angle for the four tasks. The smallest mean reach angle error was observed during the DRS task (DRS, $M_1=4.12±3.24^\circ$, $M_2=3.72±2.95^\circ$), and the largest reach angle error was observed during the MRF task ($M_1=8.63±6.22^\circ$, $M_2=6.62±5.30^\circ$). When comparing the reach angle error elicited from MRS versus DRF task; in M1 the mean angle was significantly smaller when
the reach was coupled with a saccade to an invisible target (MRS), than when the reach was uncoupled but the target was visible (DRF task ($F=138.41, p=0.00$; $M1$: MRS: $6.11 \pm 4.51^\circ$, DRF: $8.52 \pm 5.72^\circ$). For M2, we did not find a significant difference between the reach angle error elicited during the MRS versus the DRF task ($p=0.83$, $F$-value=0.04; $M2$: MRS = $4.87 \pm 3.62^\circ$, DRF = $4.90 \pm 4.24^\circ$).

We next analyzed the amplitude error of the reach movements (Fig. 3D). The mean amplitude errors of the reaches differed significantly across the four tasks in both monkeys (mean ± s.t.d. $M1$: DRS = $-0.18 \pm 0.01$ cm, MRS = $-0.04 \pm 0.02$ cm, DRF = $0.33 \pm 0.3$ cm, MRF = $0.82 \pm 0.03$ cm, $p=0.001$, $F$-value=206.85; $n=1070$; $M2$: DRS = $-0.06 \pm 0.01$ cm, MRS = $0.23 \pm 0.02$ cm, DRF = $-0.08 \pm 0.02$ cm, MRF = $-0.29 \pm 0.03$ cm, $p=0.001$, $F$-value=69.78, $n=988$). Overshoot>0, Undershoot<0). Moreover, we found that the mean amplitude error was significantly different for the MRS than for the DRF task ($M1$: $p<0.001$; $M2$, $p<0.001$). This suggests that a coordinated saccade influences reach amplitude by increasing accuracy as much as target information from the visual periphery.

Taken together, the reach error and reach amplitude results reveal that visual information about the target is not the only factor contributing to reach accuracy. A coordinated saccade increases reach accuracy in the absence of target foveation (MRS task), at levels similar to peripheral visual information (DRF task). Hence, eye-hand coordination increases reach accuracy independently of target foveation at levels comparable to the contribution of information from the visual periphery.

**Control for variations in temporal coupling**
In the single target reach-and-saccade tasks, we instructed each monkey to shift gaze and reach to the same target location at the same time. This presents a concern as fluctuations in the temporal coupling between gaze and the reach could vary and alter reach accuracy according to a speed accuracy trade off factor. In particular, reach accuracy may vary with respect to the time when the saccade is emitted relative to the reach. The variability in this effector-to-effector delay could potentially alter reach accuracy in addition to the spatial coupling between the eye and hand targets. To test whether fluctuations in the temporal coupling between both effectors influenced reach accuracy, we calculated the correlation between the difference in the reach and saccade reaction times, and reach accuracy. Across all behavioral sessions, the difference between the reaction time of the reach and the reaction time of the saccade did not reliably predict the magnitude of the reach error, for M1 ($\rho=0.038$, $p=0.72$, median $\Delta$RT=36 ms n=3080 trials) or M2 ($\rho=-0.069$, $p=0.38$, median $\Delta$RT=68 ms, n=2128 trials). We obtained similar findings when we analyzed the data separately for each session. In M1, only one session displayed significant correlations ($\rho=-0.1687$, $p=0.0252$). In M2, three sessions had significant correlations, however the sign of the correlation was not consistent across days ($\rho=0.2628$, $p=0.0065$; $\rho=-0.2012$, $p=0.0135$; $\rho=-0.55$, $p=0.0038$). These results demonstrate that variability in the effector-to-effector delay did not alter reach accuracy on a trial-by-trial basis. In other words, temporal coupling between the gaze and the reach was consistent during coordinated eye-arm movements (MRS). Hence, trial-by-trial variability in the temporal coupling was not the main factor influencing reach accuracy.

**Dissociating the contribution of spatial coordination**

Spatial coupling introduced by coordinating the saccade to the same location as the reach may underlie the improvement in reach accuracy. However, since single target tasks couple spatial and temporal factors, it remains unclear whether spatial coupling of a coordinated saccade
supports reach accuracy. To more directly assess the contribution of spatial coupling to coordinated reach accuracy we designed a task in which the subject spatially dissociates the saccade from the reach, while performing both movements at the same time. Specifically, we examined reach accuracy by presenting a spatial cue comprising two targets at different locations. The dissociated-delay-reach-and-saccade (DRSd) task and dissociated-memory-reach-and-saccade (MRSd) task altered spatial coupling without altering temporal coupling (Fig. 1F-G). Table 1 reports the reaction time for the reaches and saccades performed during each task. We confirmed that temporal coupling was present in both the coordinated and dissociated tasks, by calculating the correlation between the reaction time of the reach and the saccade (Dean et al. 2011). We observed significant correlations during the coordinated and the dissociated tasks for both monkeys (M1: DRS, $\rho=0.55$, $P \leq 0.001$, 1245 trials; DRSd $\rho=0.30$, $P \leq 0.001$, 726 trials; MRS $\rho=0.52$, $P \leq 0.001$, 1116 trials; MRSd $\rho=0.42$, $P \leq 0.001$, 1936 trials; M2: DRS $\rho=0.26$, $P \leq 0.001$, 1121 trials; DRSd, $\rho=0.16$, $P \leq 0.001$, 481 trials; MRS $\rho=0.22$, $P \leq 0.001$, 1324 trials; MRSd $\rho=0.41$, $P \leq 0.001$, 1318 trials).

Figure 4 presents the magnitude of the reach error in the dissociated (DRSd and MRSd) and coordinated (DRS and MRS) tasks. The magnitude of the reach error for the coordinated tasks is significantly smaller than for the dissociation tasks, for all reach directions (asterisks, $p<0.05$). When reach and saccade movements were instructed to different spatial locations (DRSd task) the reach error was significantly larger than the error when the reach was accompanied by a coordinated saccade to a visible target (DRS task; light gray asterisks: M1: $p \leq 0.001$; M2: $p \leq 0.001$). When we removed visual information about the target, and the monkey performed a remembered reach and saccade to the same target (MRS task), the mean reach error was significantly smaller than when the monkey performed a remembered reach and saccade to different targets (MRSd, dark gray asterisks, M1: $p \leq 0.001$; M2: $p \leq 0.001$). Moreover, the mean magnitude of the reach error in the MRSd task was significantly larger in comparison to the...
coordinated (DRS and MRS) and the reach-and-fixate (DRF and MRF) tasks (M1: \( p \leq 0.001, F=219.41, df=5; \) M2: \( p \leq 0.001, F=213.49, df=5 \)). These results suggest that it is not only the presence of the saccade that improves reach accuracy. The spatial goal of the saccade compared to the reach contributes to improvements in reach accuracy. Saccade errors were significantly smaller for the coordination task than the dissociation task in both monkeys (M1, gray asterisk: \( p \leq 0.001 \); black asterisk: \( p \leq 0.001 \); M2 gray asterisk \( p \leq 0.001 \); black asterisk: \( p < 0.002 \)). These results demonstrate that the spatial coupling of a reach with a saccade contributes substantially to reach accuracy, regardless of target foveation.

Interestingly, reach accuracy in the dissociation tasks depended on an interaction between the spatial location of the reach and saccade targets. Figure 5A presents the mean reach error for each saccade and reach target location in the dissociation task. We divided the circle into four quadrants, yielding 16 different gaze-reach target combinations. For each combination, we calculated the mean reach error magnitude. In both monkeys, the mean reach errors varied 1.4-3 cm across saccade and reach target locations. In both monkeys, there was a significant interaction between saccade and reach target location in the mean hand position error (M1: \( p \leq 0.001, F=4.83, d.f.=9, 73 \) trials per quadrant, M2: \( p=0.0001, F=3.92, d.f.=9, 91 \) trials per quadrant). Similar results were found for the magnitude of the gaze position error (M1: \( p=0.0014, F=3.03, d.f.=9, n=73 \) per quadrant; M2: \( p=0.021, F=2.18, d.f.=9, n=91 \) per quadrant). We obtained similar results for the amplitude of the reach (results not shown).

The fact that the magnitude of the reach error depends significantly on the location of the reach and saccade target positions indicates that a spatial interaction between the reach and the saccade systems can influence reach accuracy. If so, we would expect to observe a relationship between saccade and reach errors during coordinated movements. Therefore, we examined
correlations between the saccade and reach errors after a coordinated reach-saccade movement (MRS) to a remembered target. Using the MRS trials allowed us to control for the influence of target foveation to reach accuracy, but preserve the contribution of a coordinated saccade.

Figure 6A presents the correlations between the absolute magnitude of the saccade and the reach errors per quadrant. In M1, saccade and reach magnitude errors were significantly correlated for the majority of the quadrants (rho values: $q_1=0.44$, $q_2=-0.08$, $q_3=0.26$, $q_4=0.11$, $p \leq 0.05$). M2 displayed significant correlations only in half of the circle (rho values: $q_1=0.12$, $q_2=0.10$, $q_3=0.06$, $q_4=-0.006$, $p \leq 0.05$). Correlations in the amplitude of the saccade and reach errors showed a similar pattern (Fig. 6B). In M1 the amplitude of the saccade and reach error were correlated in half of the circle (M1, rho values: $q_1=0.08$, $q_2=0.07$, $q_3=0.27$, $q_4=0.29$, $p \leq 0.05$); whereas in M2 the amplitude of the saccade and reach error were correlated within most of the circle (M2, rho values: $q_1=0.28$, $q_2=0.19$, $q_3=0.05$, $q_4=0.15$, $p \leq 0.05$).

During the coordinated trials (MRS), most saccades overshot the target and less than 35% of the saccades were hypometric. The magnitude of the reach error may be related to the amplitude of the saccade. To test this, we compared the magnitude of the reach error when the saccade overshot the target with when it undershot the target. In M1 there was a slight, but not significant, tendency for higher reach errors when the saccade overshot the target (mean ± s.t.d. $M1$: Overshoot: $1.4 \pm 0.71$, n=831; Undershoot: $1.3 \pm 0.7$, n=529, $p=0.068$). However, M2 didn't show a clear relation between the amplitude of the saccade and the magnitude of the reach error (mean ± s.t.d. $M2$: Overshoot: $1.1 \pm 0.6$, n=950; Undershoot: $1.0 \pm 0.56$, n=359, $p=0.25$). Therefore, the amplitude of the saccade was not a clear predictor of the magnitude of the reach error during coordinated movements (MRS task).
On the other hand, the correlation between the minimum angle formed between the target and the effector (reach/saccade) was more congruent for both monkeys with a higher degree of correlation between saccade and the reach (Fig. 6C). Gaze angle and reach angle error were significantly correlated after movements to most parts of the circle (M1 rho values: q1=0.48, q2=0.028, q3=0.25, q4=0.18, p≤0.01; M2 rho values: q1=0.23, q2=0.13, q3=0.13, q4=0.009, p≤0.05).

The above measures do not characterize variations in movement direction trial by trial. Therefore, we quantified the direction of each movement with respect to the target using the external angle. The external angle is the angle formed between the effector endpoint (gaze/hand position) and the target, as if the target were located at the center of a circle. Figure 7 presents the histograms of the external angles for the reach and gaze (M1: left panels: M2: right panels); for each quadrant of the circle (A: 0-90°, B: 90-180°, C: 180-270°, D: 270-360°). Figure 8 presents the correlation between the external angle of gaze and the reach. Gaze and reach external angles were significantly correlated for all quadrants of the circle in both monkeys. The correlations between external angles were larger and more significant than the correlations between movement amplitudes (M1, rho: q1=0.15, q2=-0.40, q3=-0.23, q4=0.42, p≤0.01; M2, rho q1=0.39, q2=0.23 q3=-0.32 q4=-0.45, p≤0.01). This demonstrates the presence of a spatial relationship between gaze and the reach endpoints for coordinated movements. The correlations measured depend on the quadrant of the circle and so may reflect other factors such as the biomechanics of the upper limb extremity.

We computed the correlation between the gaze and reach angles for movements to remembered targets during the MRSd task. We found that the strength of the correlation depends on the relative location of the saccade and reach targets. Figure 9A-B presents the
Look-reach accuracy

strength of correlation, rho, between the gaze and reach angles by combination of quadrants.

In general, correlations for movements to remembered targets were lower for the dissociated movements than for the coordinated movements (MRSd vs MRS task). Moreover, the value and significance of the correlation in the MRSd task differed significantly depending on the saccade and reach target location within the circle. We found significant (Fig 9C-D black/white quadrants, t-test statistics), and non-significant (Fig 9C-D gray quadrants) correlations depending on the combination of gaze and reach target locations. This indicates that the correlations between the movement directions in a coordinated movement depend on a spatial form of coupling between the saccade and the reach systems.

Control for efference copy of the saccade

The accuracy of coordinated reach movements may reflect the influence of an efference copy of the saccade motor command. If so, reach movement endpoints should deviate according to the direction of the saccade executed on that trial. To test for the presence of a systematic bias in reach endpoint due to the saccade motor command, we separated the trials from the memory dissociated task (MRSd) in two categories, depending on whether the saccade was performed to the same or opposite visual hemifield as the reach. We first separated the trials in two groups according to whether the saccade was performed to the right or left visual hemifield. We then examined the mean endpoint for reaches performed to the ipsilateral or contralateral hemifield to the saccade. If saccade efference copy influences reach accuracy, and hence the reach endpoint, we expect that reach endpoints will be biased towards the direction of the saccade. When reaches are made to the opposite direction of the saccade, we would expect a less precise reach, with an endpoint biased towards the saccade direction. This hypothesis predicts that the reach endpoints lie towards the inner parts of the circle when the saccade is performed.
toward the contralateral side of the circle, since the saccade efferent copy will shift the reach
towards the saccade’s direction.

Figure 10, depicts the raw (black and gray squares) and mean reach endpoints (gray line,
bin=10°) when the saccades (black and gray dots) were performed to the left (Fig 10 A,B) or the
right (Fig 10 C,D) visual hemifield. We did not observe a consistent bias of the mean reach
endpoints towards the saccade direction when the saccade and reach occurred in opposite
directions i.e. reach endpoints within the circle. Moreover, the reach endpoints were not
necessarily more precise when the saccade and reach were performed to the same side of the
visual field (p>0.05).

The influence of the saccade efferent copy on the reach may be spatially restricted to reach and
saccade movements with similar movement direction and amplitude. Under this scenario, when
the saccade and reach plan overlap in space, we expect greater and more significant
correlations between the amplitude of the hand and gaze endpoints (MRS task). A similar effect
is expected when the locations of the targets are located nearby, but do not overlap. In the MRS
task, when the eye target is located within a range of ± 30° from the hand target, the
correlations are expected to be smaller in magnitude since the reach plan and saccade efferent
copy differ in their spatial properties. In the case of the saccade and reach movements (MRSd)
directed to locations far apart, for example, when the eye target is located within a range of 180
± 30° from the hand target. The correlation between the amplitude endpoints should be low or
negative since the spatial properties of the reach and saccade are very different.

Figure 11 depicts the correlation values between the saccade and reach amplitude (Fig 11 A,C)
or the saccade and reach direction (Fig 11 B,D) when the eye and arm movements landed in
the same (MRS), nearby (MRSd E-H near, Fig 11) or far away (MRSd E-H far, Fig 11) locations.
in the circle. When the saccade and reach were coupled to the same spatial location (MRS task), most amplitude correlations were positive (gray circles) and significant (black circles \( p \leq 0.05 \)) in M1 and M2. When the saccade and reach landed within nearby locations most correlations were positive but not significant (gray diamonds) in M1. M2 presented a mixture of positive and negative correlations. When the saccade and reach landed far from each other (black and gray squares) we observed a mixture of small positive and negative amplitude correlations. Very few of these correlations were significant. Examining the correlation between the saccade and reach direction revealed similar results. Movement directions were significantly correlated (positively and negatively) when the movements were spatially overlapping (MRS, black circles). When the saccade and reach landed nearby or faraway, correlations in movement directions were smaller in magnitude and less significant.
Discussion

Here, we investigate the influence of saccades on the accuracy of coordinated reach movements. We find that a saccade made with a coordinated reach increases reach accuracy in the absence of target foveation and does so to levels similar as when the subject keeps fixation and reaches using peripheral visual information from the target. Critically, the influence of the saccade on reach accuracy is independent of visual feedback from the target. Using a novel task requiring the subjects to perform reach and saccade movements to different spatial locations, we find that the magnitude of the reach error is determined by the spatial interaction between the reach and saccade targets. Spatial coupling of the saccade to the reach elicits significant correlations not only between the saccade and reach errors, but also between the direction of the saccade and the reach with respect to the target. The degree of correlation between the direction of the saccade and the reach is related to the spatial similarity between the reach and the saccade targets. These novel findings suggest that a common spatial representation of the target coordinates a saccade movement with a reach. We propose this common representation could result from spatial interactions between the saccade and reach systems.

Spatial coupling in eye-hand coordination

The presence of significant correlations between the errors of the saccade and the reach endpoints during the eye-arm coupled task (MRS) suggests an interaction between the spatial representation of the reach and saccade metrics (Figs 6, 8). Interestingly, the magnitude of the reach error and the degree of correlation between the direction of the saccade and the reach was determined by the spatial coupling between the reach and saccade targets. Therefore, we hypothesize that a spatial interaction between the saccade and reach systems could give rise to a common spatial representation of the reach and saccade when coordinated movements occur.
This hypothesis predicts a significant correlation between the spatial metrics of the saccade and reach consistent with our observations. Naturally, a common spatial representation model does not exclude an influence of the saccade efferent-copy in reach accuracy when coordinated movements occur. The formation and maintenance of a common spatial representation may be supported by efference copy signals.

In previous reports, evidence of spatial coupling of the target has been mixed (Bekkering and Sailer 2002). Using several tasks involving eye and hand movements to a single target, (Sailer et al. 2000) reported the presence of correlations in the mean latencies of saccades and hand movements but not the errors, supporting the existence of a temporal but not spatial coupling mechanism. Another study by (van Donkelaar 1998) showed that saccade amplitude influences the control of the coupled hand movement when no visual feedback of the hand is present.

Previous work by (Kattoulas et al. 2008) demonstrated that the endpoints following coordinated eye-arm movements were significantly correlated. This suggests that the metrics of arm movements can influence saccades. These findings support evidence from (Soechting et al. 2001; Tipper 2005) that saccade-related signals can influence spatial processing in the reach system.

Our results extend this work to demonstrate the presence of an interaction between the reach and the saccade system during coordinated movements. In addition, we show that the magnitude and significance of the correlation between the saccade and the reach direction depends strongly on spatial coupling between the gaze and reach targets. Since the correlation in movement metrics occurs during a movement to a remembered target, hence in the absence of visual target information correlations cannot be due to visual acuity and may instead depend on the interaction between gaze and reach target position due to another spatial coupling.
mechanism. To test whether any discrepancy between (Sailer et al. 2000) and our results is due
to the details of the data analysis and, specifically, how correlations were computed, we re-
analyzed our data normalizing the magnitude and amplitude of the error as was done in that
study. The results hold for each quadrant of the circle when analyzing the results in this way.
We therefore propose that the results may be related to differences in the behavioral tasks
involved – specifically the memory dissociation task. By introducing two movement remembered
targets to parametrically dissociate reach and saccade directions, the memory dissociation task
contains a rich set of conditions to measure spatial interactions during coordinated movements.

Our results support the presence of a spatial interaction between both systems influencing
reach accuracy. The interaction could arise from a common spatial representation for the
planned saccade and reach when coordinated movements occur. Each time a motor plan is
executed an efferent copy of that motor plan is generated in order to keep track of the
performed movement. Therefore, reach accuracy could, in part, reflect the role of saccade
efference copy on the common spatial representation. When rapid eye movements occur the
saccade efferent copy is used to stabilize the visual field (Becker and Jurgens 1979; Umeno
and Goldberg 1997; Sommer and Wurtz 2002, 2008). During double step tasks, in which a
primary saccade is followed by a secondary saccade to another target, the accuracy of the
second saccade depends on the update of the receptive field by the efferent copy of the first
saccade (Sommer and Wurtz 2002). In single saccade tasks in which the saccade is performed
to a visually present target, such as the DRS, the efferent copy does not play a crucial role in
the accuracy of the contralateral saccade. This is most likely due to the presence of visual input
which provides the dominant source of spatial information for visually-guided behaviors. The
tasks used in the current study involve primary saccades. How the efference copy of a primary
saccade interacts with a reach during a coordinated movement is unknown. We did not find
evidence for the saccade efferent copy pulling the reach endpoints when the eye and arm
movements were performed to opposing or far away directions (Figs 10, 11). However, when the eye-arm movements were coupled to the same location, most of the amplitude and some directions of the saccade and reach endpoints correlate positively and significantly in both monkeys (Fig 11, MRS task). These results suggest that the efferent copy could potentially play a role when saccade and reach goals overlap in space. For example, the more similar the spatial relationship of the movements, the more likely the saccade efferent copy increases reach accuracy. To confirm and better quantify the influence of the saccade efferent copy to a common saccade-reach plan, additional psychophysical and electrophysiological experiments are needed.

Accurate reaching may also arise from proprioceptive eye signals (Enright 1995; Lazzari et al. 1997; Henriques et al. 2002; Ren et al. 2006; Gonzalez and Burke 2013). In our experiment, reaches were made in a dark room but we did not explicitly remove visual feedback of hand position during the reach. Therefore, visual feedback from the hand may be present and lead to fast online reach corrections (Goodale et al. 1986; Gaveau et al. 2008; Gritsenko et al. 2009; Apker et al. 2014). An efference copy of the arm movement also supports accurate reaching but it is unlikely to specifically do so as part of coordinated movements. This is because saccades are faster movements than reaches and acquire the target before the coordinated reach. Nevertheless, further studies are needed to assess the contribution of the arm efferent copy during coordinated movements. Finally, idiosyncratic differences between the monkeys could also lead to differences in reach performance.

Saccade influences on reach accuracy without target foveation
Previous work in humans has revealed the influence of saccades on pointing responses. The influence of a saccade on pointing accuracy when the targets are not foveated was demonstrated by Enright (1995). Our results are consistent with this work by showing more accurate responses when a saccade is made towards the target before pointing. We extend the results to reaching movements as opposed to pointing and we demonstrate that reach accuracy is modulated systematically by the spatial coupling between the reach and the saccade.

Differences also exist between our and Enright’s results (1995). Enright (1995) reported that when the gaze is aimed towards the target, the direction of the pointing movement was less biased than when central fixation was enforced. Enright (1995) proposed that the presence of less eccentric reaches when the eyes were aimed towards the target was due to the influence of the saccade efferent copy on the spatial memory trace used to perform the pointing movement. Our results differ from Enright (1995) as we did not observe a consistent bias in the reach endpoints towards less eccentric locations during the coupled eye-arm task (MRS), in comparison to the reach and fixate task (MRF, Fig 3).

An alternative explanation for accurate pointing to eccentric targets during central fixation involves magnification of perifoveal visual field (Bock 1986). Perifoveal magnification predicts a constant overshoot of the reach endpoints to more peripheral locations during the delay reach and fixation task (DRF) across all target directions. Our data did not match this prediction consistently across directions in the circle or for monkeys (Fig 3 A,D light green).

The differences between our findings and those of Bock (1986) and Enright (1995) merit discussion. A species difference may be important as we studied non-human primates while Bock (1986) and Enright (1995) studied human subjects. However, the differences in results are not necessarily solely attributable to a species difference. Important differences in behavioral task design exist and may also play a significant role. Unlike earlier work, we sampled all
movement directions for a given eccentricity allowing for a more detailed analysis of movement performance. In our experiments, subjects were also required to perform different single and double effector movements randomly interleaved on a trial-by-trial basis (Fig. 1, Methods). This task design allowed us to better control a variety of behavioral factors that may lead to changes in accuracy over the course of the experimental session. Since the target angle is randomly assigned on each trial, we could prevent strategic preallocation. However, to do so, we required subjects to switch the effector rule and allocate attention to a new randomly-presented location in the circle on each trial. The ability to perform interleaved trials with different spatial effector rules may alter movement performance. Consistent with this, several weeks of daily practice was necessary before stable behavioral performance was obtained in the presence of different effector rules.

Our experimental design may have diminished the bias seen by Enright (1995), when comparing the MRS versus the MRF task. Interleaving different effector tasks may have also altered the role of the perifoveal magnification effect seen in Bock (1986). Since we interleaved saccade and touch trials in which the gaze shifted towards the peripheral target, the saccade trials could have influenced the overall spatial map used during the block, modifying the over-estimation of the eccentricity to peripheral targets during the reach trials. Additional training to interleave tasks means practice-related improvements in movement performance may have masked the influence of perifoveal magnification. Further work is needed to better understand the relative role of these factors.

**Relationship between spatial and temporal coupling.**

Coordinated eye-hand movements require coupling in the temporal and spatial domain, and the different forms of coupling may reflect inter-related mechanisms. Evidence of temporal coupling between the saccade and the reach systems during coordinated movements involves: 1)
occurrence of the primary saccade at the time the hand is at peak acceleration (Helsen et al. 2000; Binsted et al. 2001); 2) anchoring of the saccade to the landing of the reach in double-step tasks (Neggers and Bekkering 2000); 3) influence of the saccade into the reaction time, initial acceleration, and final position of the hand movement (van Donkelaar 1997, 1998; Sailer et al. 2000; van Donkelaar and Staub 2000; Binsted et al. 2001; Dean et al. 2011); and 4) correlations between the reaction times of the eye and arm movements (Fisk and Goodale 1985; Gribble et al. 2002). These temporal correlations cannot be explained exclusively by a common input or modulation model, but are consistent with a model of interaction between two effector specific integrators (Dean et al. 2011).

**Neural evidence for mechanisms of coordinated behavior**

Electrophysiological and functional neuroimaging experiments have demonstrated that saccade and reach movement systems are controlled by effector-specific networks that construct multiple spatial representations (Johnson et al. 1993; Lewis and Van Essen 2000; Van Der Werf et al. 2010; Konen et al. 2013). Experiments in non-human primates show that inactivating the parietal reach region (PRR) during coordinated saccade and reach movements (Hwang et al. 2014) alters the temporal coupling of coordinated movements, while concurrently changing the reach and saccade endpoints. Inactivating PRR alone affects the saccade endpoints when the saccade was coupled with a reach. Consequently, spatial interactions between the reach and saccade systems may be present and enhance coordinated reach accuracy. For example, spatial coupling may arise from the activity of subpopulations of neurons within the saccade system whose response fields are modulated not only by the direction of the saccade but also by the direction of the reach. Similar changes may also be present in response fields of neurons within the reach system. When coordinated eye-arm movements are planned, the neural
responses of these neurons may predict reach accuracy better than neurons whose response fields are modulated by reach direction alone.

While the neural architecture of eye-arm coordination remains unknown, our results have important implications for understanding the mechanisms of visually-guided behavior. Interactions between the saccade and the reach system may be supported by neural interactions within the posterior parietal cortices (PPC (Andersen et al. 1987; Snyder et al. 1997; Batista and Andersen 2001; Cui and Andersen 2007; Hawellek et al. 2016; Wong et al. 2016)). Furthermore, the eye-hand coordination circuit could also include other brain areas extending across a larger frontal-parietal network (Battaglia-Mayer et al. 2001; Marconi et al. 2001; Pesaran et al. 2006, 2010), the supplementary eye fields (SEF, (Mushiake et al. 1996)), the pre and supplementary motor areas (pre-SMA & SMA; (Fujii et al. 2002)), and the superior colliculus (Lunenburger L. et al. 2001; Song and McPeek 2015). Recent work has shown that neural coherence in a beta frequency band (12-15 Hz) within the PPC reflects functional interactions during coordinated visual behavior. Temporal coupling during coordinated visual behavior recruits coherently-active area LIP neurons that predict reaction time correlations during coordinated movements (Dean et al. 2012). Coherently-active LIP neurons also exhibit changes in response field magnitude when a reach is made with a saccade, unlike other neurons that are not coherently active (Hagan et al. 2012). Response field selectivity of LIP and PRR neurons is phase-dependent across theta, beta and gamma frequency bands (Hawellek et al. 2016). Multiple-area recordings from the PPC during coordinated look-and-reach decisions also reveal patterns of dual coherence, in which individual neurons in area LIP are coherent with beta-frequency band neural activity in both areas (Wong et al. 2016). Dual coherent neurons predict movement choices earlier than other neurons, due to more rapid response field selectivity. Coherent neurons across different effector systems therefore hold distinct spatial information in
comparison to non-coherent neurons and may also support spatial coupling during coordinated movements.

In conclusion, the present study significantly contributes to our understanding of the mechanisms underpinning eye-hand coordinated movements in primates. We provide psychophysical evidence for a spatial interaction among the saccade and the reach systems during coordinated eye-hand movements using a novel behavioral task to parametrically vary spatial interactions between the reach and the saccade systems.
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Figure Captions

Figure 1: The visual-motor tasks. Each trial began with the appearance of a yellow cue in the center of the screen. The monkeys were required to touch and maintain fixation within the yellow square. After a baseline period of 0.5-0.8 s, a peripheral cue appeared for 0.3 s (memory trials), or permanently during the whole delay period (0.7-1.0 s, delay trials). At the end of the instructed delay period, the yellow square turned gray indicating a “go” cue, instructing the movement. A. Delay saccade and touch (DST) task in which a peripheral red cue instructed the monkey to perform a saccade to the target while maintaining touch on the central cue. B. Delayed-reach-and-fixate (DRF) task in which a peripheral green cue instructed the monkey to perform a reach to the target while maintaining fixation on the central cue. C. Delay-reach-and-saccade (DRS) task in which a peripheral yellow cue instructed the monkey to perform a reach in coordination with a saccade to the target. D. Memory-reach-and-fixate (MRF) task in which a peripheral green cue is flashed to instruct a reach to the remembered location of the yellow cue while maintaining fixation on the central cue. E. Memory-reach-and-saccade (MRS) task in which a peripheral yellow cue is flashed to instruct a reach in coordination with a saccade to the remembered target’s location. F. Dissociated-delayed-reach-and-saccade (DRSd) task in which peripheral red and green cues appeared simultaneously and instructed the monkey to saccade to the red cue and reach to the green cue. G. Dissociated-memory-reach-and-saccade (MRSd) task in which a peripheral red and green cue are flashed to instruct the monkey to saccade to the remembered location of the red cue and reach to the remembered location of the green cue.
**Figure 2. Movement accuracy metrics.** A. Scheme depicting the imaginary circle where targets were presented. The gray square depicts the center of the circle with coordinates c_x=0 and c_y=0. The green square represents the reach target (t_x, t_y). The black square represents the reach endpoint for that target (h_x, h_y). B. Scheme depicting the absolute magnitude and angle of the error for a given target and reach endpoint. C. Scheme depicting reaches of different amplitudes for a given target. Positive amplitude errors indicate the reach landed beyond target eccentricity (overshooting). Negative amplitudes indicate the reach landed within target eccentricity (undershooting). D. Scheme depicting the external angle of the effector, defined as the angle formed between the target and the movement endpoint with the target as a center. The effector could be located in a scope of 0-360° in the periphery from the target, regardless of the target’s position within in the circle. Vector difference between the target and the reach endpoint, \( \bar{D} \).

**Figure 3: A. Mean reach endpoints** for monkey 1 (M1, left) and monkey 2 (M2, right) for the four tasks: delay-reach-and-saccade (DRS, yellow); memory-reach-and-saccade (MRS, orange); delay-reach-and-fixate (DRF, light green); and memory-reach-and-fixate (MRF). Black dots depict the hand targets. Endpoints binned every 10 degrees. In both monkeys DRS and MRS trials are closer to the targets than DRF and MRF trials. **B. Reach Error Magnitude.** M1 mean ± s.e.m. (cm): DRS =0.94±0.01; MRS=1.37±0.01; DRF=1.79±0.02; MRF=2.00±0.03 (one way ANOVA, \( p=0.001, F-value=377.11, n=1070 \), Tukey-Krammer corrected, all comparison \( p<0.001 \)). M2 mean ± s.e.m (cm): DRS=0.83 ±0.01; MRS=1.07 ±0.01; DRF=1.09 ±0.02; MRF=1.44 ±0.02 (one way ANOVA, \( p=0.001, F-value=153.33, n=988 \), Tukey-Krammer corrected, all comparisons \( p<0.001 \), except for MRS vs DRS, \( p=0.9074 \)). For all panels, asterisks depict significant differences between DRF and MRS tasks. For the boxplots, diamonds, depict the mean. **C. Reach Angle Error mean, 25th and 75th percentiles.** M1: all means are significantly different from each other (\( p=0.0, F-value=257.09, df=3 \)). MRS vs DRS
are significantly different ($F$-value=138.41, $p=0.0$). M2: means are significantly different from each other ($p=0.0$, $F$-value=96.5, $df=3$), except for MRS vs DRF ($p=0.83$, $F$-value=0.04). D.

**Reach Amplitude mean, 25th and 75th percentiles.** M1: DRS = -0.18 ±0.01 cm, MRS = -0.04 ± 0.02 cm, DRF = 0.33 ± 0.3 cm, MRF= 0.82 ± 0.03 cm, $p=0.001$, $F$-value=206.85; $n=1070$; 

*Tukey-Krammer* corrected, MRS vs DRF $p<0.001$. M2: DRS = -0.06 ± 0.01 cm, MRS = 0.23 ± 0.02 cm, DRF = -0.08 ± 0.02 cm, MRF = -0.29 ± 0.03 cm, $p<0.001$, $F$-value=69.78, $n=988$.

*Tukey-Krammer* corrected, MRS vs DRF $p<0.001$.

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**Figure 4. Reach and saccade error magnitude across all tasks.** Reach error magnitude for the delay-reach-saccade (DRS), memory-reach-saccade (MRS), delay-reach-fixate (DRF), memory reach-fixate (MRF), delay-reach-saccade dissociation (DRSd), and memory-reach-saccade dissociation (MRSd) tasks. A. Reach error magnitude for M1 (mean ± sem (cm)):

DRS=0.94±0.01, MRS=1.37±0.01, DRF=1.79±0.02, MRF=2.00±0.03, DRSd=1.93±0.03, 

MRSd=2.09±0.02. B. Reach error magnitude for M2: DRS = 0.83±0.01, MRS = 1.07±0.01, DRF = 1.09±0.02, MRF = 1.44 ± 0.02, DRSd = 1.63±0.03, MRSd = 1.98±0.02. C. Saccade error magnitude for M1 (mean ± sem (°)): DRS=0.81±0.01, MRS=1.42 ± 0.02, DRSd=0.94 ± 0.01, 

MRSd=1.76 ± 0.01. D. Saccade error magnitude for M2: DRS=1.58 ± 0.02, MRS=1.97 ± 0.02, 

DRSd=1.70 ± 0.03, MRSd=2.05 ± 0.02. For both monkeys, the mean magnitude of the reach error for the coordinated tasks – DRS and MRS - was significantly smaller than for the dissociation tasks - DRSd and MRSd - for all reach directions, respectively (gray asterisks: DRS vs DRSd, M1 $p≤0.001$, M2 $p≤0.001$; black asterisks: MRS vs MRSd, M1 $p≤0.001$; M2 $p≤0.001$). The mean reach error in MRSd task was significantly greater than the coordinated tasks (DRS & MRS) and the reach-and-fixate (DRF & MRF) tasks (M1: $p≤0.001$, $F=219.41$, $df=5$; M2: $p≤0.001$, $F=213.49$, $df=5$, red asterisks). For both monkeys, the mean magnitude of the saccade error for the coordinated tasks – DRS and MRS - was significantly smaller than for
the dissociation tasks - DRSd and MRSd - for all saccade directions, respectively (gray asterisks: DRS vs DRSd, M1, p≤0.001; M2, p≤0.001; black asterisks: MRS vs MRSd M1: p≤0.001; M2:p=0.002).

Figure 5. Reach and saccade error for target locations in memory dissociation trials. A-
B. Mean reach magnitude error. Left panel: M1, mean reach error displays a significant interaction between the saccade and reach target locations (p<=0.001, F=7.04, df=9, n=73 per quadrant). Right panel: M2, presents similar results (p=0.0001, F=3.54, df=9, n=91 per quadrant). C-D. Mean saccade magnitude error. Left panel: M1 mean saccade error displays a significant interaction between the saccade and reach target locations (p<0.001, F=3.19, df=9, n=73). Right panel: M2, presents similar results: mean saccade error displays a significant interaction between the saccade and reach target locations (p=0.001, F=3.1, df=9, n=91 per quadrant).

Figure 6. Correlations between saccade and reach errors for the Memory-reach-and-saccade (MRS) task. For all panels, asterisks depict significant correlations p<0.01. Left panels: M1. Right panels: M2. A. Correlation coefficient per quadrant in the circle for the saccade and reach error magnitude. M1 displayed significant correlations in most quadrants (rho: q1=0.44, q2=-0.08, q3=0.26, q4=0.11, p≤0.05). M2 displayed significant interactions in half of them (rho: q1=0.12, q2=0.10, q3=0.06, q4=-0.006). B. Correlation coefficient per quadrant for the saccade and reach amplitude error. M1 displayed significant correlations in half of the quadrants (rho: q1=0.08, q2=0.07, q3=0.27, q4=0.29, p≤0.05). M2 displayed significant correlations within most of the circle (rho: q1=0.28, q2=0.19, q3=0.05, q4=0.15 p≤0.05). C. Correlation coefficient per quadrant for the saccade and reach angle error. M1 and M2 displayed significant correlations for most quadrants (rho: q1=0.48, q2=0.028, q3=0.25, q4=0.18, p<=0.01; rho: q1=0.23, q2=0.13, q3=0.13, q4=0.009, p<=0.05).
Figure 7. **Reach and gaze external angle histograms.** Left columns (1-2) depict reach and gaze external angles, respectively, for M1. Right columns (3-4) depict the reach and gaze external angles, respectively, for M2. A. First quadrant of the circle (0-90°). B. Second quadrant (90-180°). C. Third quadrant (180-270°). D. Fourth quadrant (270-360°).

Figure 8. **Correlation between the gaze and reach angles with respect to the target for the Memory-reach-and-saccade task (MRS).** A. Correlation coefficients for M1 per quadrant (rho: q1=0.15, q2=-0.40, q3=-0.23, q4=0.42, p≤0.01). B. Same for M2 (rho q1=0.39, q2= 0.23 q3=-0.32 q4=-0.45, p≤0.01). For each panel, asterisks depict significant correlations, p<0.01.

Figure 9: **Correlation between the gaze and reach angles in relation to the target for the dissociated memory-reach-and-saccade task (MRSd).** A-B. Correlation coefficient (rho) for saccade and reach target locations in each quadrant of the circle. For both monkeys the correlation coefficient value varied as a function of the saccade and reach target in the dissociation task. C-D. Value for the t-statistics for the correlation coefficient for saccade and reach target locations in the quadrants of the circle. For both monkeys, statistical significance varied with saccade and reach target locations.

Figure 10: **Saccade and reach endpoints.** Memory dissociation (MRSd) trials when the saccade was performed to either the left (A-B) or right (C-D) side of the visual field. Squares indicate reach endpoints when the saccade and reach were performed to the same (black) or opposing visual hemifield (gray). Dots depict gaze endpoints when the saccade and reach were made to the same (black) or opposing visual hemifield (gray). A. M1 mean reach points show a
slight shift towards the inner side of the circle when the reach-saccade are made to opposing visual hemifield (gray line). Reach error magnitudes did not differ when the saccade and reach were performed to the same (reach error mean ± std: hs=2.54 ± 1.26) or opposite visual hemifield (ho=2.31 ± 1.26, p=0.99). B. M2 presented similar results, except that saccades and reaches directed to the same visual hemifield were not very accurate (hs=2.35 ± 1.21, ho=2.27 ± 0.99, p=0.59). C. M1 mean reach endpoints did not show a clear bias when the saccade was performed to the visual hemifield opposite to the reach. Mean reach accuracy was not significantly different for the same vs opposite reach-saccade hemifield (hs=2.7 ± 1.45, ho=2.82 ± 1.49, p=0.055). D. M2 mean reach endpoints were not biased towards the saccade, when reaches were made to opposite visual hemifield. Mean reach accuracy was not significantly different (hs= 2.64 ± 1.28, ho=2.60 ± 1.30, p=0.78).

Figure 11: Correlation between the saccade and reach amplitude (A, C) or direction (B, D) when movements landed in the same, nearby or far away locations. Gaze shifted to the same location as the reach during the memory-reach-and-saccade task (MRS, dots). Gaze shifted to nearby (MRSd E-H near, diamonds) or far away (MRSd E-H far, squares) reach locations during the dissociated memory-reach-and-saccade task. Black symbols depict significant correlations (p<0.05). Gray symbols depict non-significant correlations (p>0.05). Axes depict the median locations within the circle, e.g. 0°, contains the correlations for all targets locations within 0 ± 30° range for the MRS and MRSd tasks. Same for each MRS opposing far locations, e.g. gaze shifts into a 0 ± 30° range whereas the reach lands in the opposing range 180± 30°. The minimum number of trials per location was 50.
Look-reach accuracy

Table 1.

<table>
<thead>
<tr>
<th>Behavioral Task</th>
<th>Saccade Reaction Times (ms) mean ± std</th>
<th>Reach Reaction Times (ms) mean ± std</th>
<th>Monkey</th>
</tr>
</thead>
<tbody>
<tr>
<td>DRS</td>
<td>281 ± 44</td>
<td>340 ± 45</td>
<td>M1</td>
</tr>
<tr>
<td>DRSd</td>
<td>306 ± 53</td>
<td>313 ± 47</td>
<td>M1</td>
</tr>
<tr>
<td>MRS</td>
<td>304 ± 42</td>
<td>343 ± 46</td>
<td>M1</td>
</tr>
<tr>
<td>MRSd</td>
<td>326 ± 50</td>
<td>328 ± 45</td>
<td>M1</td>
</tr>
<tr>
<td>DRS</td>
<td>287 ± 45</td>
<td>370 ± 50</td>
<td>M2</td>
</tr>
<tr>
<td>DRSd</td>
<td>280 ± 41</td>
<td>357 ± 53</td>
<td>M2</td>
</tr>
<tr>
<td>MRS</td>
<td>317 ± 49</td>
<td>372 ± 49</td>
<td>M2</td>
</tr>
<tr>
<td>MRSd</td>
<td>303 ± 36</td>
<td>353 ± 52</td>
<td>M2</td>
</tr>
</tbody>
</table>

Saccade and reach reaction times for each monkey during saccade and reach tasks.
Figure 1

A: Baseline (0.5-0.8 s)

B: Delay saccade-touch (DST)

C: Delay reach-fixate (DRF)

D: Delay reach-saccade (DRS)

E: Memory reach-fixate (MRF)

F: Memory reach-saccade (MRS)

G: Delay dissociated reach-saccade (DRSd)

H: Memory dissociated reach-saccade (MRSD)

Memory reach-saccade (MRSd)
Figure 2

A. Target location (tx, ty)
   Hand Location (hx, hy)
   Center (cx, cy)

B. Angle Error
   Magnitude Error

C. Amplitude Error
   Amp < 0 (undershoot)
   Amp = 0
   Amp > 0 (overshoot)

D. External Angle Error
   0°
   90°
   180°
   270°
Figure 3

A. X position (°) vs. Y position (°) for M1 and M2.

B. Reach Error Magnitude (cm) for M1 and M2.

C. Reach Angle (°) for M1 and M2.

D. Reach Amplitude Error (cm) for M1 and M2.
Figure 4

M1

A

Hand Error Magnitude (cm)

0.0
1.0
2.0

DRS MRS DRF MRF DRSd MRSd

*
DRS vs DRSd

* MRS vs MRSd

* MRSd vs others

M2

B

Eye Error Magnitude (°)

0.0
1.0
2.0

DRS MRS DRF MRF DRSd MRSd

*

MRSd vs others
Figure 6

**A**

<table>
<thead>
<tr>
<th>Eye-Hand Error (rho)</th>
<th>Correlation</th>
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</thead>
<tbody>
<tr>
<td>0.0</td>
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<tr>
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**B**

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<th>Eye-Hand Amplitude (rho)</th>
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**C**

<table>
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<th>Eye-Hand Angle (rho)</th>
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</thead>
<tbody>
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</tr>
<tr>
<td>0.1</td>
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<tr>
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<td>0.4</td>
</tr>
<tr>
<td>0.4</td>
<td>0.5</td>
</tr>
</tbody>
</table>

**Legend**

- *: Significant at p < 0.05

**Eye-Hand Target Location (°)**

- 0-90
- 90-180
- 180-270
- 270-360
Figure 7

<table>
<thead>
<tr>
<th>M1</th>
<th>M2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hand Angle</td>
<td>Hand Angle</td>
</tr>
<tr>
<td>Eye Angle</td>
<td>Eye Angle</td>
</tr>
</tbody>
</table>

A

B

C

D
Figure 8

A

M1

Correlation external Angle hand-eye (ρ)

0-90 90-180 180-270 270-360

* * * *

Eye-Hand Target Location (°)

B

M2

Correlation external Angle hand-eye (ρ)

0-90 90-180 180-270 270-360

* * * *

Eye-Hand Target Location (°)
Figure 9

A. Correlation External Angle Hand-Eye (\(\rho\))

B. Correlation External Angle Hand-Eye (\(\rho\))

C. Correlation External Angle Hand-Eye (\(\rho\))

D. Correlation External Angle Hand-Eye (\(\rho\))

M1

M2

Eye Target Location (°)

Hand Target Location (°)

270-360
180-270
90-180
0-90
270-360
180-270
90-180
0-90

-3 -2 -1 0 1 2 3

-0.3 -0.2 -0.1 0 0.1 0.2

t-stats

Correlation External Angle Hand-Eye (\(\rho\))

0.05 0.1 0.15 0.2 0.25
Figure 10

MRS saccade left

A

M1

ho = 2.31 ± 1.26
hs = 2.54 ± 1.26
p = 0.99

B

M2

ho = 2.27 ± 0.99
hs = 2.35 ± 2.11
p = 0.59

C

MRS saccade right

ho = 2.82 ± 1.49
hs = 2.70 ± 1.45
p = 0.05

D

ho = 2.60 ± 1.30
hs = 2.64 ± 1.28
p = 0.78
Figure 11

A  Correlation Amplitude Saccade-Reach

B  Correlation Direction Saccade-Reach

C

D

M1

M2

p<0.05

p>0.05