

# Movement order and saccade direction affect a common measure of eye-hand coordination in bimanual reaching

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**Mooshagian E, Wang C, Ferdoash A, Snyder LH.** Movement order and saccade direction affect a common measure of eye-hand coordination in bimanual reaching. *J Neurophysiol* 112: 730–739, 2014. First published May 21, 2014; doi:10.1152/jn.00234.2014.— Studies of visually guided unimanual reaching have established that a saccade usually precedes each reach and that the reaction times (RTs) for the saccade and reach are highly correlated. The correlation of eye and hand RT is commonly taken as a measure of eye-hand coordination and is thought to assist visuospatial guidance of the hand. We asked what happens during a bimanual reach task. As with a unimanual reach, a saccade was executed first. Although latencies were fastest on unimanual trials, eye and hand RT correlation was identical whether just one or both hands reached to a single target. The average correlation was significantly reduced, however, when each hand reached simultaneously to a different target. We considered three factors that might explain the drop. We found that correlation strength depended on which hand reached first and on which hand reached to the same target as the saccade. Surprisingly, these two factors were largely independent, and the identity of the hand, left or right, had little effect. Eye-hand correlation was similar to that seen with unimanual reaching only when the hand that moved to the same target as the saccade was also the first hand to move. Thus both timing as well as spatial pattern are important in determining eye-hand coordination.

monkey; reaction time; visually guided; visuomotor; hand movement

MANUAL ACTIONS RANGING FROM the mundane, like reaching for a glass of water, to the highly skilled, like swinging a bat to hit a baseball pitched at 95 mph, rely on the spatiotemporal coordination of eyes and hand(s) for accuracy. Studies of visually guided arm and hand movements have shown that saccade and reach reaction times (RT) are positively correlated on a trial-by-trial basis (Herman et al. 1981). The eye movements that accompany reaches are surprisingly stereotyped, with subjects usually looking at the reach target before moving the hand towards it (Gielen et al. 1984; Fischer and Rogal 1986; Abrams et al. 1990). This assists in the visuospatial guidance of the hand and improves reach accuracy (Neggers and Bekkering 1999). These observations have led to the extensive use of the correlation between saccade RT and reach RT as a measure of eye-hand coordination (Fisk and Goodale 1985; Snyder et al. 2002).

The idea that coordination serves to help guide arm movements suggests that correlation might diminish if the saccade was not directed to the same target as the arm movement. Under single-arm reaching conditions this seldom happens. Others have probed the coordination by training subjects to vary the timing of the saccade relative to the reach (Dean et al.

2011) or to suppress the reach entirely (Mirabella et al. 2009). We studied this issue by adding a second arm movement. This increases behavioral variability while remaining ecologically relevant. Many everyday actions require the use of both hands in concert with the eyes. Consider pouring water from a pitcher. One hand reaches for the pitcher and the other for the glass. Since eye movements cannot be made simultaneously to both targets (the pitcher and the glass), we can measure the relative contributions of spatial saccade-reach congruence (i.e., does correlation depend on the eyes moving to the same target as the hand), temporal order (i.e., does correlation depend on whether the hand moves first or second), and handedness (i.e., is the correlation always greater for one particular hand) on eye-hand coordination. Although bimanual coordination has been studied extensively, few studies have tracked eye movements and none have reported the pattern of eye-hand correlation during bimanual movements (Müri et al. 1999; Bruyn and Mason 2009; Srinivasan and Martin 2010).

In the current study, we examine how bimanual reaching affects the temporal aspects of eye-hand coordination. We found that either hand may move to where the eyes have moved and that either hand may move first. Furthermore, how well correlated each hand's RT is with the saccade RT depends on both which hand moves first and also on which hand moves to the target of the saccade. The fact that which hand moves first is a significant factor in determining eye-hand correlation implies that eye-hand coordination is not solely concerned with guidance of the hand to a target but instead reflects a more general motor strategy.

## METHODS

All procedures conformed to the *Guide for the Care and Use of Laboratory Animals* and were approved by the Washington University Institutional Animal Care and Use Committee. Two male rhesus macaques (*Macaca mulatta*; *M1* and *M2*) participated in the study. *M1* was previously trained to make unimanual reaches. *M2* was previously trained to perform a saccade task. Neither animal had previous experience with bimanual reaches, but both were trained extensively on the current experimental paradigm before beginning data collection.

**Task.** Animals first fixated on a circular white stimulus ( $1.5 \times 1.5^\circ$ ) centered on the screen in front of them. Left and right paws touched "home" pads situated at waist height and 20 cm in front of each shoulder. After 500 ms of holding the initial eye ( $\pm 3^\circ$ ) and hand positions, either one or two peripheral target(s) ( $5 \times 5^\circ$ ) appeared on the screen. When two targets appeared, they were at opposite locations relative to the fixation point, e.g., left/right or up/down (see below). After an additional 1,250 to 1,750 ms, the central eye fixation target shrank in size to a single pixel, cueing the animal to move to the peripheral target(s) in accordance with a code conveyed by target

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color. A green target instructed a left forelimb reach, a red target instructed a right forelimb reach, a blue target instructed a combined reach with both arms, and a white target instructed a saccade (no reach). Trials could be unimanual or bimanual. Bimanual trials could have a single target ("bimanual together") or two targets separated by 180° ("bimanual apart"). All trial types were interleaved. On saccade and unimanual reach trials, the unused hand(s) were required to remain on the home button(s) throughout the trial. On reach trials, eye movements were unconstrained once the go cue appeared. On bimanual trials, the left and right paws were required to hit their target(s) within 500 ms of one another. Spatial tolerances were  $\pm 3^\circ$  for reaches and  $\pm 2^\circ$  for saccades. When an error occurred (a failure to achieve or maintain fixation or to touch the home buttons throughout the delay period or a movement that did not achieve the required spatial tolerance), the trial was aborted and a short (1,500 ms) timeout ensued. Aborted trials were excluded from further analyses. Successful trials were rewarded with a drop of water or juice. Data were collected during 67 and 53 sessions in *M1* and *M2*, respectively.

**Apparatus.** Head-fixed animals sat in a custom-designed monkey chair (Crist Instruments, Hagerstown, MD) with a fully open front to allow unimpaired reaching movements. Visual stimuli were back-projected by an LCD projector onto a translucent plexiglass screen mounted vertically, 40 cm in front of the animal.

Eye position was monitored using the 120-Hz ISCAN eye-tracking laboratory (ETL-400). Touches were monitored every 2 ms using capacitive sensors, mounted at the home pads and behind the plexiglass projection screen. Touch positions on the screen were organized in a 3 × 3 grid centered on the fixation point. Plexiglass dividers were mounted on the front of the screen at the middle of each target location. The animals were trained to reach with the left paw to the left side of the divider and with the right paw to the right side of the divider. A capacitive sensor was placed to either side of each target location, such that the left and right paws activated unique sensors even when both paws reached to the same target. Animals were monitored in the testing room at all times using an infrared camera equipped with an infrared illuminator.

**Data analysis.** For all the analyses, only correct trials were considered and RTs more or less than 3 SD from the mean for each condition were excluded. For significance testing, alpha was set at 0.05.

For the analyses of overall performance, separate one-way ANOVA models were fit for each dependent measure (saccade RT, reach RT, and movement duration) with reach condition (unimanual, bimanual together, and bimanual apart) as the independent factor. Post hoc means comparisons were performed with Tukey's honestly significant difference test.

For the correlation analyses, coefficient values (Pearson *r*) were calculated separately for each arm in each target direction for each experimental session of each animal. Mean correlation coefficient values were computed by applying the Fisher *r*-to-*z* transform (Fisher 1915) on individual correlation coefficients, computing the mean of the *z*-transformed values, and finally, converting the mean *z*-transformed value back to a mean correlation coefficient.

For bimanual apart reaches, we asked if the strength of eye-hand correlation varies for the right vs. left hand, spatial congruence of the saccade and reach (did the hand move to the same target as the eyes), and temporal order of reaching (which arm moved first). For the effect of hand identity, we measured the mean eye-hand RT correlation for each hand separately (in the bimanual together task) and assigned the hand with the larger and smaller mean correlation as "dominant" and "nondominant," respectively. For saccade-reach congruence, we identified the hand that moved towards the target of the first saccade. For the temporal order, we identified the hand that began to move first. As a result, each bimanual reach trial to two different targets had a dominant and nondominant hand movement, a congruent and incongruent movement, and a first and second movement. Based on these factors, each reach was sorted into one of

eight categories, e.g., the dominant hand moves first and makes an incongruent movement, while the nondominant hand moves second and makes a congruent movement. For each session and target location, we computed the mean eye-hand RT correlation across all movements in each category.

In particular, we submitted the Fisher *r*-to-*z* transformed correlation coefficients to repeated-measures ANOVA with the within-subjects factors of Dominant Hand (dominant, nondominant), Congruence (reach direction congruent with saccade direction, reach direction incongruent with saccade direction), and Go First (arm first-to-move, arm second-to-move). We hypothesized that coordination, assayed by the degree of correlation between eye and hand RT, would be better for one particular (dominant) hand than the other, that coordination would be greater for the hand that moves to the same target as the eyes, and that coordination would be greater for the hand that moves first. We expected that these three factors (dominant hand, saccade-reach congruence, and temporal precedence) would be largely congruent, that in most cases the hand that moves first would move towards the target of the saccade, and that the same hand would move first across most trials.

## RESULTS

On interleaved trials, animals were instructed to make a saccade, a unimanual reach with the left arm, a unimanual reach with the right arm, a bimanual reach to a single target, or a bimanual reach to two different targets on opposite sides of the fovea. Each arm started from a home position near the waist. Gaze was initially at a fixation point straight in front of the animal. Targets appeared after the eyes and arms acquired their initial positions, but animals were not allowed to move either the arms or the eyes until the fixation point disappeared,  $1.50 \pm 0.25$  s after target appearance. Once the fixation point disappeared, animals were required to bring the hand(s) to the target(s) on reach trials. The eyes were unconstrained, except on saccade trials.

**Overall performance.** Although the eyes were unconstrained on reach trials, animals always made a saccade to the target. Typically, animals saccaded first to one target and then to the other. This report concerns only the first saccade and the two hand movements. Figure 1 illustrates eye-hand coordination for two example movement directions in one animal (*M2*). Movements are indicated by colored lines. Eye movements are in red, right-hand reaches are in blue, and left-hand reaches are in green. In Fig. 1, *top to bottom*, a unimanual right-hand reach, bimanual together (single target) reach, and two types of bimanual apart (two targets) reaches are shown. The average RTs, defined as the time from the go cue to the start of the movement, are indicated by the distance from the *left* side of the plot to the start of each movement line. Movement times, defined as the time from the start of the movement to the acquisition of the target, are indicated by the horizontal extent of the colored lines. Figure 1, *top*, is for a target presented below fixation at the 6-o'clock position. For this target location, when the monkey was cued to reach with the right arm only (1st row), it first moved its eyes and landed on the target (red line) before initiating a reach the reach (blue line). When both arms were required to reach towards the same target (2nd row, bimanual together), the pattern was similar: first the eyes moved to the target and then the two arms left the home position and landed on the target approximately synchronously. When each arm was required to reach to a different target (bimanual apart, right hand to below fixation at the

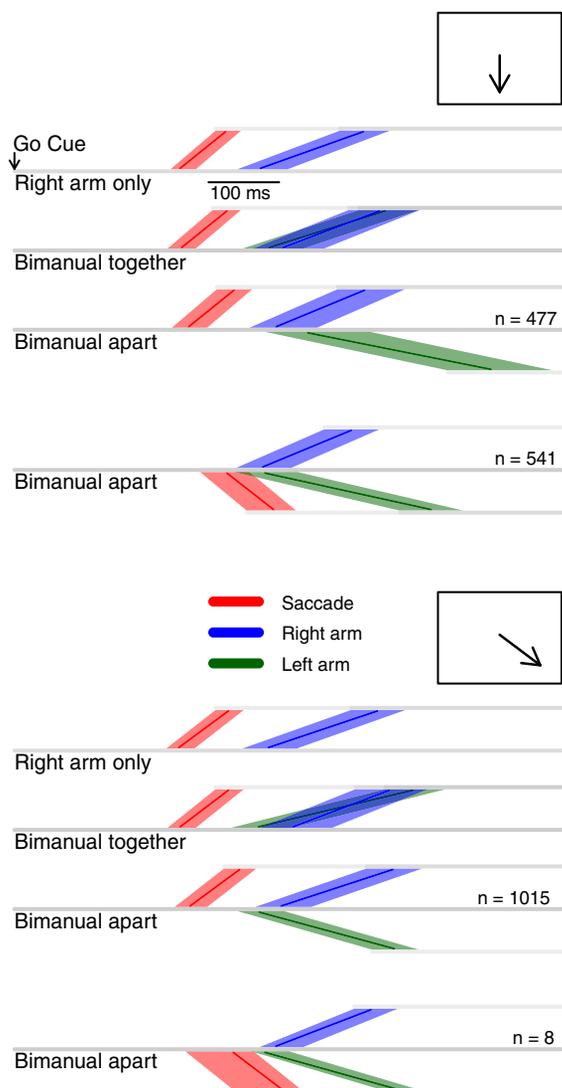


Fig. 1. Example reaction time (RT) and movement duration data for 1 monkey (*M2*). The *top* and *bottom* sets of traces each show data for one primary target direction. Each row shows a different reach type. Time is shown on the *x*-axis, increasing from *left* to *right*. The red traces represent saccades and the green, and blue traces represent left and right hand reaches, respectively. Traces for the 2 target conditions (bimanual apart) are split into 2 rows. On some trials, the saccade went to the same target as in the single target conditions (3rd row). On others, the saccade went to the opposite target (4th row). Traces are aligned on the go cue (*far left*). Movement start times are indicated by where the colored traces deflect from the lower horizontal gray line, and end times are indicated by where the colored traces meet the upper horizontal gray line. Movement time is shown by the horizontal extent of the colored trace. A shallower slope (longer line) indicates longer movement time. The dark lines within the center of each colored trace indicate the median times and the surrounding color covers values from the 15th to the 85th percentile. Values to the right indicate the number of trials for that condition. The graphic at the *top right* of each panel indicates the target direction relative to the central fixation for the single target conditions. In the bimanual apart condition the target for the left arm was located 180° from the indicated (right arm target) direction.

6-o'clock position and the left hand above fixation at the 12-o'clock position, 3rd and 4th rows), the animal made one of two different saccades. In about half of the trials (477 out of 1,018), the eyes moved to the same target as the right hand (3rd row), and in the other 541 trials, the eyes moved to the same target as the left hand (4th row).

For other target locations, the animal behaved in a more stereotyped manner (Fig. 1, *bottom*). The first two lines show unimanual right and bimanual together movements down and to the right. Behavior is similar to what was shown in Fig. 1, *top*. On bimanual apart trials, however, the animal nearly always moved his eyes to the same target as the right hand (1,015 out of 1,023 trials) and only rarely to the target of the left hand.

*M1* made substantial numbers of saccades (at least 26% to each target for two bimanual apart conditions and made saccades primarily or solely to just one target for the other six. *M2* displayed more variability, with saccades to the two targets ranging from 100/0% (completely stereotyped) to 53/47% (a nearly balanced distribution between the two options), with a mean ratio of 52/48%.

*Eye-hand coordination.* Eye and arm RTs are correlated during unimanual reaching (Herman et al. 1981; Gielen et al. 1984; Fisk and Goodale 1985; Fischer and Rogal 1986; Sailer et al. 2000; Snyder et al. 2002; Dean et al. 2011). This correlation has been taken as a measure of eye-hand coordination (Herman et al. 1981; Lünenburger et al. 2000; Snyder et al. 2002). We asked how this measure is affected by bimanual reaching. Figure 2 shows RT data for right arm movements and saccades to the 3-o'clock target in one animal (*M1*). RTs are highly positively correlated for unimanual reaches ( $r = 0.63$ ,  $P < 0.001$ ), less so for bimanual reaches together ( $r = 0.55$ ,  $P < 0.001$ ), and even less so for bimanual reaches apart ( $r = 0.43$ ,  $P < 0.001$ ).

Figure 3 shows eye-hand correlations averaged over both arms for all target directions and sessions for each animal under different conditions. As expected, correlation was strong for unimanual reaches (Pearson  $r = 0.74$  in *M1* and 0.73 in *M2*, both  $P < 0.001$ ; Fig. 3, 1st bar). Correlation was only slightly reduced when both arms moved to a single target [bimanual together:  $r = 0.73$  in *M1* and 0.70 in *M2*, not significantly different than unimanual in either animal ( $P > 0.2$ ); Fig. 3, 2nd bar; hand RT values computed using the mean of the left- and right-hand RTs]. In contrast, correlation was sharply reduced when each arm moved to its own target (bimanual apart:  $r = 0.60$  in *M1* and 0.53 in *M2*, both  $P < 0.001$ ; Fig. 3, 3rd bar). The remainder of this section is devoted to addressing what factors are responsible for reduced eye-hand correlation during bimanual apart reaching.

Eye-hand coordination is typically measured under unimanual reaching conditions. With unimanual reaching, one might assume that eye and hand RTs are coupled because the two effectors are directed to the same target. This assumption cannot be easily tested because the movement patterns are so stereotyped; the eye and hand essentially always move to the same target. With bimanual reaching to different targets, the two eyes move together in only one direction at a time. In our experiments, with targets on opposite sides of the fovea, we observed that on every trial the first saccade was directed to either one or the other target. Often a second saccade followed, directed towards the target not foveated by the first saccade. These second saccades are beyond the scope of the current report. As previously noted, the first saccade was not always directed to the same target on each trial (Fig. 1). Thus under the bimanual apart condition, it becomes possible to explore which factors contribute to the coupling of the eyes and arm. We considered three factors in particular: 1) correlation might be

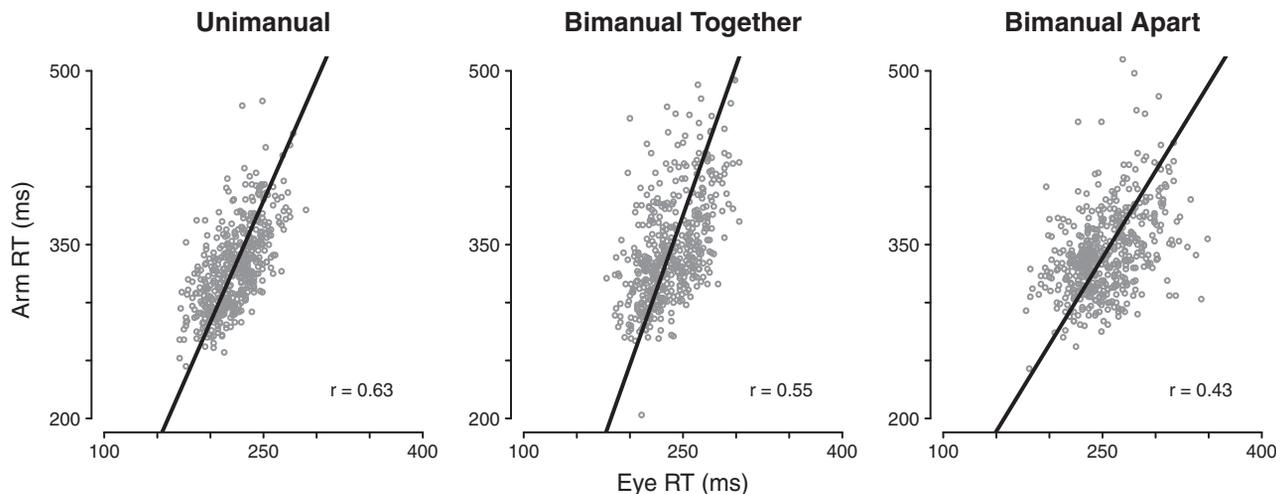


Fig. 2. Scatterplots depicting the correlation between hand RT and eye RT for unimanual right arm reaches (left), bimanual reaches directed together to the same target (middle), and bimanual reaches directed to 2 different targets (right), 180° apart from one another. In each case, the right hand moves to a target at the 3-o'clock position. Each dot represents the RT for a single trial from monkey M1.

stronger for one (dominant) hand compared with the other; 2) correlation might depend on a spatial relationship: it might be stronger for the hand that moves to the same target as the endpoint of the first saccade, compared with the hand that moves to the other target (Congruence); and 3) correlation might depend on a temporal factor: correlation might be stronger for the hand that is the first to move (Go First). One, two, or all three of these factors might influence eye-hand correlation.

We began by determining whether these three factors (Dominant Hand, Congruence, and Go First) were represented independently in our data. It could be, for example, that animals always or almost always lead with the same hand and that the first saccade is always or almost always directed to the target of the dominant hand. One could also imagine the reverse: the first saccade could always or almost always be directed to the

target of the nondominant hand. Instead, we found that all three factors were nearly independent. We first defined a dominant hand for each animal. We based this on which hand showed higher correlation with the eyes during bimanual together reaches. Note that any other definition (e.g., the hand with the faster mean RT in bimanual together trials) can at most only swap the dominant/nondominant hand assignment, which would change the sign of the effect but not its magnitude or significance. For M1, the right hand had the higher correlation ( $r = 0.75$  for bimanual together trials, compared with 0.70 for the left hand; difference  $P < 0.001$ ). This was also the case in unimanual trials, with  $r = 0.72$  for the left hand and 0.75 for the right. The eyes moved to the target of the dominant hand in 54% of bimanual apart trials, and the dominant hand moved first 62% of the time. The hand that moved first was directed to the target of the saccade in 34% of trials (chance would be 50%; Table 1). For M2, the left hand was dominant ( $r = 0.74$  for bimanual reach trials, compared with 0.66 for the right hand; difference of  $P < 0.001$ ). There was no hand difference in unimanual trials, with  $r = 0.73$  for the left and right hand. The eyes moved to the target of the dominant hand in 46% of bimanual apart trials, and the dominant hand moved first 69% of the time. The hand that moved first was directed to the target of the saccade in 68% of trials (Table 1). Although most of these values are significantly different from the chance level of 50%, none approaches either 0 or 100% in either animal. When

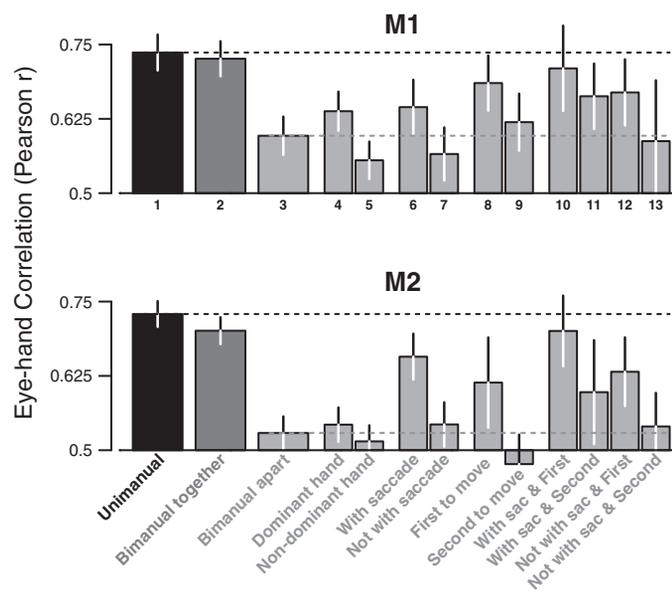


Fig. 3. Eye-hand correlations for each reach type in M1 (top) and M2 (bottom). The black dashed line indicates the eye-hand correlation for unimanual reaches. The gray dashed line indicates the eye-hand correlation for bimanual apart reaches when all trials are considered. Error bars indicate SE.

Table 1. Percentage of trials that each hand moved first and moved with the eyes

Animal/Saccade Direction	First Hand to Move		Matched
	Left	Right	
M1			
Left	9%	37%	34%
Right	29%	25%	
M2			
Left	44%	5%	68%
Right	27%	24%	

“Matched” shows the percentage of time that the hand that moved first also was the hand that moved in the same direction as the first saccade.

averaged across both animals, the hand that moved first was the dominant hand on about half of trials, the hand that moved to the same target as the eye was the dominant hand on about half of trials, and the hand that moved first was also the hand that moved to the same target as the eye on about half of trials. Thus the three factors, Dominant Hand, Congruence, and Go First, are all represented substantially independently in our data. Note that this result is itself independent of which hand is defined as dominant.

Next, we tested the contribution of each factor (Dominant Hand, Congruence, and Go First) using repeated-measures ANOVA on the mean Fisher  $r$ -to- $z$  transformed correlation coefficients (Fig. 3). We used mean values for each of the eight possible combinations of the three factors (e.g., the mean eye-hand RT correlation over all instances in which dominant hand moved to the same target as the saccade and was the first hand to move) so that our design was completely balanced. Subject ( $M1$  or  $M2$ ) was treated as a random factor. Both the  $t$ -test and ANOVA require that data values be normally distributed. Correlation coefficients are bounded at  $-1$  and  $+1$  and, therefore, are not normally distributed. We normalized the correlation coefficients by applying the Fisher  $r$ -to- $z$  transformation before any statistical testing, which maps correlation coefficients into values ranging from minus to plus infinity (Fisher 1915). Figure 3 and the text report values that have been reverse transformed back to correlation coefficients, but the beta values, representing the strength of each individual factor, are based on the transformed values. The practical effect of this transformation is that, while both the beta weightings and correlation coefficients reported below are accurate, the beta weightings do not sum to the (untransformed) correlation coefficients.

There was no main effect of Dominant Hand ( $F < 1$ ). The correlation of the eyes with the dominant hand was numerically higher than with the nondominant hand ( $r = 0.64$  vs.  $0.56$  in  $M1$ ,  $0.54$  vs.  $0.52$  in  $M2$ ; Fig. 3, 4th and 5th bars). The difference was significant in  $M1$  ( $P < 0.05$ ) but not  $M2$  ( $P > 0.2$ ).

There was a significant main effect of Congruence [ $F(1,8) = 13.48$ ,  $P = 0.006$ ,  $\beta = 0.11$ ]. Eye-hand correlations were larger for congruent movements, that is, reaches toward the saccade target compared with reaches away from the saccade target ( $r = 0.64$  vs.  $0.57$  in  $M1$  and  $0.59$  vs.  $0.47$  in  $M2$ ; Fig. 3, 6th and 7th bars). The correlation of congruent movements by themselves was significantly greater than the overall bimanual apart correlation (both  $P < 0.01$ ) but significantly less than the unimanual correlation (both  $P < 0.05$ ). There was no significant interaction between Congruence and Dominant Hand ( $F < 1$ ).

Perhaps surprisingly, there was also a significant main effect of Go First, with a beta weight more than twice as large as that of Congruence [ $F(1,8) = 31.17$ ,  $P < 0.001$ ,  $\beta = 0.28$ ]. [There was also a significant interaction between Go First and Dominant Hand,  $F(1,8) = 24.31$ ,  $P = 0.001$ .] The correlation between the eyes and the hand that moved first was greater than the correlation between the eyes and the hand that moved second ( $r = 0.64$  vs.  $0.60$  in  $M1$  and  $0.60$  vs.  $0.47$  in  $M2$ ; Fig. 3, 8th and 9th bars). The eye-hand correlation for the hand that moved first was greater than the overall bimanual apart correlation (both  $P < 0.001$ ) but less than the unimanual correlation ( $M1$ ,  $P < 0.001$ ;  $M2$ ,  $P = 0.001$ ).

As can be seen in Fig. 3, *top* and *bottom*, similar results were observed in each animal. In particular, bimanual apart correlation is substantially lower than unimanual or bimanual together correlation; hand identity has little effect on correlation (Fig. 3, 4th and 5th bars), while correlation is higher for the hand moving to the target of the saccade (Fig. 3, 6th and 7th bars) and for the hand that moves first (Fig. 3, 8th and 9th bars); and taking into account both saccade-reach congruence and movement order accounts for most of the drop in the correlation seen on bimanual apart compared with unimanual trials. In fact, the values for reaches satisfying both criteria (move first and move to the saccade target) were not significantly different from the values for unimanual correlation (both  $P > 0.05$ ; Fig. 3, 10th bar vs. 1st bar).

There was no significant interaction of Go First  $\times$  Congruence ( $F < 1$ ). The absence of a significant interaction means that these factors had independent effects on eye-hand correlation. This can be appreciated by comparing coordination when just one criterion was satisfied to when neither or both criteria were satisfied. For reaches that were initiated first but not directed to the saccade target, correlations were  $0.67$  and  $0.56$  for  $M1$  and  $M2$ , respectively (Fig. 3, 12th bar). For reaches that were directed to the saccade target but not initiated first, correlations were  $0.64$  and  $0.56$  ( $M1$  and  $M2$ ; Fig. 3, 11th bar). These values are intermediate between the values for reaches satisfying neither criterion ( $0.55$  and  $0.47$ ; Fig. 3, 13th bar) and the values for reaches satisfying both criteria ( $0.69$  and  $0.65$ ;  $M1$  and  $M2$ ).

We did not expect to find a strong influence of which hand moves first on the eye-hand RT correlation. We considered whether unexpected patterns of movement might contribute to this result. On 7% of trials, the left- and right-hand movements were completely separated in time, with one hand completing its reach before the other hand started moving. Such fractionated responses might be better described as two sequential unimanual reaching movements rather than a single bimanual movement. When fractionated trials were excluded from the analysis, the results remained largely the same. There was a significant main effect of Go First [ $F(1,8) = 12.95$ ,  $P = 0.007$ ], a trend towards an effect of Congruence [ $F(1,8) = 4.51$ ,  $P = 0.07$ ], and an interaction of Go First  $\times$  Dominant Hand [ $F(1,8) = 29.54$ ,  $P = 0.002$ ]. In a third analysis, we included only those trials in which the two hands began their movements within 200 ms of one another. Once again, the results were unchanged. There were main effects of Go First [ $F(1,8) = 29.55$ ,  $P = 0.006$ ] and Congruence [ $F(1,8) = 11.92$ ,  $P = 0.009$ ], as well as an interaction of Go First  $\times$  Dominant Hand [ $F(1, 8) = 22.21$ ,  $P = 0.002$ ].

*Saccade and reach times.* Cumulative distributions for saccade and reach RTs across all target directions, reach conditions, and animals are shown in Fig. 4. Means, SD, and comparisons among reach conditions are reported for each animal separately in Table 2. Saccades led reaches in all conditions, and in most cases, the saccade was completed before the reach was initiated. Saccades on unimanual reach trials had the fastest latencies. Saccade latencies on bimanual together trials were slower, and saccade latencies on bimanual apart trials were slowest [one-way ANOVA,  $M1$ :  $F(2,24643) = 962$ ,  $P < 0.001$ ;  $M2$ :  $F(2,50218) = 484$ ,  $P < 0.001$ ; Fig. 4, *left traces*; Table 1]. Reach latencies were faster on unimanual than bimanual trials for both animals. For  $M1$ , reach latencies for bimanual together were faster than for biman-

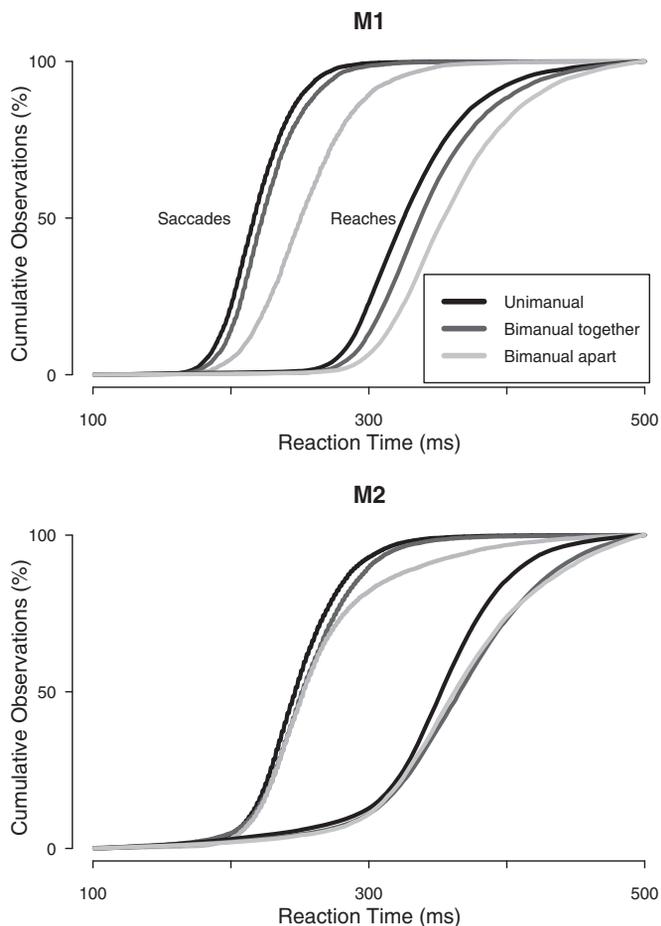


Fig. 4. Cumulative distributions of RTs for saccades (*left*) and reaches (*right*) for each animal. The *x*-axis shows time from target onset. The *y*-axis shows the cumulative percentage of trials in which the saccade or reaches had been initiated. Coordinated reaches were associated with longer saccade and reach latencies in both animals (rightward shift of dark and light gray traces relative to the black curve in each set of traces).

ual reaches apart [one-way ANOVA, *M1*:  $F(2,24650) = 784, P < 0.001$ ], whereas for *M2*, there was no difference in reach latencies between bimanual together and bimanual apart trials [*M2*:  $F(2,50432) = 369, P < 0.001$ ; Fig. 4, *right traces*; Table 2].

Unlike reach latency, there was no consistent relationship between the type of reach and reach duration (Fig. 5; Table 2). For

*M1*, unimanual reach durations were faster than bimanual together reaches, which were in turn faster than bimanual apart reaches [ $F(2,23951) = 164, P < 0.001$ ]. However, *M2* showed similar reach durations under unimanual and bimanual apart conditions and the fastest durations for bimanual together reaches [ $F(2,50370) = 193, P < 0.001$ ]. For *M1*, saccade durations were faster for unimanual reaches than bimanual together reaches, which were in turn faster than saccade durations for bimanual apart reaches [ $F(2,24647) = 19.4, P < 0.001$ ]. However, for *M2*, saccade durations did not differ for unimanual and bimanual together reaches and were instead fastest during bimanual apart reaches [ $F(2,50283) = 172, P < 0.001$ ; Table 2].

Next we checked for relationships between RT and movement duration. At the level of individual trials, movement duration might be independent of, proportional to, or inversely proportional to initial RT. Across different movement configurations, each hand may need to travel a different distance due to different starting positions, different end positions, or both. To land synchronously, movements that travel further and therefore are associated with a longer movement time might be initiated sooner, holding total travel time constant and producing an inverse relationship. Alternatively, a proportional relationship might arise if nonspecific factors have similar effects on both reaction and movement time. We found inverse and proportional relationships within different reach conditions (e.g., bimanual together trials to upward targets), but combining across directions yielded modest but significant positive correlations in each animal ( $r = 0.12$ – $0.14$ , all  $P < 0.001$ ).

**Bimanual coordination.** There was a significant correlation between the RTs of the left and right hands in both monkeys (Fig. 6). For *M1*, the correlation was significantly larger for bimanual together than apart movements (Pearson  $r = 0.78$  vs.  $0.74$ , respectively;  $P < 0.05$ , Fisher  $z$ -transformed  $r$ -test). For *M2*, the values were not significantly different from one another ( $r = 0.61$  and  $0.63$ , respectively,  $P > 0.05$ ).

Human bimanual coordination studies show that RTs for reaches to two different targets are faster when the reaches have symmetric trajectories than when they have asymmetric trajectories (Diedrichsen et al. 2001, 2006; Heuer and Klein 2006). We compared RTs in monkeys for two symmetric trajectories (right hand to the right and left hand to the left, and vice versa) and two asymmetric trajectories (right hand up and left hand down, and vice versa). Similar to humans, the

Table 2. Means, SD, and means comparisons for saccade reaction time, reach reaction time, and movement duration

Measure/Animal	Reach Condition		
	Unimanual	Bimanual Together	Bimanual Apart
Saccade RT			
<i>M1</i>	203 ± 66 (8,409)	210 ± 66 (8,317)	245 ± 62 (7,927)
<i>M2</i>	244 ± 45 (18,100)	248 ± 50 (16,896)	262 ± 65 (15,409)
Saccade duration			
<i>M1</i>	67 ± 14 (8,409)	68 ± 14 (8,317)	69 ± 14 (7,927)
<i>M2</i>	68 ± 6 (18,100)	68 ± 6 (16,896)	67 ± 9 (15,409)
Reach RT			
<i>M1</i>	332 ± 45 (8,409)	345 ± 46 (8,317)	360 ± 47 (7,927)
<i>M2</i>	349 ± 57 (18,100)	364 ± 62 (16,896)	364 ± 63 (15,409)
Reach duration			
<i>M1</i>	168 ± 34 (8,409)	174 ± 35 (8,317)	180 ± 57 (7,927)
<i>M2</i>	208 ± 50 (18,100)	197 ± 49 (16,896)	207 ± 68 (15,409)

Values are means (±SD; *n*) in ms; RT, reaction time; < and > indicate significant difference (Tukey's honestly significant difference) at  $P < 0.05$ .

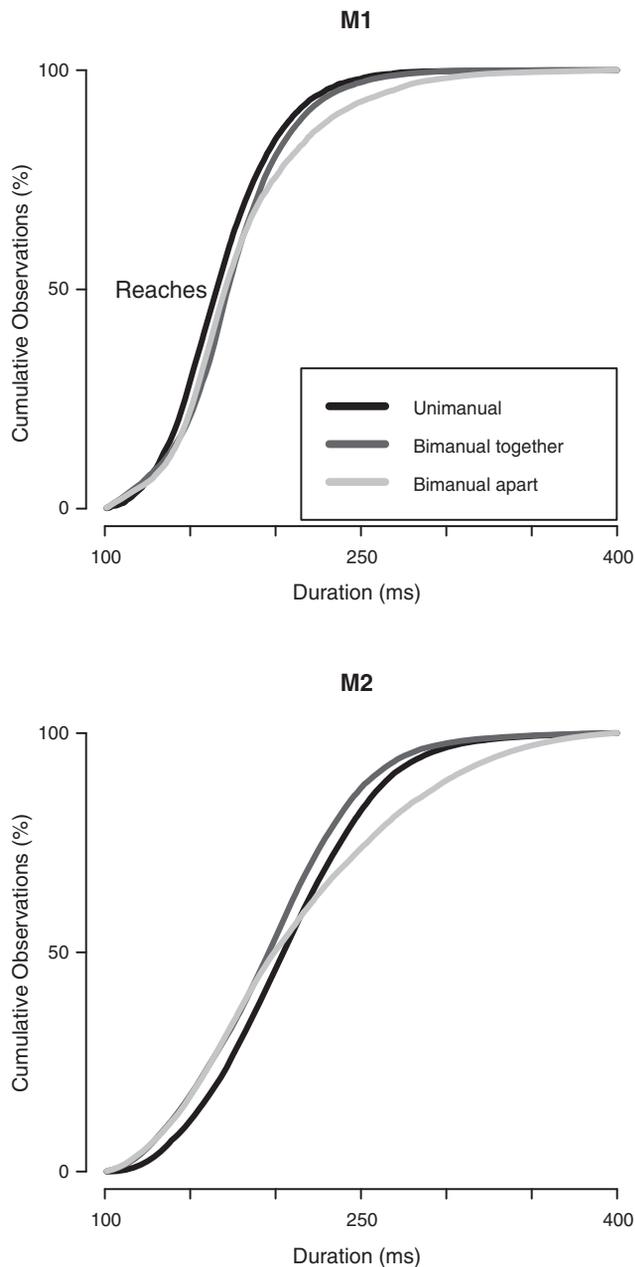


Fig. 5. Cumulative distributions of movement duration for reaches for each animal. The x-axis shows time from reach onset (RT) to reach offset. The y-axis shows the cumulative percentage of trials in which the saccade or reaches had been completed.

monkeys initiated symmetric movements more quickly than asymmetric movements, with RT differences of 6 and 13 ms, in *M1* and *M2*, respectively [one-way ANOVA; *M1*:  $F(1,6958) = 19.7$ ,  $P < 0.001$ ; *M2*:  $F(1,17573) = 82.7$ ,  $P < 0.001$ ].

## DISCUSSION

We examined hand-hand and eye-hand coordination during unimanual and bimanual reaching. Our most important finding is that eye-hand RT correlations are similar when just one or both hands move to a single target but significantly reduced when each hand moves to a different target. This reduction is accounted for by two factors. As one might have expected, coordination is stronger when the eyes and hand move to the

same target (spatial congruence). Unexpectedly, coordination is also stronger for the hand that moves first, and this effect is largely independent of spatial congruence: the hand that moves to the target is just as likely to move first as it is to move second. The fact that correlation depends not just on spatial congruence but also on movement order suggests that eye-hand coordination is involved with more than just optimizing the visual guidance of the reach.

**Hand-eye-hand coordination.** Eye and hand movements during a unimanual reach are highly stereotyped. Previous studies in humans and monkeys have shown that eye movements reliably lead hand movements and that eye and hand RTs are highly correlated on a trial-by-trial basis (Fischer and Rogal 1986). This stereotyped relationship is usually viewed as linked to visuospatial guidance. Yet in some cases, we look and reach to different locations. It is unclear, under these circumstances, whether and how eye and hand RTs might be related. Eye-hand coordination may well be affected by factors other than just saccade-reach congruence (Diaz et al. 2013a,b).

The fact that eye and hand movements are so stereotyped during unimanual reaching makes it difficult to scrutinize the factors that underlie eye-hand coordination. Previous studies have aimed to increase behavioral variability by directly training animals to modify their natural eye-hand coordination. For example, animals can be trained to reach without an accompanying eye movement (Snyder et al. 1997) or to initiate eye and hand movements in response to independent cues, which can be separated in time to tease apart the two movements (Dean et al. 2011). These approaches can be revealing, but by requiring animals to dissociate eye and hand movements, they risk bypassing the very circuitry we wish to study.

An alternative approach to producing variable patterns of eye and hand movements is to require not a single but two separate hand movements. There have been a number of studies of bimanual movements in the past, but most have focused on hand-hand coordination (Franz et al. 1991; Swinnen et al. 1996; Spijkers et al. 1997; Diedrichsen et al. 2001; Diedrichsen and Dowling 2009). In fact, only a very few studies have tracked eye movements in conjunction with a

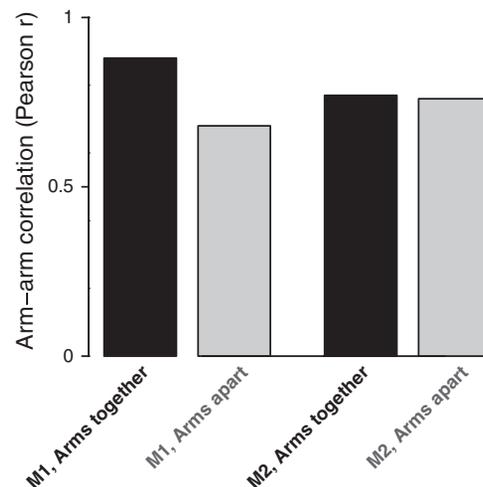


Fig. 6. Correlations between the left and right hands for bimanual reaches to same (black) or opposite (gray) targets for each monkey (*M1* and *M2*, respectively).

bimanual task (Müri et al. 1999; Hayhoe et al. 2003; Mason and Bruyn 2009; Srinivasan and Martin 2010) or reported separate data for the two hands; many studies instead collapse analyses across the left and right hands (Diedrichsen et al. 2001, 2006; Weigelt 2007; Weigelt et al. 2007). One such study showed that the pattern of eye movements can influence which hand moves first (Kokubu et al. 2009). Subjects were required to move each hand to a different target (as in our bimanual apart task) and were required to look at the two targets in a specified order. Although not specifically required, subjects initiated reaches to the two targets in that same order. In our experiments, we expected that unconstrained subjects would also match the order of their eye and hand movements. We were surprised to find instead that, in our trained macaques, the order was matched on only one-half of trials (Table 2). The fact that spatial alignment and temporal order were nearly independent might reflect overtraining, just as humans learn to, for example, reach for a gear shift or turn signal indicator without taking their eyes off the road. In any case, this dissociation offered us the opportunity to explore the factors influencing bimanual eye-hand coordination.

Our first observation was that when both hands move together to the same target, the RT correlation of each hand with the eyes is about the same as that seen in the unimanual task. When each hand moves to its own target, however, overall eye-hand correlation drops substantially. We asked what factor(s) are responsible for this drop.

While humans show varying degrees of handedness, there are few reports of handedness in monkeys. We see preferences for particular tasks, e.g., a given monkey might always accept treats with its right paw. However, these preferences are not consistent across tasks and may change over the course of months to years (unpublished observations). Nevertheless, we thought that animals might show a systematic preference to move one hand first and, furthermore, that eye-hand correlation might be systematically stronger for one hand than for the other. Neither speculation was borne out by the data.

Extrapolating from the unproven assumption that unimanual eye-hand correlation is driven primarily by the fact that the eye and hand share a common destination, we expected that, in the bimanual apart task, the hand that moves to the same target as the eye would show higher correlation than the hand that moves to the nonfoveated target. This proved to be the case, but the factor accounts for only about half of the difference between the overall bimanual apart eye-hand correlation and the unimanual correlation. The fact that the correlation between the eyes and the hand moving to the same target as the saccade falls substantially below the correlation seen on unimanual and on bimanual together trials could reflect a loss of coordination due to the complexity of the (two-target) movement. Alternatively, yet another factor could account for the difference.

We found that the hand that moves first in the bimanual apart task independently accounts for about half of the difference between the unimanual and overall bimanual eye-hand correlations. When we consider only those movements that are initiated first and are directed to the endpoint of the first saccade, we find that eye-hand coordination is

not significantly different from that seen with unimanual reaches.

Previous studies have asked whether saccades are directed to where a subject intends to reach or if the decision regarding which target to saccade towards is made first and then the hand moves to whichever target was foveated (Carey 2000). One study suggested that we look to where we intend to reach (Horstmann and Hoffmann 2005). Others have observed that arm movements made to the target of the first saccade are more accurate than those made to the secondary target, but this does not resolve the issue (Kokubu et al. 2009). Our study suggests that spatial factors are not the predominant factor in determining eye-hand coordination. This implies in turn that the two decisions (where to reach and where to saccade) might not be as tightly coupled as previously thought based on unimanual reaching studies.

One proposed strategy for handling the numerous degrees of freedom present in coordinated movements (e.g., where to reach and where to saccade) is “coordinative structures” wherein the brain groups individual movements together into a single functional unit (Bernstein 1967; Turvey 1977). Eye-hand coordination seems like a prime example of that (Pelz et al. 2001). When there is only a single target for a movement, the RT of the eyes and the arms are tightly linked as if they are being controlled as a single functional unit. When each hand moves to a different target, we found that the monkey uses one of two basic strategies. It either moves the eyes to the same target as the arm that moves first or moves the eyes to the same target as the arm that moves second. This choice has consequences for the pattern of eye-hand coordination. If the eyes move with the arm that moves first, then there is strong coordination between the eyes and that arm but weak coordination between the eyes and the other arm (Fig. 3, 10th and 13th bars). If instead the eyes move to the target of the arm that moves second, then we find an intermediate level of coordination between the eyes and each arm (Fig. 3, 11th and 12th bars). This finding does not fit with a simple version of coordinative structures, in which we would expect the structure to comprise the eyes and both arms together leading to similar high levels of eye-hand coordination for each arm, not varying degrees of eye-hand coordination depending on which strategy has been chosen. This suggests that patterns of motor coordination are graded rather than categorical, that is, very similar sets of movements can be coordinated to greater or lesser degrees.

*Relation to human literature.* Human bimanual coordination studies show that RTs for reaches to two different targets are slower when the reaches have asymmetric trajectories than when they have symmetric trajectories (Diedrichsen et al. 2001, 2006; Heuer and Klein 2006). For instance, if subjects make forward or sideways reaches with each hand, RT is shorter when the two movements are the same (symmetric) than when they are different (asymmetric) but only when the movements are cued symbolically (Diedrichsen et al. 2001). The RT cost for asymmetric compared with symmetric bimanual reaches is pronounced when reach goals are cued symbolically; exogenous targets and delay periods decrease or eliminate the effects (Heuer and Sangals 1998; Diedrichsen et al. 2001, 2004; Hazeltine et al. 2003; Weigelt et al. 2007). In our experiment, monkeys made bimanual reaches that were either symmetric

(i.e., both hands reached together to the same target along the vertical midline or each hand reached to targets on opposite sides of fixation along the horizontal midline), or asymmetric (i.e., both hands reached together to the same target at locations except along the vertical midline or each hand reached to targets 180° apart except along the horizontal midline). However, our study design also used an extended delay period between target presentation and movement initiation for the purpose of neural recording during the movement planning period. Additionally, target stimuli comprised both symbolic and spatial attributes; reach goals were directly spatially cued, while the required movement effector was cued by the color of the spatial cue. Thus one might not expect that we would observe the interference effects reported in the human literature. Nonetheless, we showed that under these conditions monkeys behave similarly to humans, with RT slowing for asymmetric reaches compared with symmetric reaches, although an order of magnitude smaller (Spijkers et al. 1997; Diedrichsen et al. 2001). To the extent that the RT cost associated with responding to symbolic cues is due to the time needed to translate the symbol into its appropriate response, the present result might be due to the animals having to select the correct effector(s) as opposed to the correct movement trajectory.

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#### DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

#### DISCLAIMER

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#### AUTHOR CONTRIBUTIONS

Author contributions: E.M., C.W., and A.F. performed experiments; E.M. and L.H.S. analyzed data; E.M. and L.H.S. interpreted results of experiments; E.M. prepared figures; E.M. drafted manuscript; E.M. and L.H.S. edited and revised manuscript; E.M. and L.H.S. approved final version of manuscript; C.W. and L.H.S. conception and design of research.

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