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The impact of head direction on lateralized choices of target and hand

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Abstract

We examined choices made by monkeys performing a task in which two food-well targets were positioned on either side of the monkey, and LEDs provided instructions on hand use and food target availability. We have previously reported that when gaze and head direction were unrestricted, lateralized choices were biased primarily by hand preference and secondarily by a preference to retrieve a target ipsilateral to the preferred hand. Here, we used a similar behavioral paradigm, but now during trial instructions the monkeys were required to maintain head direction aimed toward a left, a center, or a right fixation LED. When a lateralized head direction was required during presentation of the instructional cues, monkeys were more likely to choose the hand and target ipsilateral to the head direction. Lateralized head direction more strongly biased the monkeys' choice of hand than their choice of target, but hand preference produced even stronger bias on target choices than did head direction. Although target cues were presented before hand cues, our data indicate that target and hand choices were made interactively. We also found that the monkeys' choices were better correlated with their success rate for particular combinations of hand and target than with movement times.

Keywords

Bias; Choice; Head; Preference; Reach; Target

Introduction

In picking an apple off a tree, you move your eyes and head to look at various apples. You then pick one apple with one hand. In this way, target selection commonly is assumed to be the first step in a sequential process that guides goal-directed reaching. Alternatively, however, your choice of which apple to take might be based in part on which hand you prefer to use.

When reaching to a single target with unrestricted head and eye movements, gaze is directed at the target and then the head is turned toward the target, followed by a reach to the target

(Bartz 1966; Flanders et al. 1999; Engel and Soechting 2003). Maintaining gaze on the target optimizes the precision of reaching movements (Neggers and Bekkering 2000, 2001). Head and gaze direction therefore might be expected to bias target selection when multiple targets are present. Indeed, in both monkeys and humans, gaze direction biases target choices (Scherberger et al. 2003; Horstmann and Hoffmann 2005), and in monkeys head direction per se also has been shown to bias target choices (Scherberger et al. 2003). Does head direction influence the choice of which hand to use as well?

In previous experiments, we studied monkeys that were allowed choices between identical targets presented to the right and left, as well as choices of which hand to use. We found that when equivalent targets were presented simultaneously on the left and right, lateralized choices of target and hand were biased primarily, not by preference for a target on one side or the other, but rather by hand preference (Gardinier et al. 2006; Lee and Schieber 2006). Secondly, monkeys showed a preference to retrieve a target ipsilateral to the preferred hand. In these studies, however, the head and eye movements of the animals were neither restricted nor monitored.

Therefore, to examine how head direction influences impending lateralized choices of target and hand, we used a behavioral task similar to that of our previous experiments, but now we required each monkey to actively fix head direction left, center or right while cues were presented instructing the monkey about its available choices of target and/or hand. Although one might have expected head direction to have a prominent effect in biasing target choices, we found instead a larger effect of head direction in biasing hand choices ipsilaterally. Furthermore, our observations indicate that choices of target and hand are made, not sequentially, but interactively.

Methods

Animals

Two male monkeys (*Macaca nemestrina*; Monkey J, 11 kg body weight, and Monkey O, 12 kg) initially were trained to retrieve food pellets dispensed into wells to the right and left of midline (Fig. 1). These monkeys received cues via light emitting diodes (LEDs) instructing them as to the well into which food pellets would be dispensed and which hand could be used in retrieving a pellet (Gardinier et al. 2006). In the present study, to investigate the effect of head direction on the monkeys' choices of target and hand, we additionally required the monkeys to fix their head to the center, left or right while the instruction cues were delivered. All care and use of these purpose-bred monkeys complied with the USPHS policy on humane care and use of laboratory animals, and was approved by the University Committee on Animal Resources of the University of Rochester.

Behavioral task

After obtaining the behavioral data described in previous reports (Gardinier et al. 2006; Lee and Schieber 2006), these two monkeys underwent surgical implantation of a head post on the skull located approximately above the center of horizontal head rotation at the neck. A scleral search coil also was implanted in one eye to monitor gaze direction (Judge et al. 1980). In daily sessions thereafter, each monkey sat in a primate chair that restrained the neck, torso and legs, but allowed free movement of the head, as well as reaching movements of both arms. The primate chair was placed in a 1.24 m³ cube, housing dual oscillating magnetic fields that enabled monitoring of rotational position in the horizontal (yaw) and vertical (pitch) directions (CNC Engineering). The scleral search coil monitored gaze position, and a second search coil mounted on the head post simultaneously monitored head position. A small, red laser mounted on the same head post provided the monkey with continuous visual feedback of head direction.

During delivery of instructional cues at the beginning of each behavioral trial, the monkey was required to fixate a blue, eye-level LED at a central, left or right position. The right and left fixation LEDs were 25° from the midline. The monkey was required to direct gaze within a 20° × 20° window centered at the fixation LED, as monitored by the scleral search coil. Once the monkey was able to perform the task successfully with gaze position, both gaze and head position were required to be directed within the same window centered on the fixation LED. Because the present experiment focused on the effect of head position on lateralized choices of target and hand, we sought to have the monkey direct the head simply to the center, left or right. We did not require precise fixation and instead used relatively large windows, allowing the animals to complete many trials per days with relatively few fixation errors. Nevertheless, the monkeys generally maintained both head and gaze position close to the fixation LEDs. In some recording sessions, the scleral search coil had failed and the monkey then was required to point only its head at the fixation LEDs. In these sessions, observation with a video camera revealed that the monkey typically maintained gaze fixation on the LEDs as well. When a new scleral search coil subsequently was implanted, the monkey promptly resumed accurate fixation with both gaze and head position.

Trials of the behavioral task (Fig. 1) began when the monkey placed both the right and left hands in their respective home plate positions 5 cm to the right and left of the midline, and 13 cm below shoulder level. Correct initial positions were signaled to the monkey by illumination of two orange LEDs, one for each hand, at the bottom of the LED display. Then one of the three blue, fixation LEDs was lit, and up to 2,000 ms were allowed for acquisition of the fixation LED. Fixation, whether both gaze and head or head only, then had to be maintained, and both hands had to remain in their home plate positions, throughout the remainder of the instructional cue presentations and until appearance of the GO cue, as described below. Breaking fixation or lifting either hand before the GO cue was considered an error, and the trial was aborted immediately without reward.

Once the hands were in their home plate positions and fixation was established, an initial hold period began that varied randomly in duration. Although the minimum and maximum limits of randomly varied periods were fixed on any given day, we changed the limits from day to day to accommodate the work habits of the individual monkey. For Monkey J, the minimum initial hold period ranged from 160 to 230 ms and the maximum from 320 to 460 ms. For Monkey O, the minimum initial hold period ranged from 200 to 350 ms and the maximum from 400 to 700 ms.

At the end of this initial hold, the monkey received a 400-ms target cue, informing him whether food pellets would be dispensed in the right food well (right red LED), the left food well (left red LED), or both food wells (both red LEDs). We refer to the food wells or the pellets as the targets. The target cue then was extinguished, and a first instructed delay of randomized duration ensued. For Monkey J, on different days the minimum first instructed delay ranged from 160 to 230 ms, and the maximum from 320 to 460 ms. For Monkey O, the minimum of first instructed delay ranged from 200 to 350 ms and the maximum from 400 to 700 ms.

At the end of this first instructed delay, the monkey received another 400-ms cue informing him whether to use the right hand (right green LED), the left hand (left green LED) or either hand (both green LEDs). This hand cue then was extinguished, and a second instructed delay of randomized duration ensued. For Monkey J, the minimum second instructed delay ranged from 160 to 230 ms, and the maximum from 320 to 460 ms. For Monkey O, the minimum of the second instructed delay ranged from 200 to 350 ms, and the maximum from 700 to 1,050 ms. The second instructed delay was terminated by illumination of the GO cue, a midline yellow LED, at which time a food pellet was dispensed into the well(s) indicated by the preceding red target instruction LED(s).

Upon illumination of the GO cue, the monkey was allowed to break fixation, lift one hand, take one food pellet, and return the food pellet to its mouth. Infrared sensors monitored when the monkey's hands were in the home plate positions or in the food wells (Fig. 1, S1 and S2, respectively). These sensors enabled us to measure (1) the reaction time (from the appearance of the GO cue until the monkey lifted the required hand), (2) the reach time (from when the hand lifted off until it entered the required food well), and the (3) grasp time (from when the hand entered the food well to when it departed) in each trial.

The V-shaped food wells were located 11 cm from the midline, 18 cm in front of the monkey and were inclined 45° from the horizontal. Once the monkey's hand entered a food well, the sliding floor beneath the opposite well opened, dropping any second pellet out of the monkey's reach. Because the food pellets were small (5 mm diameter) relative to the depth of the food wells (12 mm), the monkeys used fine pinch movements to pick food pellets out of the wells.

In this way, although given choices, the monkey was allowed to lift only one hand and reach to only one food target on each trial. If the monkey lifted an allowed hand and reached into an allowed food well, we considered the trial successful. But if the monkey lifted a non-instructed hand, lifted both hands, or if the lifted hand entered an empty food well, then an error was declared; both sliding doors opened immediately, and any food pellets dropped out of reach. Likewise, if the monkey failed to lift a hand within 700 ms after illumination of the GO cue, or failed to reach into a food well within 700 ms of lifting a hand, an error was declared and the pellets were dropped out of reach. All error trials were repeated until performed correctly.

Overall, the instructions of hand and target each had three alternatives (left, right, or choice), which incorporated four different levels of choice for the monkey. In no-choice trials both the hand to be used and the target to be taken were specified by the instructions. Target-choice trials afforded the monkey a choice of taking either target but with a specified hand. Hand-choice trials afforded the monkey a choice of using either hand in reaching to a specified target. Double-choice trials afforded choices of both hand and target.

For each level of choice, four combinations of hand used and target taken were possible: left hand, left target (LHLT); left hand, right target (LHRT); right hand, left target (RHLT); and right hand, right target (RHRT). These four combinations of hand used and target taken, each at four levels of choice, resulted in 16 different possible combinations of instruction and response. To assess the monkeys' behavioral choices, trials were presented in the following ratio: one trial of each no-choice combination, two target-choice trials with the left hand required, two target-choice trials with the right hand required, two hand-choice trials with the left target required, two hand-choice trials with the right target required, and four double-choice trials. These 16 types of target and hand choices each were presented as the monkey maintained fixation in three different directions—center, left and right—resulting in a total of 48 trial presentations, all of which were randomized within a single block.

This behavioral task was controlled by TEMPO software (Reflective Computing, Olympia, WA, USA) running on client and server computers. This software generated marker codes representing the times of behavioral task events, which were collected through a data acquisition interface (micro1401, Spike2 software, Cambridge Electronic Design, Cambridge, UK) and stored on a separate computer along with vertical and horizontal components of gaze and head position, each sampled at 500 Hz.

Monkeys earned their entire daily diet of food pellets (BioServ, Frenchtown, NJ) in performing this task for 2–4 h each workday. On weekends and holidays, the monkeys received food of an equivalent weight in their home cages. Monkeys had ad libitum access to water in their home cages every day.

Data analysis

For the present study we selected behavioral sessions in which a sufficient number of evenly balanced trial presentations had been recorded to reflect the monkeys' laterality preferences. Each block of 48 randomized trials presented to the monkey included one no-choice trial of each of the 4 possible hand–target combinations—LHLT, LHRT, RHLT, and RHRT—presented with fixation maintained in each of 3 directions—left, center or right—for a total of 12 no-choice trials per block. We typically started and stopped data collection as the monkey was actively engaged in performing trials, without regard for block boundaries. We therefore retained for analysis only sessions in which each of the 12 no-choice trial types (4 combinations of hand and target per fixation) had been performed correctly at least 10 times, and in which the distribution of these correctly performed no-choice trials was not significantly different from uniform across the 12 categories (χ^2 , $p > 0.05$).

In target-choice trials, food pellets were dispensed simultaneously on both sides, whereas the monkey was required to use either its left or its right hand. Left hand-required and right hand-required target-choice trials each were presented as the monkey maintained fixation to the left, center or right, producing six combinations of hand required and fixation direction (2 hand $\times$ 3 fixation). For each of these six categories in each session, we calculated the percentage of trials in which the monkey chose the right versus left target, normalizing the total of right target-chosen and left target-chosen trials in each of the six categories to total 100%.

In hand-choice trials, a single food pellet was dispensed either on the left or on the right, and the monkey had a choice of which hand to use in retrieving the pellet. The instructional cues for left target-required and right target-required hand-choice trials each were presented as the monkey maintained fixation to the left, center or right, producing six combinations of target location and fixation direction (2 targets $\times$ 3 fixations). For each of these six categories, we calculated the percentage of trials in which the monkey chose to use its right or left hand in each session, normalizing the number of right hand-chosen and left hand-chosen trials to total 100%.

In double-choice trials, food pellets were dispensed simultaneously on both the left and the right, and the monkey was permitted to use either hand. The monkey thus made two choices: (1) the side from which to retrieve a pellet, and (2) the hand to use in retrieving the pellet. For each session, we calculated the percentage of trials in which the monkey chose each of the four possible hand–target combinations—LHLT, LHRT, RHLT, or RHRT—normalizing the total to 100% for each of the three fixation directions.

For statistical analyses these percentages were subjected to arcsine square-root transformation [transformed percentage = $\arcsin(\sqrt{\text{percentage}})$] to homogenize the variance at different percentages for subsequent ANOVAs (Hogg and Craig 1995). In most cases, ANOVAs were applied initially ($p < 0.01$), and post hoc testing was done using the Tukey honestly significant difference test ($p < 0.05$).

To quantify target laterality preferences, we calculated laterality quotients for target choices made under four combinations of fixation and hand use requirements (for simplicity omitting the central fixation condition). These laterality quotients, Q , were calculated as:

$$\begin{aligned} Q_{\text{rf|rlh|ct}} &= (\text{RTC}_{\text{rf|rlh|ct}} - \text{LTC}_{\text{rf|rlh|ct}}) / (\text{RTC}_{\text{rf|rlh|ct}} + \text{LTC}_{\text{rf|rlh|ct}}) \\ Q_{\text{lf|rlh|ct}} &= (\text{RTC}_{\text{lf|rlh|ct}} - \text{LTC}_{\text{lf|rlh|ct}}) / (\text{RTC}_{\text{lf|rlh|ct}} + \text{LTC}_{\text{lf|rlh|ct}}) \\ Q_{\text{rf|llh|ct}} &= (\text{RTC}_{\text{rf|llh|ct}} - \text{LTC}_{\text{rf|llh|ct}}) / (\text{RTC}_{\text{rf|llh|ct}} + \text{LTC}_{\text{rf|llh|ct}}) \\ Q_{\text{lf|llh|ct}} &= (\text{RTC}_{\text{lf|llh|ct}} - \text{LTC}_{\text{lf|llh|ct}}) / (\text{RTC}_{\text{lf|llh|ct}} + \text{LTC}_{\text{lf|llh|ct}}) \end{aligned}$$

where RTC and LTC represent the percentage of trials averaged across sessions in which the right and left targets were chosen (accordingly, the denominator of each of these equations sums to 100), rf and lf indicate right versus left fixation required, rh and lh indicate right versus left hand required, and ct indicates choice of target. $RTC_{rf|rh|ct}$ thus represents the percentage of trials in which the monkey was required to fix right (rf), was required to use the right hand (rh), was given a choice of target (ct), and chose the right target (RTC).

We then used these target laterality quotients to calculate the bias of target choices produced by the requirement to use the right versus the left hand when either right fixation or left fixation had been required:

$$\begin{aligned} B_{rf|l-r|lh|ct} &= Q_{rf|rh|ct} - Q_{rf|lh|ct} \\ B_{lf|r-lh|ct} &= Q_{lf|rh|ct} - Q_{lf|lh|ct} \end{aligned}$$

$B_{rf|l-r|lh|ct}$ thus quantifies the change in laterality of target choices depending on whether the right versus left hand was required, given that right fixation had been required. Positive values of B indicate that requiring a given hand increased the likelihood of ipsilateral target choices; negative values indicate that requiring a given hand increased the likelihood of contralateral target choices. Larger values of B , whether positive or negative, reflect a stronger bias of target choices depending on the hand requirement.

Using the same laterality quotients, we also calculated the bias produced by requiring fixation to one side or the other when either the right or the left hand had been required:

$$\begin{aligned} B_{r-lf|rh|ct} &= Q_{rf|rh|ct} - Q_{lf|rh|ct} \\ B_{r-lf|lh|ct} &= Q_{rf|lh|ct} - Q_{lf|lh|ct} \end{aligned}$$

Here, a positive value of B indicates that the fixation requirement increased the likelihood that the monkey would choose the ipsilateral target; a negative value indicates that the fixation requirement increased the likelihood of contralateral choices. Again, larger values of B , whether positive or negative, reflect a stronger bias of the choice of target generated by the fixation requirement. Laterality quotients (Q) and bias (B) were calculated similarly to quantify the effect of target and fixation requirements on hand choices.

Results

From Monkey J we obtained 170 sessions with a sufficient number of evenly balanced trial presentations, each including from 467 to 1391 correctly performed trials of all types: no choice, target choice, hand choice and double choice. Of these sessions, 65 were recorded with both the eye and head coils and 105 with the head coil only. From Monkey O we obtained 130 sessions, each including 484–1,345 correctly performed trials. Of these sessions, 75 were recorded with both the eye and head coils and 55 with the head coil only.

Target-choice trials

The means and standard deviations across sessions of the percentage of target-choice trials in which the right target or the left target was chosen are shown in Fig. 2a. Pooling the data from target choice trials across hand $\times$ fixation categories showed that Monkey J had a slight but significant preference for the right target (54.2%) in target-choice trials (one-way ANOVA: $F = 42.12$; $p < 0.0001$). Monkey O did not show a significant target preference.

For Monkey J, two-way ANOVA using only the right target-chosen percentages from the six hand $\times$ fixation categories demonstrated significant main effects of both hand ($F = 366.59$; $p < 0.0001$) and fixation direction ($F = 10.05$; $p < 0.0001$), with no significant interaction between these two factors. Post hoc analysis revealed that he chose the right target significantly more often when looking to the right than when looking to the center or left. For Monkey O, we found a significant main effect of the hand required ($F = 757.02$; $p < 0.0001$), but no effect of the fixation direction, nor any significant interaction between these two factors. The overall effect of requiring one hand or the other has been summarized in Table 1 (left half) by averaging the percentage of right target choices across left-, center-, and right fixation-required trials. The effect of fixation direction has been summarized by averaging the percentage of right target choices across both left- and right hand-required trials.

For all three fixation directions, both monkeys chose the right target more often when the right hand was required, and chose the left target more often when the left hand was required. For Monkey J, the percentage of right-target choices when both right fixation and right hand were required, $RTC_{rf|rh|ct}$, was 74.1, and for Monkey O $RTC_{rf|rh|ct}$ was 67.8, as shown in Fig. 2a (rightmost dark green bar for each monkey) and given in Table 2. Table 2 also gives the resulting laterality quotients, Q . Positive values of Q indicate that the monkey preferred the right target choice, negative values of Q indicate that the monkey preferred the left target choice. For example, the laterality quotient for target choices when right fixation and right hand were required, $Q_{rf|rh|ct}$, was 0.48 and 0.36 for Monkeys J and O, respectively, indicating that they both chose the right target more often under these conditions, whereas when left fixation and left hand were required, $Q_{lf|lh|ct}$ values were -0.30 and -0.46 , indicating that both monkeys chose the left target more often.

From these laterality quotients, we calculated the extent to which hand or fixation requirements biased target choices (see “Methods”). Positive values indicate that the requirement biased choices ipsilaterally; negative values, contralaterally. As summarized in Table 3, the bias of target choices produced by hand requirement was $+0.61$ for Monkey J and $+0.80$ for Monkey O when right fixation had been required; and was $+0.60$ for Monkey J and $+0.84$ for Monkey O when left fixation had been required. Requiring the monkey to use a given hand thus produced a strong bias, averaging $+0.71$, to choose the ipsilateral target.

For Monkey J, the bias of target choices produced by the requirement to fix to one side or another during delivery of the instructional cues was $+0.18$ when the right hand was required, and $+0.17$ when the left hand was required. The equivalent biases computed for Monkey O were -0.02 and $+0.01$. Requiring the monkeys to fix to the right versus left thus biased target choices only an average of $+0.10$, substantially weaker than the average bias produced by hand requirement of $+0.71$ (above). The weaker bias of target choices produced by the fixation direction was particularly apparent when the monkeys were required to use one hand after fixating to the opposite side. If required to use the left hand after fixating to the right (Fig. 2a, light green bars), both monkeys chose the left target more often, not the right target. Conversely, if required to use the right hand after fixating to the left (Fig. 2a, dark blue bars), both monkeys chose the right target more often. Hand requirement thus influenced lateralized target choices more strongly than the required fixation direction.

Hand-choice trials

The means and standard deviations of the percentage of hand-choice trials in which the right hand or the left hand was chosen in the six target $\times$ fixation categories across all sessions are illustrated for each monkey in Fig. 2b. Pooling these data across categories showed that Monkey J had a slight but significant overall preference for the right hand, using that hand on 53% of hand-choice trials (one-way ANOVA: $F = 35.25$, $p < 0.0001$), whereas Monkey O had

a strong preference for the left hand, using that hand on 81% of hand-choice trials (one-way ANOVA: $F = 4901.81$, $p < 0.0001$).

For both monkeys, two-way ANOVA of the percentage of right hand-chosen trials demonstrated significant main effects of both target location (Monkey J: $F = 74.88$, $p < 0.0001$; Monkey O: $F = 27.16$, $p < 0.0001$) and fixation direction (Monkey J: $F = 361.21$, $p < 0.0001$; Monkey O: $F = 19.75$, $p < 0.0001$) on hand choices, with no interaction between these two factors for either monkey. For hand-choice trials (Table 1, right half), the overall effect of requiring one target or the other has been summarized by averaging the percentage of right-hand choices across left-, center-, and right fixation-required trials when either the left or right target was required. The effect of fixation direction has been summarized by averaging the percentage of right-hand choices across both left- and the right target-required trials when left, center or right fixation had been required. Both monkeys chose the right hand significantly more often when required to go to the right target than when required to go to the left target. Post hoc analyses showed that Monkey J chose the right hand significantly more often when looking to the right than when looking center, and significantly less often when looking to the left, and that Monkey O chose the right hand significantly more often when fixation had been to the right versus left or center.

Thus, requiring the right target increased the likelihood that both monkeys would choose the right hand; requiring the left target increased the likelihood that both monkeys would choose the left hand (see Table 2). The bias of hand choices produced by the requirement to take the right versus left target was relatively small, however. Calculations analogous to those detailed above for target-choice trials showed that the bias of hand choice produced by requiring the right versus left target was +0.16 for Monkey J and +0.13 for Monkey O when fixation had been to the right, and was +0.22 for Monkey J and +0.12 for Monkey O when fixation had been to the left. Target requirements thus biased hand choices ipsilaterally an average of +0.16.

Fixation direction had a strong effect on Monkey J's hand choices, but less effect on Monkey O's hand choices. The bias of hand choices produced by right versus left fixation was +0.75 for Monkey J and +0.15 for Monkey O when the right target was required, and was +0.80 for Monkey J and +0.13 for Monkey O when the left target was required, averaging +0.46. In hand-choice trials, the fixation requirement thus produced a stronger bias than the target requirement, particularly in Monkey J. Because of the strong bias produced by fixation direction, Monkey J chose the right hand most often if fixation had been to the right, whether the right target (Fig. 2b, dark green bars) or the left target (light-green bars) had been required. Conversely, Monkey J chose the left hand most often if fixation direction had been to the left, whether the left target (light blue bars) or right target (dark blue bars) had been required. In contrast, Monkey O, with a much stronger hand preference than Monkey J, chose the left hand most often with each of the six combinations of target $\times$ fixation direction requirements. This monkey's strong hand preference appeared to prevail over any bias produced by target laterality or fixation direction.

Double-choice trials

Figure 2c illustrates the percentages of double-choice trials in which each monkey chose each hand–target combination when fixation had been in each direction (left, center or right). To examine overall preferences for hand and target, we pooled the proportion of choices of each of the four possible combinations of hand and target (LHLT, LHRT, RHLT, and RHRT) across the three fixation directions for each monkey. One-way ANOVA of these data over multiple sessions then confirmed that in double-choice trials neither monkey distributed choices of hand and target randomly, and instead showed significant preferences ($p < 0.0001$). In order of decreasing preference, Monkey J most often chose RHRT (37.8%), LHLT (32.1%), LHRT (15.2%) and RHLT (14.9%). The proportion of RHRT was significantly higher than the proportion of other choices. The proportion of LHLT was significantly higher than both the

proportion of LHRT and RHLT, but these two later proportions were not significantly different from one another. Monkey O most often chose LHLT (61.6%), LHRT (22.9%), RHRT (8.1%) and RHLT (5.9%). The proportions of each of these four choices all were significantly different from one another. Whereas Monkey J thus preferred reaching with either hand to the ipsilateral target, Monkey O showed a strong preference for the left hand.

In both monkeys, fixation direction during presentation of the instructional cues biased the subsequent choices of hand and target. Both monkeys tended to choose the left hand more when they had been looking to the left, and the right hand more when they had been looking to the right. The effect of fixation direction was most overt in Monkey J. In this monkey, one-way ANOVAs confirmed that the proportion of each of the four possible combinations of hand and target choices varied depending on whether the monkey had been looking to the left, center or right (i.e., the effect of fixation direction on the combined choices of hand and target; LHLT: $F = 78.63$, $p < 0.0001$; LHRT: $F = 31.50$, $p < 0.0001$; RHLT: $F = 44.81$, $p < 0.0001$; RHRT: $F = 118.09$, $p < 0.0001$). Post hoc analysis revealed that Monkey J chose LHLT significantly more often after fixation to the left than after fixation at the center, and significantly less often after fixation to the right (Table 4). Conversely, Monkey J chose RHRT significantly more often after fixation to the right than after fixation at the center, and significantly less often after fixation to the left. When Monkey J chose to make crossed reaches, it was the hand ipsilateral to the fixation direction, rather than ipsilateral to the target, that was chosen more frequently. Monkey J chose LHRT significantly more often after fixation to the left than after fixation to the right or center, and chose RHLT significantly more often after fixation to the right than after fixation to the center, and significantly less often after fixation to the left.

Though less overt, fixation direction also biased three of the four possible choices of hand and target during double-choice trials in Monkey O (one-way ANOVAs; LHLT: $F = 6.34$, $p = 0.0019$; RHLT: $F = 6.91$, $p = 0.0011$; RHRT: $F = 7.85$, $p = 0.0005$). The choice of LHRT was not significantly biased by fixation direction. Post hoc analysis revealed that Monkey O chose LHLT significantly more often after fixation to the left or at the center, than after fixation to the right; and conversely Monkey O chose RHRT significantly more often after fixation to the right than after fixation at the center or to the left. As for Monkey J, looking to one side increased the likelihood that Monkey O would make crossed reaches with the ipsilateral hand rather than crossed reaches to the ipsilateral target. Fixation direction during delivery of the instructional cues thus biased the likelihood of combined hand and target choices in both monkeys, with a stronger effect on hand choices than on target choices.

Furthermore, the distribution of choices of the four hand–target combinations for each fixation direction in each monkey showed that in double-choice trials the monkeys' choices of hand and target were not independent (χ^2 , $p < 0.01$). We therefore evaluated three possible types of interdependence between hand and target choices. First, if the monkey chose to take a given target immediately after the target cue, then the subsequent hand choice would be biased by the target decision as if that chosen target had been required. In this case the ratio of right versus left-hand choices in double-choice trials would be expected to follow the ratio observed when a given target was required in hand-choice trials. For example, with left gaze fixation and left target required in hand-choice trials, Monkey J chose the right versus left hand in 26.0 versus 74.0% of trials (light blue bars in Fig. 2b), a ratio of 0.351; and in left fixation double-choice trials Monkey J chose RHLT versus LHLT in 8.5 versus 48.3% trials (Fig. 2c), a ratio of 0.177. These two ratios were not particularly similar. Indeed, the plots for each monkey in Fig. 3a show that the ratios of right/left hand choices made in the six target $\times$ fixation categories of hand-choice trials overall were a poor predictor of the corresponding ratios in double-choice trials. Linear regression between the ratios in hand-choice and double-choice trials was not significant for either monkey. Although cued first, the choice of target did not dominate the choice of hand in double-choice trials.

Second, if the monkeys' hand preference led to their target choices, then target choices would be biased by hand decisions as if a given hand had been required. In this case the ratio of right versus left target choices in double-choice trials would be expected to follow the ratio observed when a given hand was required in target-choice trials. Indeed, the right/left target ratios from target-choice trials were a good predictor of the corresponding ratios in double-choice trials (Fig. 3b). Linear regression between the ratios in target-choice and double-choice trials was significant for each monkey ($p < 0.01$), with R^2 of 0.92 and 0.95 in monkeys J and O, respectively, and the line of unity slope through the origin lay within the 95% confidence intervals of the best-fit lines. Thus, it appears that hand choices had a large influence on target choices in double-choice trials.

We also considered a third possibility, that both (1) the bias produced by choosing a given target on hand choices was equivalent to the bias produced by requiring that target in hand-choice trials, and simultaneously (2) the bias produced by choosing a given hand on target choices was equivalent to having required that hand in target-choice trials. In this case, the fraction of double-choice trials in which a given hand–target combination was chosen should be predicted by the product of (1) the fraction of that combination chosen in hand-choice trials, and (2) the fraction of that combination chosen in target-choice trials. For example, during left fixation, the fraction of target-choice trials with the left hand required in which Monkey J chose the left target (65.1% or 0.651, leftmost light blue bar in Fig. 2a) multiplied by the fraction of hand-choice trials with the left target required in which Monkey J chose the left hand (74.0% or 0.740, leftmost light blue bar in Fig. 2b), gave a product of 0.481 ($= 0.651 \times 0.740$), while the fraction of double-choice trials in which Monkey J chose the combination LHLT was 0.483 (or 48.3%, left-most blue bar in Fig. 2c). The product of target-choice and hand-choice fractions was the best predictor of double-choice fractions across all four hand–target combinations in all three fixation directions, for both monkeys (Fig. 3c). Linear regression between for each monkey was highly significant ($p < 10^{-9}$), with R^2 of 0.98 and 0.99 in monkeys J and O, respectively, and 95% confidence intervals indicated that the best-fit line for each monkey did not differ from a line of unity slope through the origin. These observations suggest that target choices and hand choices biased one another interactively in double-choice trials.

Potential behavioral sources of choice bias

Success rates—To examine whether success rates influenced the monkeys' choices of hand and/or target, we calculated the percentage of fully instructed no-choice trials in which the monkey successfully lifted the instructed hand, reached to the instructed food well, and grasped the food pellet. For each combination of hand and target in each fixation direction, the percentage of successful no-choice trials averaged across sessions is shown in Fig. 4. Hand, target and fixation direction, all influenced Monkey J's success rate in no-choice trials (three-way ANOVA; hand: $F = 8.37$; $p = 0.004$; target: $F = 129.02$; $p < 0.0001$; fixation: $F = 343.49$; $p < 0.0001$). Monkey J was more successful on trials in which he was instructed to go to the left target (61.1%) than the right target (54.1%), and he was more successful when instructed to use the left hand (58.5%) than the right hand (56.7%). Post hoc analysis showed that Monkey J was significantly more successful on trials in which fixation had been central (68.7%), as compared to left (52.9%) or right (51.2%). A significant interaction was present between hand and target ($F = 244.05$; $p < 0.0001$). No interaction was found between fixation and hand or fixation and target.

Monkey O's success rate in no-choice trials was influenced by the hand and fixation, but not target requirements (hand: $F = 149.35$, $p < 0.0001$; target: $F = 5.04$, $p = 0.025$; fixation: $F = 316.40$, $p < 0.0001$). Monkey O was more successful when required to use the left hand (66.1%) than the right (56.7%). Post hoc analysis showed that Monkey O was significantly more successful when fixation had been central (73.4%) than left (59.3%) or right (51.5%). For

Monkey O, significant interactions on the proportion of successful trials were present between hand and target ($F = 110.98$; $p < 0.0001$), between fixation and target ($F = 6.10$; $p = 0.0023$), and between the fixation and hand ($F = 8.39$; $p = 0.0002$).

In conclusion, both monkeys were more successful when fixation had been central as compared to left or right, and tended to be more successful when making ipsilateral reaches (LHLT or RHRT) as compared to crossed reaches (LHRT or RHLT). We therefore examined the correlation between the monkeys' success rate in the different types of no-choice trials (LHLT, LHRT, RHLT and RHRT), and the fraction of double-choice trials in which the monkey chose each of these four combinations of hand and target (Spearman's Rho rank correlation) for each of the three fixation directions. Both monkeys showed a modest but significant correlation ($p < 0.0001$; Monkey J, $\text{Rho} = 0.32$; Monkey O, $\text{Rho} = 0.35$), suggesting that the distribution of hand and target choices in double-choice trials in part might have been based on the likelihood of successfully retrieving a pellet.

Movement times—We also considered the possibility that the monkeys might react, reach and/or grasp more quickly for some combinations of hand, target and fixation direction than for others. For each session we therefore calculated the average reaction time, reach time and grasp time in successful no-choice trials with each combination of hand, target and fixation direction. We then calculated the mean and standard deviation of these movement times across sessions; these values are given in Table 5. For Monkey J, although reaction time did not vary significantly, reach times varied depending on hand and fixation but not in relation to the target (three-way ANOVA; hand: $F = 7.74$, $p = 0.006$; fixation: $F = 5.76$; $p = 0.003$). Monkey J was faster reaching when required to use the left hand than the right hand. Monkey J's grasp times also varied in relation to hand, target and fixation (three-way ANOVA; hand: $F = 9.46$, $p = 0.0021$; target: $F = 8.53$, $p = 0.0035$ and fixation: $F = 6.35$, $p = 0.0018$). Monkey J was faster grasping when required to use the right hand than the left. He was also faster grasping when required to take the right target compared to the left. In Monkey O, none of the three times—reaction time, reach time or grasp time—varied significantly in relation to hand, target or fixation requirements.

We then examined the correlation between the monkeys' movement times in the different types of no-choice trials (LHLT, LHRT, RHLT and RHRT), and the fraction of double-choice trials in which the monkey chose each of these four combinations of hand and target. Monkey J showed a weak though significant inverse correlation between grasp time and the fraction of double-choice trials in which the monkey chose each of these four combinations of hand and target ($\text{Rho} = -0.072$; $p = 0.0013$), but no correlation was found with reaction or reach times. Monkey O showed a significant inverse correlation between the reach time and the proportion of different double-choice combinations ($\text{Rho} = -0.140$; $p < 0.0001$), but no correlation was found with reaction or grasp times. Correlations between movement times and double-choice likelihood for the various hand–target combinations thus were much weaker than the correlations between success and double choices.

Discussion

We previously studied the present monkeys performing the same choice task, but with no restrictions on head direction (Gardinier et al. 2006). As in the present experiments, we dissociated hand preference and target preference by incorporating some trials in which the monkey was required to use a given hand when choosing between right and left targets, and other trials in which the monkey chose between hands when required to take a given target. When required to use a given hand, the monkeys preferred the ipsilateral target, but when required to take a given target, they tended to use their preferred hand whether the target was on the right or left. With unrestricted head direction, lateralized choices of hand and target thus

were biased primarily by hand preference and secondarily by a preference to take a target ipsilateral to the preferred hand.

In the present study, we investigated the impact of head direction on these lateralized choices of hand and target. To do so, we added three fixation LEDs to the left, center and right of the monkeys' midline, and required them to fix their head toward one of these LEDs as target and hand instructions were presented for each trial. Under these conditions, we found that both hand and fixation requirements biased the monkeys' target choices in favor of the ipsilateral target, with the bias created by hand requirements being stronger than that created by fixation requirements (Gardinier et al. 2006). In addition, both target and fixation requirements biased the monkeys' hand choices in favor of the ipsilateral hand, but here the fixation requirement created a much stronger bias than the target requirement. When our monkeys were required to maintain the head fixed to one side or the other during cue presentation, their lateralized choices thus were biased most strongly by hand preference, secondarily by head direction, and least by target location. While this rank order of bias strength was common to both monkeys, differences between the two individuals were evident as well. In Monkey O for example, with a much stronger hand preference than Monkey J, head direction produced a substantially weaker bias of hand choices.

The influence of success likelihood and movement time on choices of target and hand

We also examined the possibility that either the likelihood of success or movement speed might influence the monkeys' simultaneous choices of hand and target in the three fixation directions. Our results suggest that the monkeys' prior experience with success and failure using the various hand–target combinations, more than the speed with which they retrieved food pellets, may have influenced their choices. When given a double choice, our monkeys more often chose hand–target combinations with which they were more successful when required to use a specific hand to take a specific target. While this finding might seem intuitively obvious, monkeys with a hand preference nevertheless show a tendency to switch hands in successive trials, possibly to minimize fatigue (Lee and Schieber 2006). Furthermore, macaques are likely to show a hand preference even when they perform equally well with either hand (Andrews 1999), and they do not necessarily prefer to use their more skillful hand to perform a given task (Kinoshita 1998). In unfamiliar situations where the individual has little prior experience with success and failure, for example, estimates of the likelihood of success may have less influence on choices.

When humans are instructed to move 'as fast as possible,' the laterality of the target and the arm have clear effects on response times (Carson et al. 1995; Velay et al. 2001; Barthelemy and Boulinguez 2002). For example, reaching across the body midline takes longer (Barthelemy and Boulinguez 2002), which can be attributed largely to biomechanical factors (Carey et al. 1996; Carey and Ottode Haart 2001). Here, we found only small differences in movement times across conditions, which were significant for only one monkey, and only weak inverse correlations were present between the monkeys' choices and movement times. Our monkeys were allowed relatively generous reaction, reach and grasp times, and were permitted to work to satiation each day, however, minimizing any incentive to perform quickly. Greater influence of movement times on choices might be observed in other situations that require more rapid performance.

Interaction of target and hand choices

In previous studies with no fixation requirements, we found that inverting the order of target and hand cue presentation had no effect on the monkeys' distribution of the four hand–target combinations chosen in double-choice trials (Gardinier et al. 2006). Similarly in the present study, although the target cue always was presented first and the hand cue second, the monkeys

did not choose the target first and thereafter choose the hand; nor were double-choices driven entirely by hand preferences. We found instead that the distribution of hand–target combinations chosen in double-choice trials was predicted most closely by the product of (1) the fraction of target choices given the hand, and (2) the fraction of hand choices given the target. This finding suggests that choices of hand–target combinations in double-choice trials were made in an interactive fashion, once the monkey knew that both target and hand choices were to be made.

Influence of head direction on choices of target and hand

Scherberger et al. (2003) previously reported that passively fixing the head to the right or the left shifted monkeys' preference for both saccade and reach targets rightward or leftward an equivalent amount. When the head was held passively to the left, for example, monkeys preferred more leftward targets for reaching, as did our monkeys that actively maintained their head position. Furthermore, in this prior study (Scherberger et al. 2003), the simultaneously presented targets were located equidistant from and relatively close to (16°) the visual fixation point, well within the range in which gaze shifts are made with ocular saccades but no head movement (Freedman and Sparks 1997). In our study, however, the reaching target ipsilateral to head fixation was approximately aligned with the head, where small saccades easily could have foveated the ipsi-lateral target to support accurate reaching (Weymouth 1958; Ballard et al. 1992), whereas the contralateral target was $\sim 50^\circ$ away, and a large gaze shift, likely to include substantial head movement, would have been required to foveate that target (Freedman and Sparks 1997). This difference in the gaze shifts needed to foveate the target may have contributed to the bias produced by fixation direction in favor of the ipsilateral target.

In our right and left fixation trials, the animal maintained both head and eye position in the required direction while the instructional cues were presented close to the midline. Thus, the instructions cues were received primarily by the ipsilateral cerebral hemisphere. With the head fixed actively on the right, for example, the instruction LEDs lay in the left visual field, which is projected to the right hemisphere. In theory, this might have favored use of the arm contralateral to the fixation LED, because transfer of information across the corpus callosum for use with the ipsilateral arm takes several milliseconds (Marzi et al. 1991; Berlucchi et al. 1995). Our animals had more than adequate time to react, reach and grasp, however, and any advantage conferred by visuomotor processing within a given hemisphere may have had relatively little effect on the monkeys' choices.

Although we anticipated that active fixation of the head to one side or the other would bias choices in favor of the ipsilateral target (Scherberger et al. 2003), we were surprised to find that head direction produced a substantially stronger bias in favor of the ipsilateral hand. Even in double-choice trials, head fixation to the right or left increased the proportion of crossed reaches made with the ipsilateral arm, despite the greater biomechanical costs of crossing the midline. If hand choice had been dominated by the biomechanical cost of arm movements (Soechting and Flanders 1992, 1995), our monkeys would never have crossed the midline, even less so when the head already had been turned toward the arm. This suggests that other factors engender the bias produced by head direction on hand choices. Such a bias might result in part from the tonic neck reflex, which increases the excitability of extensor muscles in the upper extremity ipsilateral to the turned head (Aiello et al. 1988) favoring extensor force production for reaching with that arm (Shea et al. 1995). In addition, higher-order cognitive processes might favor choosing the effector ipsilateral to head direction. Turning the head in one direction, for example, might increase neural activity in the contralateral cerebral hemisphere, lowering the threshold for activation of arm-related neurons in that hemisphere through cortico-cortical facilitation.

Interactions between gaze direction and arm movements may be crucial to the unimanual feeding behavior characteristic of primates (MacNeilage et al. 1987). Whatever the underlying mechanism, the bias produced by head direction appears ethologically well suited for feeding behavior in an arboreal niche. Perched amid fruit in a tree, the animal looks around itself until it finds a desirable target. The head and eyes already being turned in one direction biases the choice of which arm to use in reaching to grasp a piece of fruit, most likely one on the same side.

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References

- Aiello I, Rosati G, Sau GF, Patraskakis S, Bissakou M, Traccis S. Tonic neck reflexes on upper limb flexor tone in man. *Exp Neurol* 1988;101:41–49. [PubMed: 3391259]
- Andrews MW. Emergence of handedness in bonnet macaques (*Macaca radiata*) on a task they were equally capable of performing with the left or right hand. *Percept Mot Skills* 1999;88:1280–1282. [PubMed: 10485111]
- Ballard DH, Hayhoe MM, Li F, Whitehead SD. Hand-eye coordination during sequential tasks. *Philos Trans R Soc Lond B Biol Sci* 1992;337:331–338. (discussion 338–339). [PubMed: 1359587]
- Barthelemy S, Boultinguez P. Manual asymmetries in the directional coding of reaching: further evidence for hemispatial effects and right hemisphere dominance for movement planning. *Exp Brain Res* 2002;147:305–312. [PubMed: 12428138]
- Bartz AE. Eye and head movements in peripheral vision: nature of compensatory eye movements. *Science* 1966;152:1644–1645. [PubMed: 5936888]
- Berlucchi G, Aglioti S, Marzi CA, Tassinari G. Corpus callosum and simple visuomotor integration. *Neuropsychologia* 1995;33:923–936. [PubMed: 8524454]
- Carey DP, Otto-de Haart EG. Hemispatial differences in visually guided aiming are neither hemispatial nor visual. *Neuropsychologia* 2001;39:885–894. [PubMed: 11516441]
- Carey DP, Hargreaves EL, Goodale MA. Reaching to ipsilateral or contralateral targets: within-hemisphere visuomotor processing cannot explain hemispatial differences in motor control. *Exp Brain Res* 1996;112:496–504. [PubMed: 9007551]
- Carson RG, Chua R, Goodman D, Byblow WD, Elliott D. The preparation of aiming movements. *Brain Cogn* 1995;28:133–154. [PubMed: 7546669]
- Engel KC, Soechting JF. Interactions between ocular motor and manual responses during two-dimensional tracking. *Prog Brain Res* 2003;142:141–153. [PubMed: 12693259]
- Flanders M, Daghestani L, Berthoz A. Reaching beyond reach. *Exp Brain Res* 1999;126:19–30. [PubMed: 10333004]
- Freedman EG, Sparks DL. Eye-head coordination during head-unrestrained gaze shifts in rhesus monkeys. *J Neurophysiol* 1997;77:2328–2348. [PubMed: 9163361]
- Gardinier J, Franco V, Schieber MH. Interactions between lateralized choices of hand and target. *Exp Brain Res* 2006;170:149–159. [PubMed: 16328287]
- Hogg, RV.; Craig, AT. Introduction to mathematical statistics. Prentice Hall; Lebanon, IN: 1995.
- Horstmann A, Hoffmann KP. Target selection in eye-hand coordination: do we reach to where we look or do we look to where we reach? *Exp Brain Res* 2005;167:187–195. [PubMed: 16044304]
- Judge SJ, Richmond BJ, Chu FC. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vis Res* 1980;20:535–538. [PubMed: 6776685]
- Kinoshita M. Do monkeys choose the more skillful hand in manual problem-solving? *Percept Mot Skills* 1998;87:83–89. [PubMed: 9760629]

- Lee D, Schieber MH. Serial correlation in lateralized choices of hand and target. *Exp Brain Res* 2006;174:499–509. [PubMed: 16715180]
- MacNeillage PF, Studdert-Kennedy MG, Lindblom B. Primate handedness reconsidered. *Behav Brain Sci* 1987;10:247–303.
- Marzi CA, Bisiacchi P, Nicoletti R. Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia* 1991;29:1163–1177. [PubMed: 1838793]
- Neggers SF, Bekkering H. Ocular gaze is anchored to the target of an ongoing pointing movement. *J Neurophysiol* 2000;83:639–651. [PubMed: 10669480]
- Neggers SF, Bekkering H. Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. *J Neurophysiol* 2001;86:961–970. [PubMed: 11495964]
- Scherberger H, Goodale MA, Andersen RA. Target selection for reaching and saccades share a similar behavioral reference frame in the macaque. *J Neurophysiol* 2003;89:1456–1466. [PubMed: 12612028]
- Shea CH, Guadagnoli MA, Dean M. Responses biases: tonic neck response and after contraction phenomenon. *J Mot Behav* 1995;27:41–51.
- Soechting JF, Flanders M. Moving in three-dimensional space: frames of reference, vectors, and coordinate systems. *Annu Rev Neurosci* 1992;15:167–191. [PubMed: 1575441]
- Soechting JF, Flanders M. Psychophysical approaches to motor control. *Curr Opin Neurobiol* 1995;5:742–748. [PubMed: 8805407]
- Velay JL, Daffaure V, Raphael N, Benoit-Dubrocard S. Hemispheric asymmetry and interhemispheric transfer in pointing depend on the spatial components of the movement. *Cortex* 2001;37:75–90. [PubMed: 11292163]
- Weymouth FW. Visual sensory units and the minimal angle of resolution. *Am J Ophthalmol* 1958;46:102–113. [PubMed: 13545337]

Fig. 1.

Behavioral task. A series of panels illustrates the LED display viewed by the monkey during different periods of a single trial. To start a trial the monkey placed both hands in home plate positions (*lower left photo*). The monkey was informed of correct initial hand positioning (detected via infrared sensors, S1) by illumination of *left and right orange LEDs* at the bottom of the LED display (*panel 1*). Then, one of three *blue* fixation point LEDs was illuminated (fixation LED) on the monkey's left (illustrated here as a *blue filled circle*; *panel 2*) or right, or at center. The monkey directed both his head and eyes toward this fixation point in order to acquire fixation (*panel 3*, *gray arrow and box*). Following an initial hold period (*panel 4*), a second set of *red* LEDs gave the target instruction. Food pellets could be dispensed on the left only (*left red LED only*), on the right only (*right red LED only*) or on both sides (choice of target: both *red LEDs*). In this example the right LED came on (*panel 5*), instructing the monkey that a food pellet would be dispensed only in the right food well. An instructed delay followed the target cue (*panel 6*), followed by a third set of LEDs instructing the monkey which hand to use (*green LEDs*). In the example illustrated, both *green LEDs* were illuminated (*panel 7*), instructing the monkey that he could choose to use either hand in reaching to the target. Following another instructed delay (*panel 8*), a *central yellow LED* was lit as a GO cue (*panel 9*). The monkey then was allowed to break fixation and reach for the food pellet (*upper right photo*). Thus, in the illustrated trial, left fixation and right target were required, but the monkey to use its left hand. Movement times were measured using infrared sensors at the home plates (*arrowhead; S1*) and in the food wells (*arrowhead; S2*)

Fig. 2.

Choices made in different types of trials. *Bar graphs* show the percentage of each of the four possible hand–target combinations chosen under different conditions by Monkey J and Monkey O. *Error bars* represent one standard deviation from the mean across sessions. For each monkey, the *left column of panels with blue bars* represents choices made when fixation had been directed to the left, the *middle column with red bars* represents choices when fixation had been at center; the *right column with green bars* represents fixation to the right. **a** In target-choice trials (*top row*), for each fixation direction, each monkey's choices of right versus left target have been normalized to total 100% for trials in which the left hand was required (*light colors*), and to total 100% for trials in which the right hand was required (*dark colors*). For all three fixation directions, both monkeys chose the left target more often when the left hand was required, and chose the right target more often when the right hand was required. **b** In hand-choice trials (*middle row*), each monkey's choices of right versus left hand have been normalized to total 100% for trials in which the left (*light colors*) or the right (*dark colors*) target had been required with fixation in each direction. Requiring the monkey to take a food pellet on its left increased the likelihood that it would choose its left hand; requiring the monkey to take a food pellet on its right increased the likelihood that it would choose its right hand. **c** In double-choice trials (*bottom row*), choices of the four possible combinations of hand and target have been normalized to total 100% for each fixation direction.

Fig. 3.

Predicting the distribution of hand–target combinations chosen in double-choice trials. For each monkey, J (*top*) and O (*bottom*), the distribution of different hand–target combinations in double-choice trials was predicted using the distribution of choices in one choice trials based on three different models. **a** Target choice dominant. For each fixation direction (*black* left, *gray* center, *white* right), the right/left ratio of hand choices made when the right or the left target was chosen in double-choice trials (*ordinate*) has been plotted against the right/left ratio of hand choices in hand-choice trials (*abscissa*), where the right or left target decision had been made externally for the monkey by requiring a given target. **b** Hand choice dominant. The right/left ratio of target choices made when the right or the left hand was chosen in double-choice trials (*ordinate*) has been plotted against the right/left ratio of target choices in target-choice trials (*abscissa*), where the right or left hand decision had been made externally for the monkey by requiring a given hand. **c** Hand and target choices interact. The fraction of double-choice trials in which each hand–target combination was chosen (*ordinate*) has been plotted against the product of (1) the fraction of hand-choice trials in which that target was required and that hand was chosen and (2) the fraction of target-choice trials in which that hand was required and that target was chosen (*abscissa*). In each plot, the best-fit line (*solid*) is compared to a line of unity slope through the origin (*dotted*)

Fig. 4. Success in no-choice trials. Percentage of successful trials for Monkey J (**a**) and Monkey O (**b**) when required to retrieve a particular target and required to use a particular hand in no-choice trials. For each monkey, the *left column with black bars* represents trials in which left fixation was required; the *middle column with gray bars*, center fixation; and the *right column with white bars*, right fixation. *Each bar* represents the mean ($\pm$ standard deviation) percentage of successful trials averaged across all sessions for that combination of fixation, hand and target requirement. For each required hand–target combination, both monkeys were more successful when fixation had been at the center than either left or right

Table 1

Overall effects of hand, target and gaze in target- and hand-choice trials

Right-target choices (%) in target-choice trials				Right-hand choices (%) in hand-choice trials			
Effect of hand		Effect of fixation direction		Effect of target		Effect of fixation direction	
Left hand	Right hand	Left gaze	Right gaze	Left target	Right target	Left gaze	Right gaze
Monkey J 36.6	69.9	50.0	58.8	48.3	58.5	31.4	58.5
Monkey O 28.2	68.5	47.9	47.6	16.2	21.8	16.7	16.6
							70.3
							23.7

Table 2

Percentage of target and hand choices and resulting laterality quotients

	Left fixation				Right fixation				Right versus left laterality quotients			
	Left hand		Right hand		Left hand		Right hand					
	Left target	Right target	Left target	Right target	Left target	Right target	Left target	Right target				
Target choice (%)	LTC lf lh ct	RTC lf lh ct	LTC lf rh ct	RTC lf rh ct	LTC lf lh ct	RTC lf lh ct	LTC rf rh ct	RTC rf rh ct	$\bar{Q}$ lf lh ct	$\bar{Q}$ rf lh ct	$\bar{Q}$ lf rh ct	$\bar{Q}$ rf rh ct
Monkey J	65.1	34.9	35.0	65.0	56.5	43.5	25.9	74.1	-0.30	-0.13	+0.30	+0.48
Monkey O	73.1	26.9	31.0	69.0	72.5	27.5	32.2	67.8	-0.46	-0.45	+0.38	+0.36
Hand choice (%)	LHC lf lh ch	LHC lf rh ch	RHC lf lh ch	RHC lf rh ch	LHC rf lh ch	LHC rf rh ch	RHC rf lh ch	RHC rf rh ch	$\bar{Q}$ lf lh ch	$\bar{Q}$ lf rh ch	$\bar{Q}$ rf lh ch	$\bar{Q}$ rf rh ch
Monkey J	74.0	63.2	26.0	36.8	33.8	25.6	66.2	74.4	-0.48	+0.32	-0.26	+0.49
Monkey O	86.2	80.3	13.8	19.7	79.7	72.9	20.4	27.0	-0.72	-0.59	-0.61	-0.46

Table 3

Biasing of target and hand choices

	By hand required		By fixation required	
	Left fixation required	Right fixation required	Left hand required	Right hand required
Bias of target choices				
Monkey J	+0.60	+0.61	+0.17	+0.18
Monkey O	+0.84	+0.80	+0.01	−0.02
Bias of hand choices				
Monkey J	+0.22	+0.16	+0.80	+0.75
Monkey O	+0.12	+0.13	+0.13	+0.15

Table 4

Effect of gaze in double-choice trials

	Percent choice (%)		
	Left gaze	Center gaze	Right gaze
Left hand left target choice (LHLT)			
Monkey J	48.3	31.2	17.0
Monkey O	64.6	62.4	57.7
Left hand right target choice (LHRT)			
Monkey J	22.4	11.4	11.8
Monkey O	22.9	22.8	23.0
Right hand left target choice (RHLT)			
Monkey J	8.5	16.1	20.0
Monkey O	3.2	4.4	6.5
Right hand right target (RHRT)			
Monkey J	20.8	41.3	51.2
Monkey O	9.3	10.5	12.8

Table 5
Times associated with different combinations of hand and target in no-choice trials

	Left fixation				Center fixation				Right fixation			
	Left hand		Right hand		Left hand		Right hand		Left hand		Right hand	
	Left target	Right target	Left target	Right target	Left target	Right target	Left target	Right target	Left target	Right target	Left target	Right target
Monkey J												
Reaction time (ms)	475 ± 68	473 ± 71	475 ± 68	474 ± 69	474 ± 70	473 ± 72	475 ± 68	475 ± 69	475 ± 71	472 ± 72	475 ± 68	474 ± 70
Reach time (ms)	320 ± 45	325 ± 49	331 ± 48	329 ± 46	313 ± 51	316 ± 51	321 ± 49	319 ± 47	316 ± 49	321 ± 50	326 ± 49	321 ± 48
Grasp time (ms)	417 ± 50	428 ± 57	427 ± 52	401 ± 51	424 ± 48	435 ± 49	435 ± 48	411 ± 47	415 ± 47	427 ± 49	426 ± 50	404 ± 51
Monkey O												
Reaction time (ms)	540 ± 165	540 ± 167	537 ± 152	537 ± 153	554 ± 180	550 ± 169	544 ± 151	542 ± 151	557 ± 199	554 ± 192	552 ± 181	552 ± 183
Reach time (ms)	241 ± 87	252 ± 84	259 ± 81	251 ± 83	235 ± 79	243 ± 78	250 ± 73	242 ± 73	240 ± 84	248 ± 82	259 ± 79	253 ± 82
Grasp time (ms)	524 ± 81	522 ± 79	530 ± 80	518 ± 78	510 ± 63	517 ± 66	524 ± 61	513 ± 60	526 ± 74	524 ± 77	520 ± 70	515 ± 72