# Simultaneous encoding of the direction and orientation of potential targets during reach planning: evidence of multiple competing reach plans

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**Stewart BM, Baugh LA, Gallivan JP, Flanagan JR.** Simultaneous encoding of the direction and orientation of potential targets during reach planning: evidence of multiple competing reach plans. *J Neurophysiol* 110: 807–816, 2013. First published May 22, 2013; doi:10.1152/jn.00131.2013.—Reaches performed in many natural situations involve selecting a specific target from a number of alternatives. Recent studies show that before reaching, multiple potential reach targets are encoded in brain regions involved in action control and that, when people are required to initiate the reach before the target is specified, initial hand direction is biased by the spatial distribution of potential targets. These findings have led to the suggestion that the brain, during planning, simultaneously prepares multiple reaches to potential targets. In addition to hand direction, reach planning often involves specifying other parameters such as wrist orientation. For example, when posting a letter in a mail slot, both the location and orientation of the slot must be encoded to control hand direction and orientation. Therefore, if the brain prepares multiple reaches to potential targets and if these targets require the specification of hand direction and orientation, then both of these variables should be biased by the spatial distribution of potential targets. To test this prediction, we examined a task in which participants moved a hand-held rectangular tool toward multiple rectangular targets of varying location and orientation, one of which was selected, with equal probability as the actual target after movement initiation. We found that initial hand direction and orientation were biased by the spatial distributions of potential target locations and orientations, respectively. This result is consistent with the idea that the brain, in cases of target uncertainty, simultaneously plans fully specified reaching movements to all potential targets.

visually guided reaching; decision making; goal-directed action; human

VISUALLY GUIDED GOAL-DIRECTED reaching requires that action-relevant features of a target, such as its location, orientation, and shape, be extracted and transformed into a series of coordinated motor commands (Baldauf and Deubel 2010; Cisek 2007; Jeannerod 1981, 1984, 1988; Jeannerod et al. 1995; Tunik et al. 2005). Serial models of movement planning assume that a target for action must be selected before the movement metrics can be specified and the movement implemented (McClelland 1979; Miller et al. 1960; Schall 2002a,b; Sternberg 1969). However, recent studies examining situations in which a single reach target must be selected from a number of competing alternatives have challenged this serial model. Specifically, it has been argued, on the basis of neurophysiological data, that multiple potential targets are encoded in parallel before deciding between them (Cisek 2007, 2012;

Cisek and Kalaska 2002, 2005). This parallel encoding provides a potential neural basis for the ability of individuals to quickly adjust motor output and make online corrections when the initial target changes (Brenner and Smeets 1997; Gomi 2008; Resulaj et al. 2009).

Parallel encoding is also consistent with findings from recent behavioral studies showing that when reaching toward multiple potential targets, one of which becomes cued after reach onset, the initial direction of the reach is biased by the spatial distribution of potential targets. For example, if two potential targets are presented that have equal probabilities of being selected as the target, participants initially aim toward the midpoint (Chapman et al. 2010a; Gallivan et al. 2011a; see also Ghez et al. 1997). One interpretation of these behavioral results is that the initial arm movement arises from the parallel specification of competing reach plans linked to potential targets (Chapman et al. 2010a). However, there are other possible interpretations. For example, participants may first select an initial movement direction based on the distribution of potential target locations and then begin moving in this direction.

The aim of the current study was to provide an important test of the multiple reach plan hypothesis using a task in which participants moved a hand-held rectangular tool toward multiple potential rectangular targets of varying location and orientation, one of which was selected as the actual target after movement initiation. Reaching to such targets involves specifying both hand direction and orientation, and there is strong evidence that the control of these two parameters is integrated (Desmurget et al. 1995, 1996; Fan et al. 2006). We reasoned that if the initial movement trajectories reflect the simultaneous planning of fully elaborated multiple reaches, then in addition to the initial hand direction being biased by the distribution of potential target positions, the initial hand orientation should be biased by the distribution of potential target orientations. Alternatively, if participants are solely concerned with the locations of the potential targets and select an initial movement direction based on these locations, then we would not expect initial hand orientation to be biased by the distribution of potential target orientations. Such a situation could occur if participants aimed to minimize a cost function associated with corrective translational movements of the hand such as the variance of durations or energy outlays of these movements (for reviews dealing with cost functions, see Diedrichsen et al. 2010 and Todorov 2004).

## METHODS

*Participants and general procedure.* Fourteen right-handed participants (9 female; age range: 20–31 yr old) recruited from Queen's

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University took part in this experiment after providing informed written consent. The Queen's University General Research Ethics Board approved all experimental procedures, and the participants received financial compensation (12 CAD/h) for their time.

On a given trial, one, two, or three potential targets were presented on a vertical screen. These potential targets were unfilled rectangles that varied in location and orientation. When instructed by an auditory signal, participants were required, as quickly and accurately as possible, to align a hand-held rectangular bar to both the location and orientation of the cued target by positioning the hand and orienting the wrist. Importantly, however, the actual target was not filled in (i.e., cued) until the hand movement was initiated, and all potential targets in the display had an equal probability of being cued as the actual target.

*Apparatus.* Seated participants grasped an oval Plexiglas tool with a rectangular protrusion (6 cm long and 1 cm wide), henceforth referred to as the tool-tip (Fig. 1*A*). Participants used the tool-tip to contact rectangular targets of the same size (i.e., 6 by 1 cm) projected onto a display screen. An electromagnetic position sensor (LIBERTY; Polhemus, Burlington, VT) embedded in the tool-tip measured both the position and orientation of the tool in 3 dimensions (240 samples per second). The tool was grasped with a power grip such that its orientation was closely coupled to the orientation of the wrist.

The task involved moving the tool-tip from its start position (shown in Fig. 1*A*), resting vertically on the tabletop, to contact targets rear-projected (Electrohome 9500LC Ultra) on a screen covered with Plexiglas. The projector had a refresh rate of 185 frames per second and a computer-to-projector lag of 3 ms. The screen was located 30 cm from the tool-tip starting location (in the *y*-axis) and was ~50 cm from the eyes (in the *y*-axis). The top and bottom edges of the tool were flat, and thus participants could easily hold the tool in a vertical upright position at the start of each trial (as they were instructed to do). Two photodiodes, placed on the top left and bottom right side of the screen, were used to record the time at which potential targets were displayed and the time at which the actual target was cued. The

table and screen borders were constructed from wood and brass screws to prevent distortion of the electromagnetic signals from the position sensor.

*Stimuli.* Target displays consisted of one, two, or three rectangular targets (Fig. 1*B*). The centers of the potential targets were positioned 20 cm to either the left or right of the midline of the screen. The potential targets were oriented 20° either clockwise (CW) or counterclockwise (CCW) from the vertical (*z*-axis). On 2-target trials, the two potential targets were displayed on either side of midline. On 3-target trials, two of the potential targets always appeared on one side of the display with the remaining target appearing on the other side of the display. The centers of the two potential targets displayed on one side of the display were 6.64 cm apart in the vertical dimension. Target displays consisted of all possible combinations of position and orientation. Thus, as shown in Fig. 1*B*, there were 4 1-target displays, 4 2-target displays, and 16 3-target displays. The 3-target displays can be partitioned into 3 types: 3-target same displays, in which all 3 potential targets have the same orientation; 3-target "paired" displays, in which the 2 potential targets located on the same side of the display have the same orientation; and 3-target "unpaired" displays, in which the 2 potential targets located on the same side of the display have different orientations, such that the 2 potential targets with the same orientation are on opposite sides of the display.

*Procedure.* At the start of each trial, the participant placed the hand-held tool at the "home" position (Fig. 1*A*). At the home position, the tool was held vertically and upright, with the contact surface facing forward and the bottom edge of the tool resting on the tabletop. In this position, the position-angle sensor embedded in tool-tip was aligned with the center of the screen in the *y-z* plane. A tongue depressor, taped to the tabletop, helped the participant align the tool at the home position but did not impede movement of the tool toward the screen. Figure 1*C* shows the sequence of events for a single (3-target) trial as well as the hand *y-* and *x*-positions and hand roll as a function of time. Once the tool was held at the home position (with the sensor held within 1.25 cm of the home position for 200 ms), a fixation cross
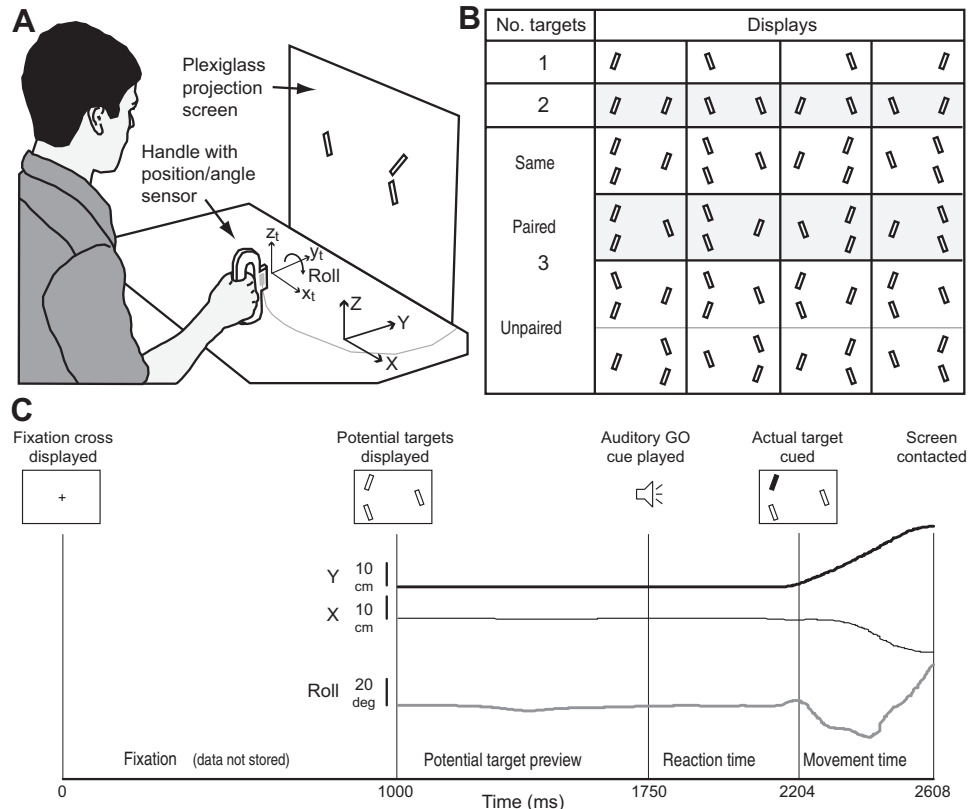


Fig. 1. Apparatus and target displays. *A*: participants moved a hand-held tool (t) with a rectangular contact surface toward a display with potential rectangular targets of varying position and orientation. *B*: on a given trial, 1, 2, or 3 potential targets were presented, with a total of 24 different configurations. *C*: time course of a single 3-target trial showing hand *x-* and *y*-positions and hand roll as well as key events. After a fixation cross was displayed for 1,000 ms, the potential targets were displayed for 750 ms. An auditory signal then instructed the participant to reach, and 1 of the potential targets was cued (filled in) as the actual target at the time of movement initiation. deg, Degrees.

was displayed for 1,000 ms. Immediately thereafter, the potential targets were displayed for 750 ms. An auditory "beep" (100 ms, 1,000 Hz) was then played, providing the go signal or cue for the participant to begin reaching toward the screen. Once the tool-tip was displaced 2.5 cm from the start position, the actual target was cued (filled in black). Participants were required to initiate the movement within 500 ms of the go (auditory) signal and, once the actual target was cued, had 500 ms to make contact with the screen. The position and orientation of the sensor at the time at which the contact surface of the tool-tip contacted the screen was used to determine whether a particular trial was a "hit" or a "miss." The trial was considered to be a hit if the position of the sensor in the *x*-*z* plane was within 1 cm of the target center point and the roll angle of the sensor was within 10° of the target orientation. Otherwise, the trial was considered to be a miss. A feedback message was displayed on the screen after each trial. If the tool-tip contacted the screen within the aforementioned time restrictions (i.e., <500-ms reaction time and <500-ms movement time), the feedback message indicated whether the particular trial was a hit or a miss. The feedback message displayed for trials that were not completed within a 500-ms movement time was either "too slow: hit" or "too slow: miss." If the participant began moving too early (i.e., before 100 ms after the auditory go signal) or too late (i.e., >500 ms after the auditory go signal), the trial was aborted, the potential targets were removed from the screen, and the message too early or too late was displayed, respectively. Before beginning the experiment, participants completed 50 practice trials so that they would be comfortable with the time restrictions and accuracy requirements of the task. During the experiment, participants performed 600 experimental trials that were separated into 4 blocks of 150 trials. Each block included 25 1-target trials, 25 2-target trials, and 100 3-target trials presented in a random order. Mandatory breaks were given between each block to prevent participants from becoming fatigued. The breaks ended when the participants felt they were ready to continue. The experiment took ~1 h to complete.

*Data analysis.* Position and orientation signals from the tool-tip position sensor were smoothed using a fourth-order, zero-phase-lag, low-pass Butterworth filter with a cutoff frequency of 14 Hz. The velocities of the hand in *x*, *y*, and *z* were obtained using a central differential equation, and the tangential velocity (or speed) of the handle was computed as the resultant of the *x*-, *y*-, and *z*-velocities. Our analysis focused on the horizontal (*x*)-position of the tool-tip and the CW or CCW roll of the tool-tip. Note that roll was measured as the orientation of the tool-tip about the *y*-axis of a coordinate system anchored to the tool (*y*$_t$-axis in Fig. 1*A*).

Because we were interested in examining the initial trajectory produced in response to target uncertainty in the display, our analysis focused on the movement of the tool-tip before when corrections could be made based on visual feedback about the actual target being cued. To this end, we determined the *x* (or lateral)-position and roll angle of the tool-tip when the tool-tip had moved 40% of the *y*-distance from the start position to the screen. Previous studies have used 60% of the distance from the start position to distinguish the point before correction (Chapman et al. 2010a; Gallivan et al. 2011a; Wood et al. 2011). However, we found that corrections could sometimes be observed using the 60% criteria, whereas, as will be demonstrated in the results, this was very rarely the case with the 40% criteria. In any event, all of the analyses reported in the current paper were also carried out using 50 and 60% of the distance from the start position to the screen, and these analyses yielded very similar results.

Previous studies examining reaching to multiple potential targets have reported that a substantial proportion of participants consistently adopt a strategy of selecting one of the potential targets in the display, initiating a movement toward that target, and attempting to correct if another potential target is specified as the target (Chapman et al. 2010a; Gallivan et al. 2011a). We wished to exclude such participants (as previous studies have done) because their data cannot be used to test between the competing hypotheses under investigation. To iden-

tify such participants, we examined the distribution of tool-tip *x*-positions, determined at the time the tool-tip reached 40% of the *y*-distance to the screen, in all 2-target trials. Figure 2 shows separate distributions for each participant (gray and red lines). For comparison, the combined distributions (across subjects) for all 1-target trials with the target on the left (green line) or right (blue line) are shown. The four distributions shown in red are from participants who were excluded from further analysis. Two of these participants exhibited a strong right-side bias, suggesting that they selected the right target.
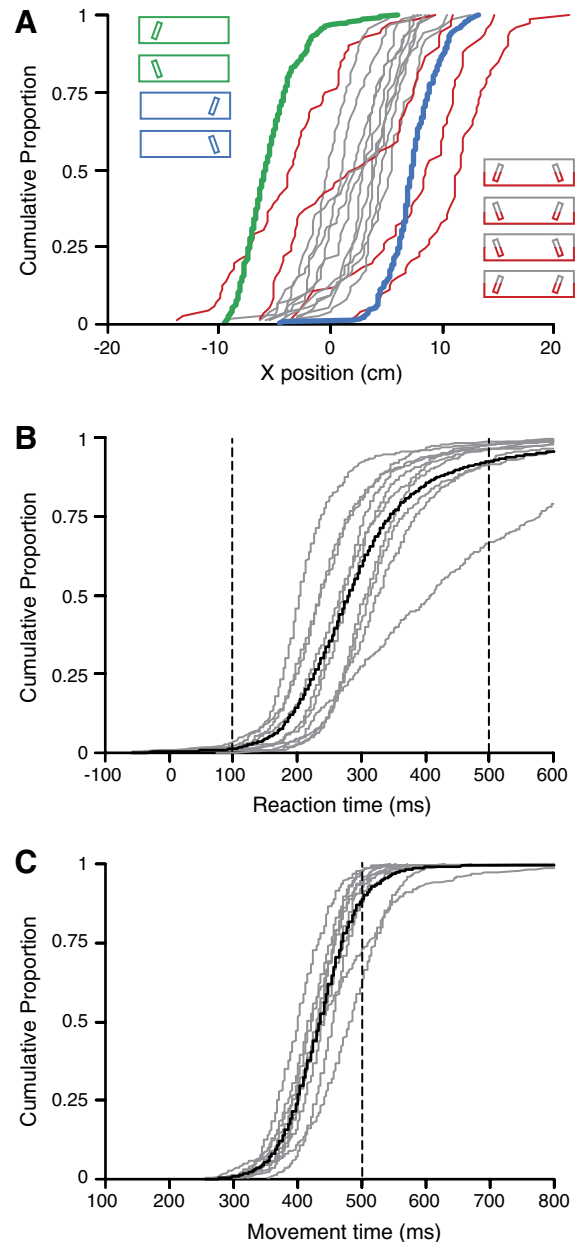


Fig. 2. *A*: cumulative frequency distributions, expressed as proportions, showing, for 2-target trials, the *x*-position of the tool-tip when the *y*-position of the hand reached 40% of the distance from the start position to the screen. The gray lines show the distributions from the 10 participants analyzed in this study. The red lines show distributions from the 4 participants who were excluded from analysis. For comparison, the green and red lines show the distributions for 1-target left and 1-target right trials, respectively, combining data from all analyzed participants. *B* and *C*: cumulative frequency distributions showing, for all trials, reaction time (*B*) and movement time (*C*). The gray lines show distributions of each participant, and the thicker black line shows the distribution across all participants.

One exhibited a strong left-side bias, suggesting that they selected the left target. The other participant exhibited a bimodal distribution, suggesting that they randomly selected either the left or right target in a given trial. The 10 remaining participants (gray lines) were used in all analyses.

As noted above, participants in the current study viewed the potential targets for 750 ms before receiving the auditory go cue. In contrast, in several previous studies using a similar approach, the actual presentation of the potential targets served as the go cue (Chapman et al. 2010a; Gallivan et al. 2011a). We opted for a 750-ms target display viewing period (i.e., before movement onset) because we found, in pilot testing, that over half of the participants exhibited a strong (typically right-side) bias when required to move as soon as possible after presentation of the target display.

In total, 90% of all trials were completed within the reaction time restrictions (Fig. 2B), 87% of all trials were completed within the movement time restriction (Fig. 2C), and 79% of all trials were completed within both the reaction time and movement time restrictions. Only the latter trials were included in the analysis. Because we were primarily interested in the initial trajectory of the movement, before the online correction when the final target was cued, both misses and hits were included in the analysis.

We used repeated-measures ANOVA and paired *t*-tests to assess experimental effects. Bonferroni corrections were used to compensate for multiple comparisons. An $\alpha$-level of 0.05 was considered to be significant.

## RESULTS

*Errors rates.* The average percentages of successful target hits, based on participant means, in 1-, 2-, and 3-target trials were 91.4% (SE = 2.5%), 89.3% (SE = 2.2%), and 88.0% (SE = 2.4%), respectively. One-way repeated-measures ANOVA failed to reveal a significant effect of target number on the percentage of target hits ($F_{2,18} = 1.01$; $P = 0.385$). Misses could arise from errors in the location and/or the orientation of

the handle. A paired *t*-test failed to reveal a significant difference between the percentages of location [mean (M) = 5.1%, SE = 1.1%] and orientation (M = 5.7%, SE = 1.5%) errors ($P = 0.72$; data collapsed across all 1-, 2-, and 3-target trials), suggesting that participants were not attending to one target feature at the expense of the other.

*Representative movement paths.* Figure 3 shows, for individual trials generated by a single participant, movement paths in the *x-y* (horizontal) and roll-*y* planes. Thus these plots illustrate how the lateral position and roll angle of the tool-tip evolved over time as the hand approaches the screen (i.e., as *y* increased). Figure 3, *A* and *B*, shows paths from four 2-target trials and two 1-target trials. The paths are color-coded to indicate the target configuration (see *inset*; filled targets denote the actual target cued on that particular trial). Whereas the hand moved in an approximately straight line (in the horizontal plane) toward the single target in the 1-target trials, in the 2-target trials, the hand was initially directed approximately halfway between the two potential targets (i.e., midpoint or "averaged" location). The hand direction then veered toward the actual target (cued after movement onset) at around the time that *y*-position of the hand reached 40% of the distance to the screen (denoted by the horizontal dashed line in Fig. 3A). On the 1-target trials, the roll angle began changing toward the orientation of the target right from the start of the movement. In contrast, on the 2-target trials in which the two potential targets had opposite orientations (i.e., +20 and −20°), hand roll stayed at ~0° for the initial part of the movement and only veered toward the orientation of the cued target when the *y*-position of the hand reach 40% of the distance to the screen (Fig. 3B). Critically, on 2-target trials in which the two potential targets had the same orientation, hand roll began changing toward this orientation right from the start of the movement, as
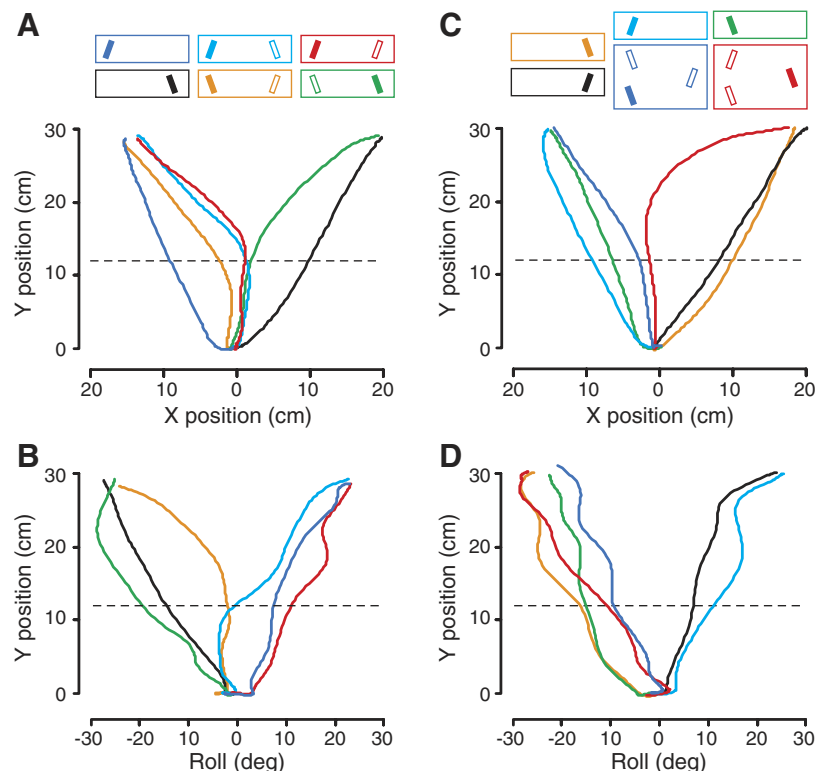


Fig. 3. Exemplar movement paths from a representative participant. *A*: *x-y* paths of the hand for single 1- and 2-target trials. The *inset* shows the target configuration for each trial, and the filled potential target indicates the target that was selected after movement onset (note that the target configurations are color-coded to indicate correspondence with the associated movement paths). *B*: roll-*y* paths of the hand for the same trials shown in *A*. *C* and *D*: same as *A* and *B* except that paths are shown for single 1- and 3-target trials. Horizontal dashed black lines indicate 40% of the distance from the start position to the screen.

in the 1-target trials. These results suggest that, on 2-target trials, both the orientation and the location of the potential targets are encoded and transformed into appropriate motor commands controlling hand direction and roll.

Figure 3, *C* and *D*, shows paths from two 3-target trials and four 1-target trials. Again, on 1-target trials, right from the start of the movement the hand moved in a straight line toward the target and the roll angle began changing toward the orientation of the target. On 3-target trials, the initial direction of the hand was biased (relative to the initial direction seen in 2-target trials) toward the side of the display with two targets, although the initial direction was closer to the midline than in the 1-target trials (compare the red and blue lines with the green and cyan lines in Fig. 3*C*). Likewise, the initial path in roll-*y* space was biased toward the angle shared by two of the three targets, regardless of whether these two targets were on the same side (blue line) or opposite sides (red line) of the display. However, the initial roll-*y* direction on these 3-target trials was closer to midline than in the 1-target trials (compare red and blue lines with the green and orange lines in Fig. 3*D*). These findings suggest that on 3-target trials, as in 2-target trials, both the orientation and the location of the potential targets are encoded and transformed into motor commands controlling hand direction and roll.

*Cumulative frequency distributions.* Cumulative frequency distributions of the *x*-position and roll of the tool-tip, at the time when the *y*-position of the tool-tip reached 40% of the distance from the start position to the screen, are shown for select target configurations in Fig. 4. These distributions include all trials from all participants. Overall, we observed a right-side bias in initial hand direction (Fig. 4*A*) that may arise, at least in part, from the fact that our participants were



Fig. 4. Distributions of initial *x*-positions and roll angles. *A* and *B*: cumulative frequency distributions, expressed as proportions, showing the *x*-position (*A*) and orientation (*B*) of the tool-tip when the *y*-position of the hand reached 40% of the distance from the start position to the screen. Distributions for selected 1-, 2-, and 3-target configurations are shown and color-coded (*inset*). Vertical dashed black lines indicate 0 cm in the *x*-position (*A*) and 0° rotation (*B*).

right-handed (Chapman et al. 2010a; Gallivan et al. 2011a). These distributions indicate that the pattern of results illustrated by the single trials shown in Fig. 3 hold across all trials and participants. In 2-target trials, the hand was initially directed between the two targets, and in 3-target trials the initial hand direction shifted (relative to the 2-target trials) toward the side of the display with two targets. The distribution of roll angles (Fig. 4*B*) on the 2-target trials in which the targets had the same orientation (blue line) was very similar to distributions on 1-target trials with the same target orientation (orange and cyan lines). The initial roll angle on the 2-target trials in which the targets had opposite orientations (green and lime lines) was in-between the roll angles on 1-target trials with CW and CCW targets, although the roll angle was somewhat biased by the orientation of the right-side potential target (compare lime and green lines). On 3-target trials, the initial roll angle was shifted (relative to the distribution on 2-target trials with opposite target orientations) toward the angle shared by two of the three targets, regardless of whether these two targets were on the same side (black line) or different sides (red line) of the display. Importantly, these distributions indicate that the influence of multiple potential targets on initial hand direction and roll occurred at the level of individual trials, something that could not be inferred by only examining the average initial hand direction and roll across trials.

*Effects of target configuration in 1- and 2-target trials.* To assess statistically the effects described above, we first compared 1- and 2-target trials. Figure 5*A* shows the average *x*-position of the hand at the time when the *y*-position of the hand reached 40% of the distance to the screen (based on participants' means) for 1-target left, 1-target right, and 2-targets trials, collapsed across target orientations in each case. One-way repeated-measures ANOVA revealed a significant effect of target condition ($F_{2,18} = 165.6$, $P < 0.001$). On 2-target trials, the *x*-position of the hand (M = 2.71 cm, SE = 0.50 cm) was intermediate between the *x*-positions observed when one target was presented on the left (M = −5.63 cm, SE = 0.67 cm) or right (M = 6.98 cm, SE = 0.41 cm). Bonferroni-corrected pairwise comparisons indicated that all conditions were significantly different from one another ($P < 0.001$ in all 3 cases).

Figure 5*B* shows the average roll angle of the hand at the time when the *y*-position of the hand reached 40% of the distance to the screen (based on participants' means) for 1-target CW and 1-target CCW trials (collapsed across target locations) as well as 2-target CW (both targets CW), 2-target CCW (both targets CCW), and 2-target CW+CCW (1 target CW and 1 CCW) trials. One-way repeated-measures ANOVA revealed a reliable effect of target condition ($F_{4,36} = 107.3$, $P < 0.001$). Bonferroni-corrected pairwise comparisons indicated that all conditions were significantly different from one another ($P < 0.001$) with two important exceptions: the initial roll angle on 1-target CW trials (M = 9.82°, SE = 0.84°) was not reliably different ($P > 0.99$) from the roll angle on 2-targets CW trials (M = 9.75°, SE = 1.24°), and the roll angle on 1-target CCW trials (M = −12.20°, SE = 1.49°) was not reliably different ($P = 0.56$) from the roll angle on 2-target CCW trials (M = 10.52°, SE = 1.72°). Note that when we combined the 1-target CW and CCW trials and also combined the 2-target CW and CCW trials, after negating the roll angle in all CCW trials to obtain a normalized roll angle (see *inset* in
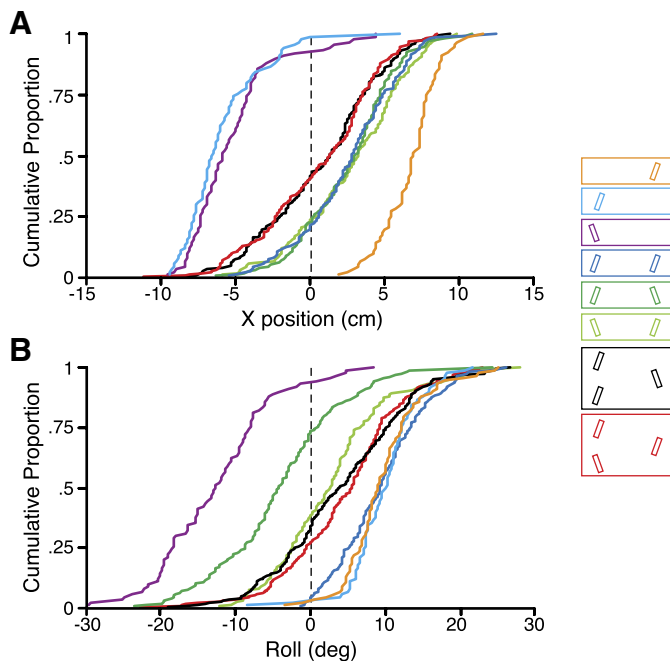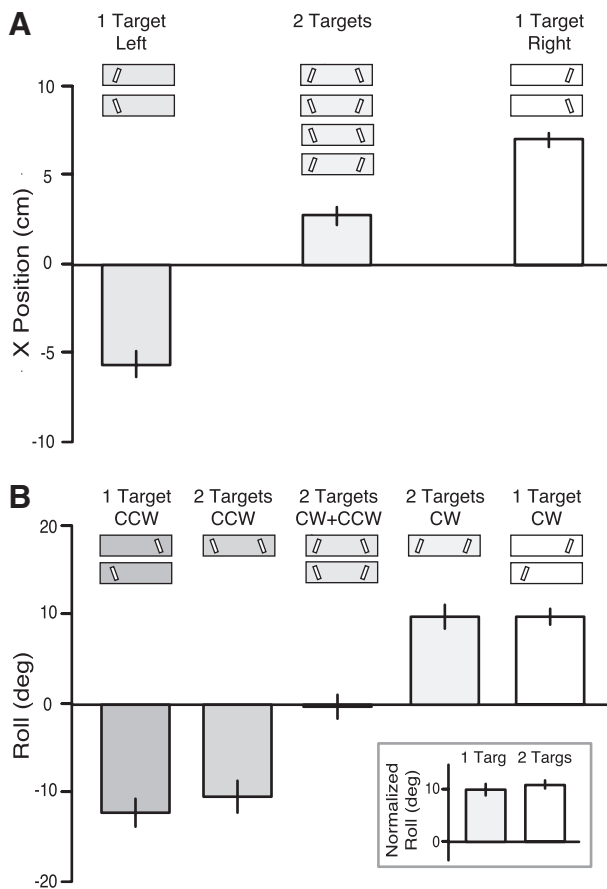
Fig. 5. Average initial *x*-positions and roll angles for 1- and 2-target trials. *A* and *B*: average *x*-position (*A*) and orientation (*B*) of the tool-tip when the *y*-position of the hand reached 40% of the distance from the start position to the screen. Averages based on participant means. Vertical lines on bars represent ±1 SE. Target configurations from which the trials used to compute participant means were taken are shown. CCW, counterclockwise; CW, clockwise. The *inset* in *B* shows normalized roll in 1- and 2-target (Targ) trials.

Fig. 5*B*), we still failed to find a significant difference between 1-target and 2-target trials even when using an uncorrected paired *t*-test ($P = 0.199$).

The above results show that on 2-target trials, participants directed their initial hand movement between the two potential targets, albeit with a right-side bias. When the two potential targets had opposite orientations, the initial roll angle was close to 0 on average (M = $-0.30°$, SE = $1.25°$). However, when the two potential targets had the same orientation, the initial roll angle was not different from that seen on 1-target trials with the same target orientation. These results are consistent with the spatial averaging behavior reported previously (Chapman et al. 2010a; Gallivan et al. 2011a) but show, rather importantly, that this averaging applies to both the location and orientation of the potential targets.

*Effects of target configuration in 3-target trials.* Figure 6*A* shows the average *x*-position of the hand at the time when the *y*-position of the hand reached 40% of the distance to the screen (based on participants' means) for all 3-target trials in which two targets were on the left and all 3-target trials in which two targets were on the right, collapsed across target orientations in each case. A paired *t*-test revealed that the *x*-position of the hand on 2-target left trials (M = 0.90 cm,

SE = 0.66 cm) was significantly different ($P = 0.006$) from that of 2-target right trials (M = 4.10 cm, SE = 0.67 cm). Thus, although a clear right-side bias was observed, the initial direction of the hand was strongly influenced by the spatial distribution of potential targets.

We predicted that on 3-target trials, the initial roll angle of the tool-tip (i.e., the roll angle at the time when the *y*-position of the hand reached 40% of the distance to the screen) would be greatest, in absolute terms, when all three potential targets had the same orientation (3-target-same trials). We also expected that when the two potential targets on one side of the display had the same orientation and the single potential target on the other side had the opposite orientation (3-target-paired trials), the initial roll angle would more closely match the orientation of the two potential targets located on the one side. However, we considered two possibilities on 3-target trials in which the two potential targets on one side of the display had opposite orientations (3-target-unpaired trials). On the one hand, if the processing of target locations biases the processing of target orientations, such that the orientations of the two potential targets on one side of the display would be weighted more heavily than the orientation of the single potential target on the other side, then we would expect the bias in initial roll angle to be greater in 3-target-paired trials than in 3-target-unpaired trials. On the other hand, if locations and orientations are processed independently and in parallel, consistent with the idea of multiple independent motor plans, then we would not expect any difference between 3-target-paired and 3-target-unpaired trials.

To evaluate these possibilities, we examined the normalized roll angle on 3-target-same trials, 3-target-paired trials, and 3-target-unpaired trials. Specifically, we negated the initial roll angle on trials in which two of the potential targets had a CCW orientation (to obtain normalized roll) and then collapsed across the four 3-target-same configurations, the four 3-target-paired configurations, and the eight 3-target-unpaired config-



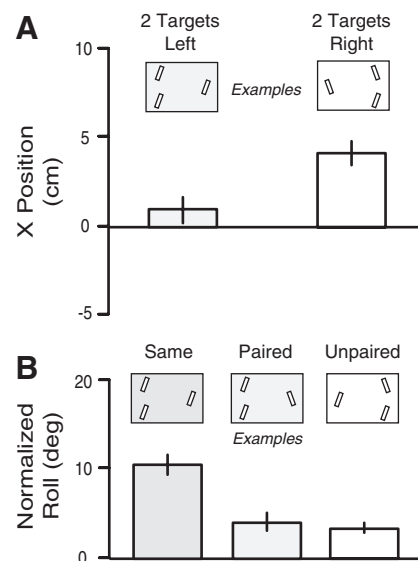Fig. 6. Average initial *x*-positions and roll angles for 3-target trials. *A* and *B*: average *x*-position (*A*) and orientation (*B*) of the tool-tip when the *y*-position of the hand reached 40% of the distance from the start position to the screen. Averages based on participant means. Vertical lines on bars represent ±1 SE. *Insets* provide example target configurations from which the trials used to compute participant means were taken.

urations separately (see Fig. 1B for reference). Figure 6B shows the average initial roll angle (based on participants' means) for each of these three 3-target conditions (same, paired, and unpaired). One-way repeated-measures ANOVA revealed a reliable effect of target condition ($F_{3,18} = 23.3$, $P < 0.001$). To explore this effect further, we carried out two orthogonal comparisons: one comparing the roll angle in the 3-target-same condition to the roll angle in the combination of the 3-target-paired and 3-target-unpaired conditions and the other comparing the roll angles in the 3-target-paired and 3-target-unpaired conditions. The roll angle was significantly greater in the 3-target-same condition compared with the other two conditions combined ($P < 0.001$), but there was no reliable difference between the 3-target-paired and 3-target-unpaired conditions ($P = 0.626$). Pairwise comparisons (with Bonferroni correction) revealed that the roll angle was greater in the 3-target-same condition than in each of the other conditions ($P = 0.002$ in both cases). These results support the hypothesis that participants independently integrate information about potential target locations and orientations in specifying their initial reach motor commands.

## DISCUSSION

The aim of the current study was to provide a test of the hypothesis that during reach planning, the brain specifies multiple competing action plans in parallel before choosing among the alternatives (Chapman et al. 2010a; Cisek 2007). Using a task in which participants were asked to initiate reaches toward multiple potential targets that varied in both location and orientation, before one of the potential targets was cued as the target, we found that the initial movement trajectory took into account not only the locations of potential targets, but also their orientations. This finding is consistent with the idea that, under conditions of target uncertainty, the brain simultaneously prepares multiple fully elaborated reaching movements, which are integrated to generate an initial movement tuned to the distribution of potential targets.

Our results show that participants were not solely concerned with the locations of the potential targets when launching the initial movement. Such a situation could occur if participants sought to minimize a cost function associated with corrective translational movements of the hand, such as the variance of durations or energy outlays of these movements. Because of the large inertia associated with changing the position of the hand, one might reasonably expect the initial movement to be strongly influenced by the distribution of potential target locations. In contrast, because of the relatively small inertia associated with changing the orientation of the hand, one might expect hand orientation to be specified only after the target is cued and during the corrective movement to that target. However, we cannot rule out the possibility that the initial hand movement is selected to minimize costs associated with corrective changes in both hand position and hand orientation.

*Neurophysiological basis of spatial averaging behavior.* Particularly convincing evidence that the brain encodes multiple potential reach targets in parallel before selecting between them comes from neurophysiological investigations in nonhuman primates (NHPs). Neurons in dorsal premotor cortex (dPM) have been shown to encode simultaneously multiple target locations for reaching before the animal being instructed

on which movement to make (Cisek and Kalaska 2005). Similarly, neurons in parietal cortex and the superior colliculus have been shown to encode simultaneously multiple target locations for eye movements before the animal selecting one of them for fixation (Basso and Wurtz 1997; Platt and Glimcher 1997). Results from behavioral studies of arm and eye movements made to targets in the presence of other competing targets and/or distractors appear to reflect directly this simultaneous coding of multiple competing targets at the neural level. When two potential targets (or 1 target and 1 distractor) appear in close proximity, the initial trajectories (and often endpoints) of target-directed arm and eye movements often land between them at a midpoint location (Arai et al. 2004; Chapman et al. 2010a,b; Gallivan et al. 2011a; Ghez et al. 1997; McSorley et al. 2006; Sailer et al. 2002; Song and Nakayama 2008; Tipper et al. 1997; Welsh et al. 1999; Wood et al. 2011), a behavior often referred to as the "global effect" or spatial averaging (see Van der Stigchel et al. 2006 for review). To explain this behavioral effect, it has been suggested that closely spaced target stimuli create overlapping hills of activity in the corresponding motor maps of structures involved in movements of the eye and arm (Cisek 2006; McPeek et al. 2003; Port and Wurtz 2003), with the final movement vector being determined by an averaging of these competing signals (Findlay and Walker 1999; Godijn and Theeuwes 2002; Tipper et al. 2000). This suggestion is highly consistent with neural findings in the superior colliculus of NHPs showing that in situations in which spatially averaged eye movements are produced, maximal activity can appear at a midpoint location between both targets (e.g., Glimcher and Sparks 1993).

To date, evidence for the parallel encoding of multiple targets as well as competing motor plans (and related interpretations of the resultant behavioral spatial averaging effects) has been directly linked to the location of potential targets in space and the spatial direction of movements to these targets. However, in everyday behavior, hand movements are not directed to single points in space but rather to objects, and planning such actions involves further specifying additional object properties such as size, shape, and orientation (Jeannerod et al. 1995). Importantly, the results of the current study suggest that the parallel encoding of multiple reach targets, and specification of potential movements to these targets, occurs also with respect to orientation, a highly grasp-relevant target property. These findings lend behavioral support to recent neurophysiological evidence from NHPs showing that during grasp planning toward a single target object (a handle), parietal neurons involved in hand preshaping appear to represent simultaneously multiple potential grasp movements before one is selected for action (Baumann et al. 2009).

*Neural mechanisms involved in object processing for reaching.* Numerous studies have provided evidence that the fron-toparietal network contains two distinct circuits for visuomotor control: the dorsolateral circuit involving connections from the anterior intraparietal area (AIP) to ventral premotor cortex, thought to be specialized for grasping, and the dorsomedial circuit (DMC) involving connections between V6A/medial intraparietal area to dPM, thought to be specialized for reaching (Andersen and Buneo 2002; Grafton 2010; Jeannerod 1988; Johnson and Grafton 2003; Matelli and Luppino 2000; Rizzolatti and Matelli 2003; Sakata and Taira 1994; Sakata et

al. 1998). This body of work provides support for the highly influential two-channel framework, which proposes that the control of reach-to-grasp actions can be subdivided into a reach component that selectively processes extrinsic object properties such as target distance and location and a grasp component that selectively processes intrinsic object properties such as size and shape (Jeannerod 1981). However, a clear dissociation between reach- and grasp-related processes has not always been observed at the neural level (Fattori et al. 2009, 2010; Grol et al. 2007). Moreover, the status of object orientation within this two-channel framework remains unclear. For example, object orientation is coded in areas more traditionally implicated in hand preshaping, like AIP (Baumann et al. 2009), as well as in areas traditionally involved in reaching, including monkey V6A (Fattori et al. 2009) and its putative human homolog, superior parieto-occipital cortex (Gallivan et al. 2011b; Vesia et al. 2010), both part of the DMC. The idea that the coding of different object properties, such as location, orientation, and size, is distributed across, and integrated within, different regions and circuits is arguably more consistent with the model of grasping proposed by Smeets and Brenner (1999). According to this model, reach-to-grasp actions involve planning separate movements of each digit (e.g., the thumb and index finger) to grasp points on the object that are selected by integrating information about object location, orientation, size, and shape.

As noted above, previous studies have shown that in reaching tasks in which both hand direction and orientation need to be specified, the control of these two parameters is highly integrated (Desmurget et al. 1995, 1996; Fan et al. 2006). One possible interpretation of this finding is that the motor system plans these reaches in six dimensions, specifying the trajectory of the hand in terms of both position and orientation in three-dimensional space. Note that this notion could also account for the current results. Specifically, the motor system may plan multiple reaches to potential targets in six dimensions, with the initial movement arising from a weighted average of these plans.

*Parallel object feature processing within the broader context of visual cognition.* In the field of visual cognition, there is evidence suggesting that visual short-term memory (VSTM), the working memory system that temporarily stores visual information for use in ongoing cognitive tasks, can be subdivided into spatial (e.g., location) and object-based (e.g., orientation, color) subsystems. For example, in certain dual-task designs, the maintenance of spatial and object-based VSTM can be dissociated (Hyun and Luck 2007; Woodman and Luck 2004; Woodman et al. 2001), and there appear to be cases in which brain damage may impair one system but not the other (Hanley et al. 1991). In the context of the current results, one possibility is that, during action planning, the VSTM system is recruited to process simultaneously all the object locations and their associated orientations in the visual display and then quickly relay this information to the sensorimotor system to form a corresponding set of fully elaborated competing motor plans, any of which can be immediately implemented once the final target has been cued. These proposed links between the VSTM and sensorimotor systems are in line with the recent observation that the capacity limit of three to four objects for recall in VSTM tasks (e.g., Luck and Vogel 1997) closely matches the upper limit for the number of targets that can be

simultaneously encoded for action, as revealed through the spatial averaging of reach trajectories (Gallivan et al. 2011a). This matching may be no coincidence; it seems likely that the processes of the VSTM and sensorimotor systems reflect interrelated components of a common underlying mechanism involved in generating goal-directed behavior. Indeed, this would provide a parsimonious explanation as to why functional MRI activity in the intraparietal sulcus is closely linked to not only VSTM performance on perceptual tasks (Todd and Marois 2004; Xu and Chun 2006), but also the planning and generation of reaching and grasping actions (e.g., Gallivan et al. 2013).

Much like the averaging of competing movement plans that appears to occur at the neural level (e.g., Glimcher and Sparks 1993), the averaging of spatial and object-based information also appears to be a basic strategy employed by sensory and cognitive systems. For instance, MacEvoy and colleagues (2009) showed, using intrinsic signal optical imaging, that the patterns of early visual cortex (V1) activity evoked by superimposed contrast gratings could be predicted by the averages of responses to their individual constituent gratings. Likewise, it was found that visual responses to object pairs in the lateral occipital complex, a brain area predominantly implicated in object-related processing (Malach et al. 1995), could also be predicted by the averages of responses to the individual constituent objects (MacEvoy and Epstein 2009, 2011). One possibility, suggested by these authors, is that this type of population-level averaging response may reflect part of a general neural coding scheme that preserves detailed information about visual stimuli in the environment while, at the same time, preventing a saturation of neural responses as the number of objects in the visual scene is increased (MacEvoy and Epstein 2009, 2011). This simple neural mechanism would seem particularly advantageous for processing the multiple motor-relevant features of objects in the environment in cases of target uncertainty and may be what ultimately underlies the target orientation and location biases observed here in the initial movement vectors.

*Conclusion.* Increasing neural and behavioral evidence from sensorimotor tasks as well as current models of decision-making suggest that the simultaneous preparation of competing actions reflects an inherent computational strategy employed by the brain (Andersen and Cui 2009; Beck et al. 2008; Cisek 2012; Wang 2008). As well-argued elsewhere, the parallel specification of multiple potential movements may confer important evolutionary advantages in a continuously changing environment, allowing one to switch efficiently between different actions in a moment's notice (Cisek 2007). Here, we provide behavioral evidence consistent with this framework, showing that the initial trajectory of the hand in a rapid reach task reflects the parallel and independent coding of potential target locations and orientations during planning.

## DISCLOSURES

## AUTHOR CONTRIBUTIONS

B.M.S., L.A.B., J.P.G., and J.R.F. conception and design of research; B.M.S. performed experiments; B.M.S. and J.R.F. analyzed data; B.M.S., L.A.B., J.P.G., and J.R.F. interpreted results of experiments; B.M.S. and J.R.F. prepared figures; B.M.S., J.P.G., and J.R.F. drafted manuscript; B.M.S., L.A.B., J.P.G., and J.R.F. edited and revised manuscript; B.M.S., L.A.B., J.P.G., and J.R.F. approved final version of manuscript.

## REFERENCES

**Andersen RA, Buneo CA.** Intentional maps in posterior parietal cortex. *Annu Rev Neurosci* 25: 189–220, 2002.

**Andersen RA, Cui H.** Intention, action planning, and decision making in parietal-frontal circuits. *Neuron* 63: 568–583, 2009.

**Arai K, McPeek RM, Keller EL.** Properties of saccadic responses in monkey when multiple competing visual stimuli are present. *J Neurophysiol* 91: 890–900, 2004.

**Baldauf D, Deubel H.** Attentional landscapes in reaching and grasping. *Vision Res* 50: 999–1013, 2010.

**Basso MA, Wurtz RH.** Modulation of neuronal activity by target uncertainty. *Nature* 389: 66–69, 1997.

**Baumann MA, Fluet MC, Scherberger H.** Context-specific grasp movement representation in the macaque anterior intraparietal area. *J Neurosci* 29: 6436–6448, 2009.

**Beck JM, Ma WJ, Kiani R, Hanks T, Churchland AK, Roitman J, Shadlen MN, Latham PE, Pouget A.** Probabilistic population codes for bayesian decision making. *Neuron* 60: 1142–1152, 2008.

**Brenner E, Smeets JB.** Fast responses of the human hand to changes in target position. *J Mot Behav* 29: 297–310, 1997.

**Chapman CS, Gallivan JP, Wood DK, Milne JL, Culham JC, Goodale MA.** Reaching for the unknown: multiple target encoding and real-time decision-making in a rapid reach task. *Cognition* 116: 168–176, 2010a.

**Chapman CS, Gallivan JP, Wood DK, Milne JL, Culham JC, Goodale MA.** Short-term motor plasticity revealed in a visuomotor decision-making task. *Behav Brain Res* 214: 130–134, 2010b.

**Cisek P.** Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos Trans R Soc Lond B Biol Sci* 362: 1585–1599, 2007.

**Cisek P.** Integrated neural processes for defining potential actions and deciding between them: a computational model. *J Neurosci* 26: 9761–9770, 2006.

**Cisek P.** Making decisions through a distributed consensus. *Curr Opin Neurobiol* 22: 927–936, 2012.

**Cisek P, Kalaska JF.** Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron* 45: 801–814, 2005.

**Cisek P, Kalaska JF.** Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *J Neurophysiol* 87: 1149–1154, 2002.

**Desmurget M, Prablanc C, Arzi M, Rossetti Y, Paulignan Y, Urquizar C.** Integrated control of hand transport and orientation during prehension movements. *Exp Brain Res* 110: 265–278, 1996.

**Desmurget M, Prablanc C, Rossetti Y, Arzi M, Paulignan Y, Urquizar C, Mignot JC.** Postural and synergic control for three-dimensional movements of reaching and grasping. *J Neurophysiol* 74: 905–910, 1995.

**Diedrichsen J, Shadmehr R, Ivry RB.** The coordination of movement: optimal feedback control and beyond. *Trends Cogn Sci* 14: 31–39, 2010.

**Fan J, He J, Tillery SI.** Control of hand orientation and arm movement during reach and grasp. *Exp Brain Res* 171: 283–296, 2006.

**Fattori P, Breveglieri R, Marzocchi N, Filippini D, Bosco A, Galletti C.** Hand orientation during reach-to-grasp movements modulates neuronal activity in the medial posterior parietal area V6A. *J Neurosci* 29: 1928–1936, 2009.

**Fattori P, Raos V, Breveglieri R, Bosco A, Marzocchi N, Galletti C.** The dorsomedial pathway is not just for reaching: grasping neurons in the medial parieto-occipital cortex of the macaque monkey. *J Neurosci* 30: 342–349, 2010.

**Findlay JM, Walker R.** A model of saccade generation based on parallel processing and competitive inhibition. *Behav Brain Sci* 22: 661–721, 1999.

**Gallivan JP, Chapman CS, Wood DK, Milne JL, Ansari D, Culham JC, Goodale MA.** One to four, and nothing more: nonconscious parallel individuation of objects during action planning. *Psychol Sci* 22: 803–811, 2011a.

**Gallivan JP, McLean DA, Flanagan JR, Culham JC.** Where one hand meets the other: limb-specific and action-dependent movement plans decoded from preparatory signals in single human frontoparietal brain areas. *J Neurosci* 33: 1991–2008, 2013.

**Gallivan JP, McLean DA, Smith FW, Culham JC.** Decoding effector-dependent and effector-independent movement intentions from human parieto-frontal brain activity. *J Neurosci* 31: 17149–17168, 2011b.

**Ghez C, Favilla M, Ghilardi MF, Gordon J, Bermejo R, Pullman S.** Discrete and continuous planning of hand movements and isometric force trajectories. *Exp Brain Res* 115: 217–233, 1997.

**Glimcher PW, Sparks DL.** Representation of averaging saccades in the superior colliculus of the monkey. *Exp Brain Res* 95: 429–435, 1993.

**Godijn R, Theeuwes J.** Programming of endogenous and exogenous saccades: evidence for a competitive integration model. *J Exp Psychol Hum Percept Perform* 28: 1039–1054, 2002.

**Gomi H.** Implicit online corrections of reaching movements. *Curr Opin Neurobiol* 18: 558–564, 2008.

**Grafton ST.** The cognitive neuroscience of prehension: recent developments. *Exp Brain Res* 204: 475–491, 2010.

**Grol MJ, Majdandzic J, Stephan KE, Verhagen L, Dijkerman C, Bekkering H, Verstraten F, Toni I.** Parieto-frontal connectivity during visually guided grasping. *J Neurosci* 27: 11877–11887, 2007.

**Hanley JR, Young AW, Pearson NA.** Impairment of the visuo-spatial sketch pad. *Q J Exp Psychol A* 43: 101–125, 1991.

**Hyun JS, Luck SJ.** Visual working memory as the substrate for mental rotation. *Psychon Bull Rev* 14: 154–158, 2007.

**Jeannerod M.** Intersegmental coordination during reaching at natural visual objects. In: *Attention and Performance IX*, edited by Long J and Baddeley A. New York: Lawrence Erlbaum Associates, 1981, p. 153–168.

**Jeannerod M.** *The Neural and Behavioural Organization of Goal-Directed Movements*. Oxford, UK: Oxford Univ. Press Psychology Series no. 5, 1988.

**Jeannerod M.** The timing of natural prehension movements. *J Mot Behav* 16: 235–254, 1984.

**Jeannerod M, Arbib MA, Rizzolatti G, Sakata H.** Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci* 18: 314–320, 1995.

**Johnson SH, Grafton ST.** From 'acting on' to 'acting with': the functional anatomy of object-oriented action schemata. *Prog Brain Res* 142: 127–139, 2003.

**Luck SJ, Vogel EK.** The capacity of visual working memory for features and conjunctions. *Nature* 390: 279–281, 1997.

**MacEvoy SP, Epstein RA.** Constructing scenes from objects in human occipitotemporal cortex. *Nat Neurosci* 14: 1323–1329, 2011.

**MacEvoy SP, Epstein RA.** Decoding the representation of multiple simultaneous objects in human occipitotemporal cortex. *Curr Biol* 19: 943–947, 2009.

**MacEvoy SP, Tucker TR, Fitzpatrick D.** A precise form of divisive suppression supports population coding in the primary visual cortex. *Nat Neurosci* 12: 637–645, 2009.

**Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB.** Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc Natl Acad Sci USA* 92: 8135–8139, 1995.

**Matelli M, Luppino G.** Parietofrontal circuits: parallel channels for sensory-motor integrations. *Adv Neurol* 84: 51–61, 2000.

**McClelland JL.** On the time relations of mental processes: an examination of systems of processes in cascade. *Psychol Rev* 86: 287–330, 1979.

**McPeek RM, Han JH, Keller EL.** Competition between saccade goals in the superior colliculus produces saccade curvature. *J Neurophysiol* 89: 2577–2590, 2003.

**McSorley E, Haggard P, Walker R.** Time course of oculomotor inhibition revealed by saccade trajectory modulation. *J Neurophysiol* 96: 1420–1424, 2006.

**Miller GA, Galanter E, Pribram KH.** *Plans and the Structure of Behavior*. New York: Henry Holt, 1960.

**Platt ML, Glimcher PW.** Responses of intraparietal neurons to saccadic targets and visual distractors. *J Neurophysiol* 78: 1574–1589, 1997.

**Port NL, Wurtz RH.** Sequential activity of simultaneously recorded neurons in the superior colliculus during curved saccades. *J Neurophysiol* 90: 1887–1903, 2003.

**Resulaj A, Kiani R, Wolpert DM, Shadlen MN.** Changes of mind in decision-making. *Nature* 461: 263–266, 2009.

**Rizzolatti G, Matelli M.** Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 153: 146–157, 2003.

**Sailer U, Eggert T, Ditterich J, Straube A.** Global effect of a nearby distractor on targeting eye and hand movements. *J Exp Psychol Hum Percept Perform* 28: 1432–1446, 2002.

**Sakata H, Taira M.** Parietal control of hand action. *Curr Opin Neurobiol* 4: 847–856, 1994.

**Sakata H, Taira M, Kusunoki M, Murata A, Tanaka Y, Tsutsui K.** Neural coding of 3D features of objects for hand action in the parietal cortex of the monkey. *Philos Trans R Soc Lond B Biol Sci* 353: 1363–1373, 1998.

**Schall JD.** Decision making: neural correlates of response time. *Curr Biol* 12: R800–R801, 2002a.

**Schall JD.** The neural selection and control of saccades by the frontal eye field. *Philos Trans R Soc Lond B Biol Sci* 357: 1073–1082, 2002b.

**Smeets JB, Brenner E.** A new view on grasping. *Motor Control* 3: 237–271, 1999.

**Song JH, Nakayama K.** Target selection in visual search as revealed by movement trajectories. *Vision Res* 48: 853–861, 2008.

**Sternberg S.** Memory-scanning: mental processes revealed by reaction-time experiments. *Am Sci* 57: 421–457, 1969.

**Tipper SP, Howard DV, Houghton G.** Behavioral consequences of selection from population codes. In: *Attention Perform*, edited by Monsell S and Driver J. Cambridge, MA: MIT Press, 2000, p. 223–245.

**Tipper SP, Howard LA, Jackson SR.** Selective reaching to grasp: evidence for distractor interference effects. *Vis Cogn* 4: 1–38, 1997.

**Todd JJ, Marois R.** Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature* 428: 751–754, 2004.

**Todorov E.** Optimality principles in sensorimotor control. *Nat Neurosci* 7: 907–915, 2004.

**Tunik E, Frey SH, Grafton ST.** Virtual lesions of the anterior intraparietal area disrupt goal-dependent on-line adjustments of grasp. *Nat Neurosci* 8: 505–511, 2005.

**Van der Stigchel S, Meeter M, Theeuwes J.** Eye movement trajectories and what they tell us. *Neurosci Biobehav Rev* 30: 666–679, 2006.

**Vesia M, Prime SL, Yan X, Sergio LE, Crawford JD.** Specificity of human parietal saccade and reach regions during transcranial magnetic stimulation. *J Neurosci* 30: 13053–13065, 2010.

**Wang XJ.** Decision making in recurrent neuronal circuits. *Neuron* 60: 215–234, 2008.

**Welsh TN, Elliott D, Weeks DJ.** Hand deviations toward distractors. Evidence for response competition. *Exp Brain Res* 127: 207–212, 1999.

**Wood DK, Gallivan JP, Chapman CS, Milne JL, Culham JC, Goodale MA.** Visual salience dominates early visuomotor competition in reaching behavior. *J Vis* 11: 16, 2011.

**Woodman GF, Luck SJ.** Visual search is slowed when visuospatial working memory is occupied. *Psychon Bull Rev* 11: 269–274, 2004.

**Woodman GF, Vogel EK, Luck SJ.** Visual search remains efficient when visual working memory is full. *Psychol Sci* 12: 219–224, 2001.

**Xu Y, Chun MM.** Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature* 440: 91–95, 2006.