RESEARCH ARTICLE

# Selection of wrist posture in conditions of motor ambiguity

**Daniel K. Wood · Melvyn A. Goodale**

**Abstract** In our everyday motor interactions with objects, we often encounter situations where the features of an object are determinate (i.e., not perceptually ambiguous), but the mapping between those features and appropriate movement patterns is indeterminate, resulting in a lack of any clear preference for one posture over another. We call this indeterminacy in stimulus-response mapping 'motor ambiguity'. Here, we use a grasping task to investigate the decision mechanisms that mediate the basic behavior of selecting one wrist posture over another in conditions of motor ambiguity. Using one of two possible wrist postures, participants grasped a dowel that was presented at various orientations. At most orientations, there was a clear preference for one wrist posture over the other. Within a small range of orientations, however, participants were variable in their posture selection due to the fact that the dowel was ambiguous with respect to the hand posture it afforded. We observed longer reaction times (RT) during 'ambiguous' trials than during the 'unambiguous' trials. In two subsequent experiments, we explored the effects of foreknowledge and trial history on the selection of wrist posture. We found that foreknowledge led to shorter RT unless the previous trial involved selecting a posture in the ambiguous region, in which case foreknowledge gave no RT advantage. These results are discussed within the context of existing models of sensorimotor decision making.

**Keywords** Affordances · Orientation · Competition · Decision making · Action selection · Ambiguity

## Introduction

When one is faced with the everyday task of using a precision grip to pick up a pencil, most orientations of the pencil clearly afford a variation of just one of the two possible wrist posture patterns (see Fig. 1). In such cases, the straightforward one-to-one mapping of pencil orientation to coordinative pattern can be attributed to the fact that, with respect to the pencil's orientation, both wrist postures have an absolute critical boundary past which it is impossible, due to the mechanical properties of the relevant limb segments and joints, to perform the grasp. Of course, since the wrist postures become increasingly uncomfortable as they approach their respective absolute critical boundaries, people tend to switch between wrist posture patterns at preferred critical boundaries (PCB) instead (Mark et al. 1997; Stasik and Mark 2005). In wrist posture selection tasks similar to the pencil example described above, a number of factors (aside from a simple biomechanical cost function) can influence the bias of the PCB, where the bias is the control parameter's critical value at which pronated and supinated grasping patterns are equally probable. For the purposes of the present study, the more relevant point is the robustness of the finding that average posture selection within the PCB is better described by a logistic function (see Fig. 3a, c) than by a step function (Kent et al. 2009; van Bergen et al. 2007; Kelso et al. 1994;

D. K. Wood · M. A. Goodale
Department of Psychology, Centre for Brain and Mind,
University of Western Ontario,
London, ON N6A 5C2, Canada

M. A. Goodale (✉)
Department of Psychology, University of Western Ontario,
London, ON N6A 5C2, Canada
e-mail: mgoodale@uwo.ca

**Fig. 1** *Columns* show the two possible categorical wrist postures for our task. *Rows* show examples of dowel orientations inside and outside of the ambiguous region (i.e., the PCB)
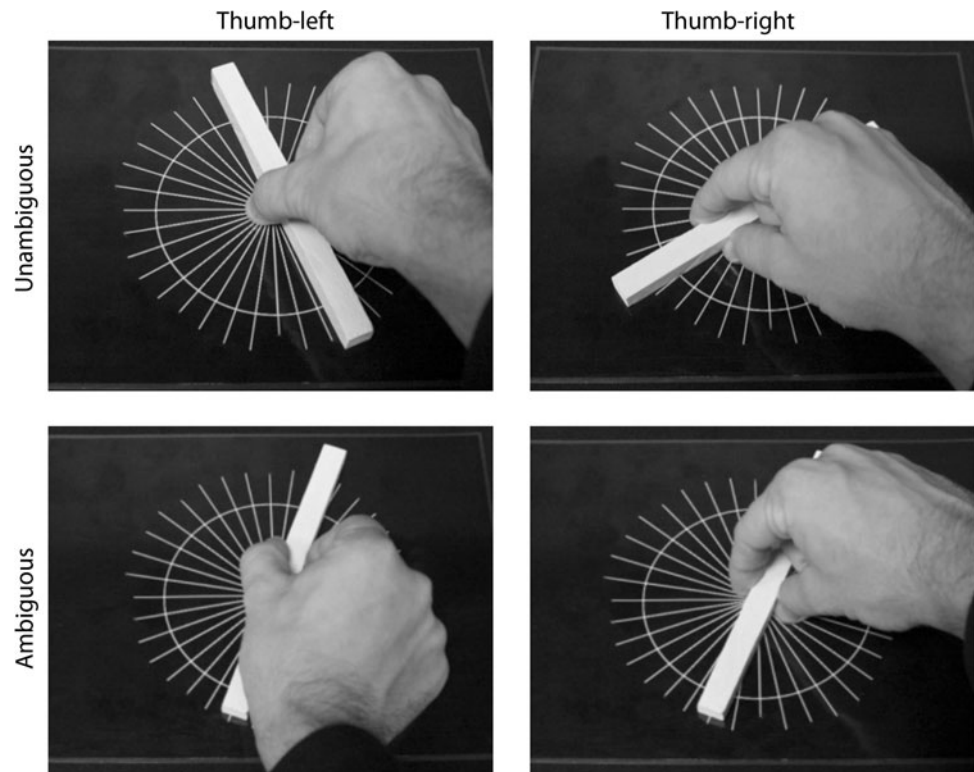


Stelmach et al. 1994; Dijkerman et al. 2009; Rosenbaum et al. 1992).

Why is the function describing the transition from one action pattern to another across the PCB gradual instead of discrete? One possible clue comes from electrophysiological studies where neural activity in parietal cortex was recorded while a monkey viewed a random dot motion (RDM) coherence display and reported the perceived direction of motion coherence with a saccade (Gold and Shadlen 2007). In general, these studies have found that neurons in lateral intraparietal cortex (area LIP) are able to treat motion-related activity (from area MT) as evidence for or against a given saccade choice (i.e., a given perceptual interpretation of the stimulus). The gain of that motion-related signal gradually accumulates in LIP cells until the discharge rate reaches a saccade initiation threshold. If evidence from the motion signal is low due to a low coherence display, other modulatory influences (including stochastic noise) play a larger role in determining the fate of the perceptual decision as computed by LIP, resulting in the familiar logistic transition between perceptual decisions (and, by extension, between saccade directions). In a RT version of this task, Roitman and Shadlen (2002) found that the speed and the accuracy of perceptual decisions, as well as the slope of the change in discharge rate for LIP neurons, increased as a function of motion strength. Even on low coherence trials (including error trials), the sign of the change in firing rate predicted

the perceptual choice, and the slope of that change still predicted RT. Similar results have been observed in a vibrotactile frequency discrimination paradigm (Romo et al. 2004).

Past work with the RDM paradigm demonstrates how the use of a psychophysical task within a decision-making paradigm was able to shed light upon a possible explanation for the distribution of categorical responses and RTs during discrimination in conditions of perceptual ambiguity (i.e., the low coherence condition). We hypothesized that neural mechanisms similar to those responsible for perceptual decision making are responsible for the selection of coordinative patterns during critical boundary tasks. A corollary of this hypothesis is that, just as the RDM task creates a condition in which the information given by the stimulus is insufficient to determine a stable identity or categorical parameter value for the stimulus (i.e., perceptual ambiguity), critical boundary tasks create a condition in which the identity and all relevant spatial parameters of the stimulus are perceptually stable, but those parameters fail to determine a stable categorical motor response. One might call this condition 'motor ambiguity'.

The thing that distinguishes motor ambiguity dilemmas from the traditional degrees of freedom problem is the categorical nature of the motor responses in the former. The degrees of freedom problem (Bernstein 1967) is the problem of parameterizing a goal action that could, due to the overabundance of mechanical degrees of freedom

inherent in effectors like a human arm, be accomplished in an infinite number of ways. Motor ambiguity, however, is an instability between only a few patterns of coordination (i.e., systematic couplings between degrees of freedom). A coordinative pattern already presupposes, if not a full solution, at least enough of a solution to the degrees of freedom problem to qualify the planned movement as a member of some equivalence class of movements. The work of Kelso (1995; Buchanan et al. 1996) is helpful in articulating this distinction.

The motor ambiguity hypothesis predicts higher RT for trials within the PCB. The primary motivation for the present study was to use a wrist posture selection task to test this prediction. At first, this prediction seems to be a straightforward extension of Hick's law (Hick 1952), which states that there is a linear relationship between RT and the log of the number of stimulus-response (S-R) alternatives in a choice RT task. However, Hick's law can be attenuated by practice (Longstreth et al. 1985) and fully violated by S-R mappings with high compatibility (Fitts and Seeger 1953; Leonard 1959). Since the act of reaching to grasp a dowel is both a highly practiced and hyper-compatible response to seeing a dowel, one might be inclined to predict a violation of Hick's law in the case of the wrist posture selection task.

Is there any other theoretical framework that would not predict higher RT in conditions of motor ambiguity? In optimal feedback control theory (Todorov and Jordan 2002), the minimal intervention principle states that an optimal feedback controller allows variability in task-irrelevant dimensions of a movement by allowing those dimensions to be controlled by noise. To the degree that two coordinative patterns can accomplish the same goal with equal cost, they represent a task-irrelevant dimension of the movement. An optimal feedback controller should then relegate this level of movement parameterization to stochastic noise in the system, resulting in variable posture selection. As these costs become imbalanced (e.g., as skeletomuscular constraints and dowel orientation render one of the candidate wrist postures increasingly uncomfortable), this level of parameterization should become task-relevant and the controller should bias the selection. Under the assumption that there can be gradation in the degree to which an optimal feedback controller treats any movement dimension as task-relevant, this minimal intervention principle would predict the behavior that has been observed in the wrist posture selection task, namely, the logistic transition between postures as a function of dowel orientation. Interestingly, because this transition region emerges out of a differential contribution of stochastic noise to the selection of a coordination pattern (with the largest contribution resulting in each posture being selected, on average, an equal number of times), the minimal intervention principle *should* predict, all other things being equal, that RT would not increase within the PCB.

While a number of past studies have investigated kinematic aspects of the wrist posture selection task in general, these have tended to focus on issues like the contribution of forearm rotation to the coordinative dynamics of reaching movements (Desmurget et al. 1996; Gentilucci et al. 1996; Soechting and Flanders 1993; Rand and Stelmach 2005; Stelmach et al. 1994; Lacquaniti and Soechting 1982), with no focus upon the PCB. There are, however, a few exceptions. For example, van Bergen et al. (2007) showed that movement time (MT) is a linear function of the degree of forearm rotation required to execute a grasp (i.e., the longest MTs will occur in the PCB, where the most extreme forearm rotations occur). Johnson (2000) replicated this finding and went on to show that it takes participants longer to vocally indicate which wrist posture they would use if the posture they end up choosing is one that they would rate as highly awkward (i.e., vocal RT goes up for prospective grasping judgments within the PCB, where the most awkward wrist postures occur). Frak et al. (2001) combined RT and MT into a composite measure ('response time') and found that response time increased when participants adopted highly rotated wrist postures.

Thus, whenever RT has been used as a measure in past incarnations of the wrist posture selection task, it has either been used for prospective judgments instead of actual movements, or it has been combined with MT, which would complicate any efforts to make inferences about how the movement was planned. We are not aware of any past studies that have examined RT differences for actual movements in a critical boundary task, or in any other task that represents a pure motor discrimination in the way that a critical boundary task does. Here, we report the results of three separate experiments designed to explore a behavioral prediction of the hypothesis that the resolution of motor ambiguity is accomplished by neural mechanisms similar to those shown to be responsible for resolving perceptual ambiguity.

## Experiment 1

### Participants

There were nine volunteers (four males, ages 18–30) in Experiment 1. All participants were right-handed (determined by self-report) and had normal visual acuity. Written informed consent was obtained from all participants, and the local ethics review board approved the protocols for all experiments. All participants were naïve to the experimental predictions.

Apparatus and design

The stimulus object was a white, rectangular wooden dowel (175 × 15 × 15 mm). It was presented at the participant's midline, 40 cm from the table's edge (black surface, 1 m × 1 m). Reaction times were collected with the release of a start button (located 15 cm from edge of table). Participants wore LCD goggles (PLATO goggles; Translucent Technologies, Toronto, ON, Canada).

The dowel was presented at 21 orientations (5° increments from 115° to 215°; see Fig. 2a). Each of the six experimental blocks consisted of all 21 orientations presented three times in one of three orders: clockwise, counter-clockwise, and pseudo-randomized. Each participant completed two sessions (separated by at least 5 h) of 378 trials. Participants were explicitly informed of the nature of the trial order for the upcoming block.

Kinematic data were collected with an OptoTRAK (Northern Digital, Waterloo, ON, Canada) optoelectronic recording system. The IREDs were placed on the proximal left corner of the index finger nail, the proximal right corner of the thumb nail, and the midpoint of the dorsal surface of the wrist in line with the ulnar styloid process. The OptoTRAK was simultaneously triggered with the opening of the goggles at the beginning of each trial. It then recorded the position of the IREDs for 1,500 ms at a rate of 100 Hz.

Procedure

Participants sat at the table with their midline aligned with the start button. They were instructed to pinch together the right thumb and index finger while depressing the start button at the beginning of each trial. Between trials, participants heard white noise in headphones (to mask unintentional auditory cues that might allow participants to make a decision prior to the start of the trial) and the

goggles remained closed. After a beep, the white noise stopped and after a variable interval (500–3,500 ms), the goggles opened. The participants were told that as soon as the goggles became transparent, they were to reach out and, as quickly and accurately as possible, pick up the dowel with a precision grip at its middle, lift it slightly, and then put it back down. The goggles remained transparent for 1,500 ms after the release of the start button. There were short breaks between blocks, and participants were always informed of the nature of the upcoming block (i.e., clockwise, counter-clockwise, or random) prior to its initiation.

Statistical analyses

All analyses were conducted with one-way repeated-measures ANOVA. Simple main effects analyses were performed where significant interactions were observed, and multiple comparisons were carried out using Bonferroni-adjusted alpha levels.

Data processing

Wrist posture selection was coded with reference to the long edge of the dowel that the thumb of the participant was touching; precision grips where the thumb touched the right edge of the dowel were termed "thumb-right" wrist postures, while those where the thumb touched the left edge were termed "thumb-left" (Fig. 1). The probability $P$ of using a thumb-right wrist posture at orientation $t$ was described by the following logistic function:

$$P = \frac{e^{b_0 + b_1 t}}{1 + e^{b_0 + b_1 t}} \qquad (1)$$

where $b_0$ and $b_1$ are coefficient estimates based on an initial general linear model (binary logit) fit. The points at which
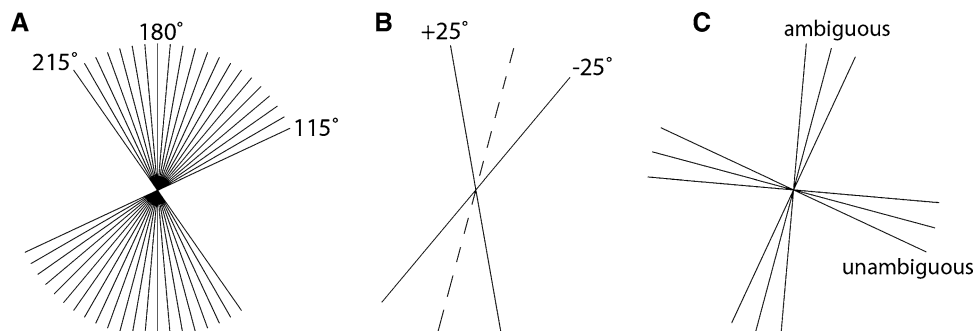


Fig. 2 The possible stimulus orientations in Experiments 1–3. **a** In Experiment 1, there were 21 orientations, moving from 115° to 215° in 5° increments. **b** In Experiment 2, there were only two possible orientations: 25° clockwise and counter-clockwise from the switch point (shown here as a *dotted line* for reference). **c** In Experiment 3,

there were six possible orientations, comprised of two regions with three orientations each. The ambiguous region consisted of the switch point and the orientations 10° clockwise and counter-clockwise from the switch point. The orientations in the unambiguous region were simply orthogonal to the three orientations in the ambiguous region

this sigmoid function reached the 75th and 25th percentile of thumb-right probability (Fig. 3a) were respectively rounded down and up to the nearest multiple of 5 and subsequently defined as the boundaries of that participant's PCB. We called this the "ambiguous" region. Based on participants' performance, this ambiguous region consisted of an average of 18° (min = 15, max = 25) for the randomized condition, 16° (min = 10, max = 20) for clockwise, and 16° (min = 15, max = 20) for counter-clockwise. The orientations outside of the participant's ambiguous region were grouped into either the left (i.e., counter-clockwise of the ambiguous region) or right (i.e., clockwise of the ambiguous region) regions. This analysis, which was conducted within each trial-order condition for each participant (Fig. 3c), resulted in a three-level variable that we used to analyze our other dependent measures, primarily RT (i.e., the time between the opening of the LCD goggles and the button release) and MT (i.e., the time between the button release and contact with the dowel).

Missing data points in the Optotrak recording were linearly interpolated. Fourteen trials in total were discarded because of excessive missing points in the kinematic data.

The beginning of the reach was defined as the time at which the velocity of the wrist IRED exceeded 20 mm/s, while the end of the reach was defined as the time at which the velocity of the wrist IRED dipped below 5% of the maximum velocity during the reach. An outlier analysis was conducted for all measures of interest. All trials with scores 3 standard deviations above or below the mean for each participant were discarded. Overall, 102 trials were excluded from analysis (approximately 1.5% of total trials).

## Results and discussion

### Wrist posture selection

To better understand any possible influences that the trial-order manipulation was having upon the selection of wrist postures, we first tested whether trial order had any effect on the switch point (i.e., 50th percentile on the sigmoid curve). If trial order was a factor in determining posture selection in the ambiguous region, one would expect switch
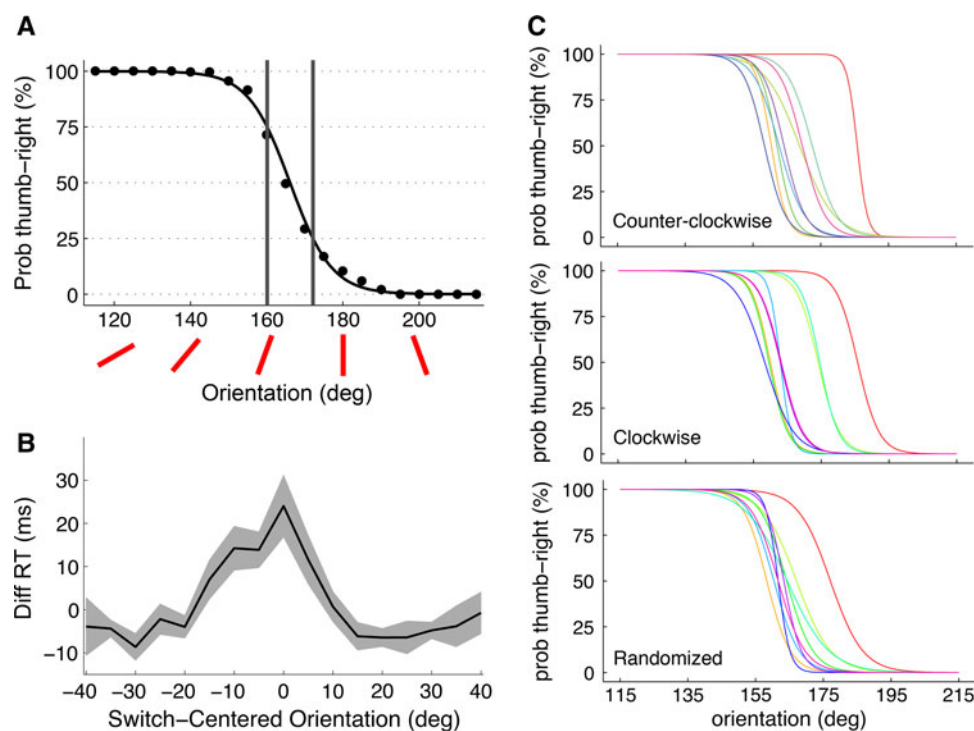


**Fig. 3** Characterization of the ambiguous region. **a** Boundaries of the ambiguous region were determined by marking 75th and 25th percentiles (*gray bars*) on a logistic fit of the average probability of using a thumb-right posture. The data shown here represent an average across all participants and all trial-order conditions. **b** After determining each participant's switch point (i.e., the 50th percentile; designated here as '0'), we recoded orientation as a function of angular distance from the switch point. Shown here for descriptive purposes are mean difference scores for RT (i.e., RT of current trial minus within-subject mean RT) at each switch-centered orientation, averaged across trial-order conditions. Shaded area represents standard error of the mean. There is a clear peak in RT at the switch point. **c** Average wrist posture selection for each of the 9 participants in the counter-clockwise (*top*), clockwise (*middle*), and randomized (*bottom*) trial orders. These three plots give a sense of the intersubject variability in participants' wrist posture selection

points during the clockwise condition to be further clockwise (i.e., lower values) and vice versa for the counterclockwise condition, with switch points for the randomized condition ending up somewhere between those of the other two conditions. There was, however, no significant effect of trial order on switch point, $F(2,16) = 2.5$, $P = 0.1$. Even if this test had reached significance, it is likely that it would have been driven primarily by the fact that switch points for the randomized condition tended to be located farther clockwise than for the clockwise and counterclockwise conditions.

We were also interested in seeing whether trial order had an effect on the width of the ambiguous region, which is effectively a measure of the slope of the sigmoid curve. This could be considered an indirect measure of the amount of ambiguity experienced by a given participant. There was, however, no detectable effect of trial order on the width of the ambiguous region.

Kinematic and temporal measures

We were interested in searching the kinematics of participants' reach-to-grasp movements for evidence of the posture selection process occurring in-flight. First, we tested whether there was any effect of region or trial order on the average peak velocity during a reach. If participants were hesitating or switching mid-flight during ambiguous trials, one might expect to see lower peak velocities during those trials. There was a significant main effect of region, $F(2,16) = 13.0$, $P < 0.001$, $\eta_P^2 = 0.62$. Trials in the right region ($M = 1,275$ mm/s) led to significantly faster peak velocities than those in the left region ($M = 1,210$ mm/s). However, trials in the ambiguous region ($M = 1,242$ mm/s) were not significantly different from those in any other region, 95% CI $\pm 14.9$. To follow up on this effect of region, we conducted a separate analysis in which we tested whether wrist posture had an effect (or interacted with the region factor) on peak velocity. This analysis revealed that the apparent effect of region on peak velocity is due to an effect of wrist posture, $F(1,8) = 21.8$, $P < 0.005$, $\eta_P^2 = 0.73$. Thumb-left wrist postures ($M = 1,217$ mm/s) led to slower peak velocities than thumb-right wrist postures ($M = 1,271$ mm/s), regardless of region, 95% CI $\pm 16.4$.

The analysis of percent time to peak velocity revealed a main effect of region, $F(2,16) = 25.2$, $P < 0.001$, $\eta_P^2 = 0.76$. Reaches in the right region ($M = 46.3\%$) and ambiguous region ($M = 46.2\%$) had lower percent time to peak velocity than reaches in the left region ($M = 48.7\%$), 95% CI $\pm 0.56\%$. A follow-up analysis (region × wrist posture) revealed a significant interaction, $F(1,8) = 5.8$, $P < 0.05$, $\eta_P^2 = 0.418$. Reaches with thumb-left wrist postures in the left region ($M = 48.7\%$) had higher percent

time to peak velocity than reaches with thumb-right wrist postures in right region ($M = 46\%$) and thumb-left wrist postures in the ambiguous region ($M = 46\%$), 95% CI $\pm 0.87\%$.

When the initial ANOVAs were performed for RT and MT in Experiment 1, there was no significant difference between the clockwise and counterclockwise conditions in any of the regions. We therefore collapsed them into one common trial-order condition, which we called the *successive* condition. Likewise, since there was no detectable difference between left and right regions, trials in these regions were grouped into one common *unambiguous* region. The MT data were analyzed with a region (ambiguous, unambiguous) by trial-order (successive, random) repeated-measures ANOVA. We found an effect of region, $F(1,8) = 31.1$, $P < 0.001$, $\eta_P^2 = 0.8$. Movements during ambiguous trials ($M = 689$ ms) took longer than those in unambiguous trials ($M = 645$ ms, 95% CI $\pm 7.8$), $t(8) = 5.5$, $P < 0.001$.

The RT data were also analyzed with a region (ambiguous, unambiguous) by trial-order (successive, random) repeated-measures ANOVA. There was a significant region × trial-order interaction in the RT data, $F(1,8) = 6.4$, $P < 0.05$, $\eta_P^2 = 0.44$. No difference between trial-order conditions was found for trials in the ambiguous region. Reaction times for unambiguous trials, however, were faster during successive conditions ($M = 325$ ms) than during the randomized condition ($M = 346$ ms), $t(8) = 5$, $P < 0.001$. Within the randomized condition, movements during ambiguous trials ($M = 355$ ms) took longer to initiate than those in unambiguous trials, $t(8) = 4.2$, $P < 0.005$. Likewise, within the successive condition, movements during ambiguous trials ($M = 348$ ms, 95% CI $\pm 6.5$) took longer to initiate than those in unambiguous trials, $t(8) = 3.9$, $P < 0.005$. In other words, when the dowel was oriented within the ambiguous region, it took participants longer to both initiate their movements (Fig. 4a) and complete those movements.

Given that more than one of the kinematic measures showed an effect of region that was, upon further analysis, explained by an effect of wrist posture, we considered it important to test whether the prominent effect of region on reaction time was also due to an effect of wrist posture. There was a significant interaction between grip and region, $F(1,8) = 8.4$, $P < 0.05$, $\eta_P^2 = 0.51$. The rise in RT for trials in the ambiguous region was attenuated (although still prominent) for thumb-left wrist postures (i.e., a mean difference of 15.6 ms between trials in ambiguous and unambiguous region) compared to the same effect for thumb-right wrist postures (a mean difference of 30.3 ms between trials in ambiguous and unambiguous region, 95% CI $\pm 5.9$). After correction for multiple comparisons, there was no significant difference
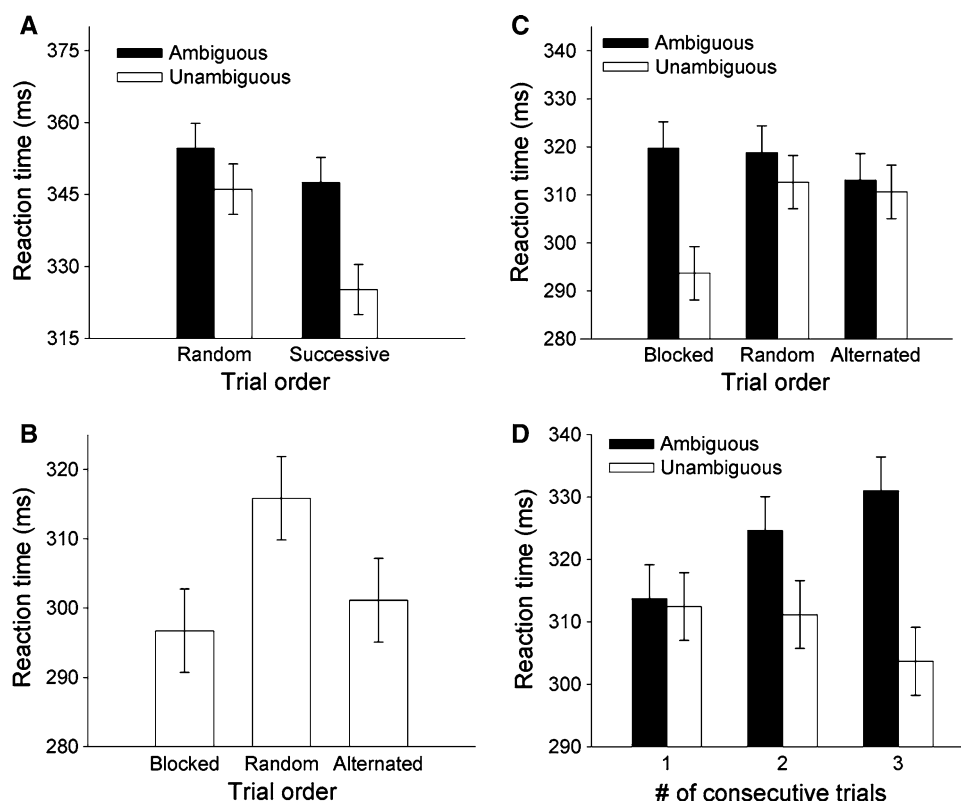
**Fig. 4** Reaction time results. **a** Experiment 1. In the randomized and successive blocks, RT was longer for ambiguous than for unambiguous trials. RT in the unambiguous condition was longer for randomized than for successive trials. **b** Experiment 2. While there was no RT difference between blocked and alternated trials, both conditions had faster RT than the randomized condition. **c** Experiment 3. Blocked unambiguous trials had faster RT than blocked ambiguous trials. This difference (much smaller, but in the same direction) was also observed in the randomized condition. There was no mean RT difference between ambiguous and unambiguous trials in the alternated condition. **d** Experiment 3, *effect of trial-type repetition*. As the number of consecutive trials increased, RT differences between ambiguous and unambiguous trials steadily increased. *Error bars* indicate 95% confidence intervals derived from MSE term from the repeated-measures ANOVAs

between RTs for thumb-left and thumb-right wrist postures, regardless of region.

Finally, in light of past work that suggests RT is sometimes correlated with the speed of the upcoming movement (Klapp and Erwin 1976), we were interested in testing whether RT was correlated with either MT or peak velocity in this task. We were unable to detect any significant correlations. This remained the case when we broke the correlation tests up by the selected wrist posture.

## Experiment 2

Experiments 2 and 3 were designed to follow up on the finding (from Experiment 1) that RTs in the unambiguous regions were longer in the randomized trial order than they were in the successive trial orders. This difference could have been due to either (a) a lack of explicit foreknowledge of the upcoming trial type in the randomized condition, or (b) a mixed trial history (i.e., a cost of switching, which was minimized in the unmixed trial histories of the successive conditions). There is an extensive body of work showing that switching between task sets incurs a cost in RT (Monsell 2003). However, it has been shown that switching costs can be eliminated by precuing if S-R pairings are hyper-compatible, as saccading or reaching to a target have been shown to be (Hunt and Klein 2002). If it is the case that this trial-order effect was due to switching, it is still not entirely clear what participants were switching between. The effect could have been due to switching between (a) two distinct wrist postures or (b) conditions of ambiguity and unambiguity. Our primary motivation for conducting Experiments 2 and 3 was to clarify this result. In Experiment 2, our aim was to investigate the effects of foreknowledge and/or trial history while presentations of the stimulus switched between two unambiguous orientations of the dowel. Aside from any changes described below, Experiment 2 was identical to Experiment 1.

Participants

Eighteen right-handed volunteers (nine men, ages 18–52) were included in this study.

Apparatus and design

The dowel was only ever presented at two orientations: one at 25° counter-clockwise and one at 25° clockwise from the switch point (i.e., the orientation at which there was a 50% probability of choosing thumb-right). These were meant to be clear cases of orientations that afforded a thumb-left and thumb-right wrist posture, respectively (Fig. 2b). There were three blocks of trials, and each block consisted of 60 trials in one of three conditions: blocked, alternated, or pseudo-randomized. In the blocked condition, there were 30 consecutive trials with the dowel in one of the orientations, followed by 30 consecutive trials in the other orientation. In the alternated condition, the orientation of the dowel simply alternated back and forth between the two orientations. In the pseudo-randomized condition, 30 trials of each of the two orientations were randomly mixed.

We identified each participant's switch point during a short diagnostic procedure prior to the session. This procedure consisted of placing the dowel 5° clockwise if a thumb-left posture was selected in the previous trial, and counter-clockwise if that posture was thumb-right. Occasionally, to keep the procedure from being too obvious, the dowel was placed at a random orientation. This process continued until the participant consistently switched wrist postures between two adjacent dowel orientations, and the midpoint between these two orientations was defined as the switch point.

During piloting for Experiment 2, we noticed that movements of a participant's shoulders (e.g., swiveling in the chair, shifting weight, etc.) produced shifts in that participant's current switch point. In Experiment 1, this tendency may have led to the ultimately trivial result of slightly less precise demarcations between regions, which most likely resulted in more variability in our temporal and kinematic analyses. However, in Experiments 2 and 3, it was essential to maintain a precise and consistent switch point throughout an experimental session. Therefore, a chinrest was used to minimize shifting of the participant's body during the experiment, ensuring that dowels within the ambiguous region were inducing motor ambiguity. The addition of the chinrest made it necessary to present the stimulus to the right of midline (based on earlier an earlier pilot experiment, we chose a distance of 20 cm) to prevent the chinrest from blocking the elbow during reaches in which the participant used a thumb-left wrist posture. During the earlier pilot testing, we observed that presenting the stimulus in this location (when compared to the central

location) produced a strong trend of shifting the entire ambiguous region an average of 10° in the clockwise direction, $P = 0.055$. That this effect did not quite reach significance can be explained by the fact that, while six out of seven pilot subjects had more clockwise switch points for the rightward stimulus location, one of the participants (who had to be reminded several times to stay in one position throughout the experiment) had the opposite pattern of performance. Indeed, removing this subject from the analysis results in a significant difference between the two locations, $t(4) = 6.3$, $P < 0.005$. Thus, this pilot work supports the straightforward notion that the switch point (and, ipso facto, the ambiguous region) is largely determined by the geometry of the relationship between the object to be grasped and the body of the person who is grasping it.

Data processing

No kinematic data were collected. Only reaction times were recorded and analyzed. In Experiment 2, the outlier analysis resulted in the exclusion of 83 trials (approximately 3.8% of total trials).

Results and discussion

In Experiment 2, we manipulated both the participant's trial history and explicit foreknowledge regarding which of two unambiguous dowel orientations would be presented in an upcoming trial. In the blocked condition, the participants had an unmixed trial history and explicit foreknowledge of the upcoming trial type. In the randomized condition, participants had a mixed trial history and no foreknowledge of the upcoming trial type. Neither of these conditions alone, therefore, could settle whether the trial-order effect discovered in Experiment 1 was due to trial history or explicit foreknowledge. The alternated condition, in which participants had a mixed trial history and explicit foreknowledge of the upcoming trial type, was the crucial condition. If this condition led to RTs similar to those observed in the randomized condition, one might conclude that trial history was the most significant determinant of the participant's motor planning. If, however, RTs in the alternated condition looked more like those in the blocked condition, one might conclude that explicit foreknowledge of upcoming trial type was the determining factor.

Reaction times were analyzed with a three-level single factor repeated-measures ANOVA, where the factor was trial order (randomized, alternated, or blocked). There was a significant effect of trial order, $F(2,34) = 8.2$, $P < 0.001$, $\eta_P^2 = 0.33$ (Fig. 4b). When the dowel was switched

between two unambiguous orientations, participants initiated movements slower when trials were presented in a random order ($M = 316$ ms) than when they were presented in a blocked order ($M = 297$ ms), $t(17) = 3.2$, $P < 0.05$. Participants initiated movements faster when trials were presented in an alternated order ($M = 301$ ms, 95% CI $\pm$ 7) than when they were presented in a random order, $t(17) = 3.4$, $P < 0.01$. No significant difference between the alternated and blocked trials was detected. Our results suggest that when the dowel was switched between two unambiguous orientations, foreknowledge was an important factor in determining RT.

## Experiment 3

Experiment 3 was a continuation of an effort that began with Experiment 2, namely, the effort to discover whether the trial-order effect observed in the unambiguous region in Experiment 1 was due to a switching cost (i.e., switching more frequently between different categorical wrist postures in the randomized condition) or a lack of explicit foreknowledge regarding the upcoming trial type in the randomized condition. In Experiment 2, we found that randomized switching between two unambiguous orientations led to longer RT compared to the blocked condition, but that providing participants with explicit foreknowledge in the alternated condition eliminated this RT cost. Since it was still unclear whether any possible switching costs in Experiment 1 were due to switching between unambiguous orientations or to switching between ambiguous and unambiguous orientations, we designed Experiment 3 to investigate the effects of foreknowledge and/or trial history while presentations of the stimulus switched between ambiguous and unambiguous orientations of the dowel. Aside from any changes described below, Experiment 3 was identical to Experiment 2.

### Participants

Fourteen volunteers (six men, ages 18–52) participated in Experiment 3. Thirteen of these participants had already participated in Experiment 2 (but had not been debriefed, and were thus still naïve).

### Apparatus and design

We reasoned that if we included only one possible orientation in the ambiguous region, participants would simply choose a default wrist posture. Including more than one orientation increased the probability that both of the wrist postures were possible affordances when the stimulus was presented in the ambiguous region. Therefore, the dowel

was presented at three ambiguous and three unambiguous orientations (directly perpendicular to the three ambiguous). Within both clusters of three orientations, the two outer orientations were 10° to either side of the middle orientation. In order to determine each participant's ambiguous region, a diagnostic procedure identical to the one performed prior to Experiment 2 was performed at the beginning of each session. The middle orientation of the ambiguous region was the switch point. While the ambiguous orientations were designed to afford both a thumb-left and thumb-right wrist posture, the unambiguous orientations afforded only one wrist posture, best characterized as thumb-down. Thus, there were two basic regions in which the dowel was presented: ambiguous and unambiguous (Fig. 2c). As in Experiment 2, we included three separate blocks of trials, each consisting of the object being presented in one of three trial orders: blocked, alternated, or pseudo-randomized. There were 42 repetitions of each region within each block type, resulting in a total of 252 trials.

### Data processing and statistical analysis

In Experiment 3, we removed 93 outliers (approximately 2.6% of total trials). The F-ratio of one ANOVA was Huyhn-Feldt corrected due to a sphericity violation.

## Results and discussion

Reaction time was analyzed with a repeated-measures ANOVA with factors of region (ambiguous or unambiguous) and block type (blocked, randomized, or alternated). There was a significant interaction between region and block type, $F(1.3,16.3) = 8.1$, $P < 0.01$, $\eta_P^2 = 0.38$ (degrees of freedom were Huynh–Feldt corrected for a sphericity violation; see Kirk 1995). In blocked trials, RTs were slower for ambiguous orientations ($M = 319.67$ ms) than for unambiguous orientations ($M = 294$ ms), $t(13) = 3.2$, $P < 0.01$. There was a smaller, though still significant, difference between the random ambiguous ($M = 319$ ms) and the random unambiguous trials ($M = 313$ ms), $t(13) = 2.4$, $P < 0.05$. In the alternated trials, however, there was no significant difference between the unambiguous orientations ($M = 311$ ms), and the ambiguous orientations ($M = 313$ ms, 95% CI $\pm$ 6.5), $t(13) = 0.7$, $P = 0.52$. Effectively, this means that if a participant had just recently finished a trial in the ambiguous region, and had explicit foreknowledge that the next trial would be unambiguous (and therefore knew precisely which wrist posture would be used), the possession of that foreknowledge provided no RT advantage in the planning of reach-to-grasp movements (Fig. 4c).

In order to see how RT was affected by ambiguity on a trial-to-trial basis, RT scores were analyzed again in a $2 \times 3$ repeated-measures ANOVA, where the within-subject factors were region (ambiguous, unambiguous) and sequential rank (one, two, or three consecutive trials). There was a significant interaction, $F(2,26) = 8.9$, $P = 0.001$, $\eta_P^2 = 0.41$. There was no difference between the first ambiguous ($M = 314$ ms) and the first unambiguous ($M = 312$ ms) trial in a sequence. After two consecutive trials, however, RTs for ambiguous trials ($M = 325$ ms) were slower than those for unambiguous trials ($M = 311$ ms), $t(13) = 2.9$, $P < 0.01$. After three consecutive trials, the difference between ambiguous trials ($M = 331$ ms) and unambiguous trials ($M = 304$ ms, 95% CI $\pm 6.35$) was even larger, $t(13) = 4.1$, $P < 0.001$. As the number of consecutive trials increased, the difference in average RTs increased between ambiguous and unambiguous trials (Fig. 4d). There was also a simple main effect of sequential rank within the ambiguous region, $F(2,26) = 6.5$, $P < 0.005$. The first ambiguous trial was faster than the second and third consecutive trials, but the second and third trials were not significantly different from each other, 95% CI $\pm 7$.

## General discussion

We used the wrist-posture selection task to investigate some of the temporal aspects of reach-to-grasp movements in conditions of motor ambiguity. Our analysis of peak velocity and percent time to peak velocity revealed that these two were dominated by the biomechanical differences inherent in the two possible wrist posture classes. The primary finding of Experiment 1 was that RT, which presumably reflects the time needed for the motor system to select a particular posture, increases with motor ambiguity. This finding was replicated in Experiment 3. We also found that participants were faster at initiating movements in successive conditions than they were in the randomized condition (albeit only in the unambiguous regions). Experiments 2 and 3 helped us determine whether these effects were due to explicit foreknowledge or trial history. We found that explicit foreknowledge did lead to shorter RTs when participants were required to switch between two different wrist postures for two corresponding unambiguous dowel orientations (Experiment 2), but not when participants were required to use those same categorical wrist postures while switching between an ambiguous and an unambiguous region (Experiment 3). Instead, what we observed in Experiment 3 was a 'homogenization effect'— i.e., an eradication of RT differences between ambiguous and unambiguous trials in the alternated trial-order condition. The fact that homogenization occurs in the face of

foreknowledge suggests that cognitive information has little effect in this situation—a phenomenon that has been observed in a range of behavioral measures from peak grip aperture in open versus closed-loop visually guided reaching (Whitwell et al. 2008) to RT during lexical decision (Kinoshita and Mozer 2006) or a pointing task (Song and Nakayama 2007). What makes our finding of homogenization unique is its juxtaposition with the results of Experiment 2, where foreknowledge clearly did provide a RT advantage.

The analysis of RT as a function of the number of consecutive trials within a given region provides insight into the homogenization effect. In Experiment 3, as the number of consecutive trials increased, the difference in RTs increased between ambiguous and unambiguous trials. This increasing separation between easy and difficult trials has been reported in other paradigms: e.g., increasing peak grip aperture with repeated no-vision trials while grasping (Whitwell and Goodale 2009), as well as increasing RT with repeated pointing to a target among distractors (Song and Nakayama 2007) or repeated countermanding trials while performing saccades (Emeric et al. 2007). In our task, since the alternated trial-order condition allowed for only one trial in a given region before switching to the other, there was never a separation between the average RTs for the two regions, resulting in the observed homogenization. The slight separation observed in the randomized condition can be explained by the fact that sequences of at least two or three consecutive trials in a given region were mixed into the trial order.

As we indicated in the Introduction, there were at least two good reasons to predict that RT would not increase within the PCB on our task. First, although Hick's law in its most general form would predict longer RTs in the PCB due to the increase in potential S-R alternatives, other work suggests that the hyper-compatibility (Fitts and Seeger 1953; Leonard 1959) and the overpracticed nature (Longstreth et al. 1985) of the S-R alternatives in our task should result in a violation of Hick's law. One likely explanation for this discrepancy is the fact that where these violations of Hick's law were observed, there was still a one-to-one mapping between stimulus and categorical response. In our task, the increase in S-R alternatives was due to a one-to-many mapping. Thus, our results suggest a caveat to these two Hick's law caveats: when motor ambiguity is a factor, Hick's law accurately predicts an increase in RT even if S-R mappings are overpracticed and compatible.

The second reason to predict an absence of RT differences in our task comes from the minimal intervention principle (Todorov and Jordan 2002). The discrepancy between this prediction and our results does not, of course, invalidate the minimal intervention principle. Rather, it

suggests a constraint upon this principle as it applies to the control of task-irrelevant movement dimensions that may nonetheless require the mediation of a decision process. One can certainly conceive of tasks similar to ours (but minus the competitive element between S-R alternatives) where RT predictions based on the minimal intervention principle would be more likely to be supported. For example, in a speeded reaching task where any endpoint was correct, it seems probable that increasing the number of possible targets would not lead to longer RT.

Another observation from Experiment 1 was that MT was longest during trials in the ambiguous region. This effect of region upon MT was likely due to the fact that when the stimulus orientation was in the ambiguous region, all possible wrist postures required extreme joint angles. This is consistent with the findings of past studies (van Bergen et al. 2007; Frak et al. 2001; Rand and Stelmach 2005; Johnson 2000) in which MT was found to increase linearly as a function of the amount of wrist rotation involved in the movement.

One possible concern about the interpretation of our RT results might be that dowel orientations within the ambiguous region will almost always require extreme joint rotations, resulting in awkward wrist postures. These awkward postures have been correlated with longer response times (RT plus MT) for actual reaches (Frak et al. 2001) as well as longer RT for imagined prehension (Parsons 1994; Johnson 2000; Parsons 1987). Other studies have found that higher RT is correlated with increased spatial length (Munro et al. 2007) and temporal length (Klapp and Erwin 1976) of upcoming movements. It could be the case, therefore, that the increased RTs in the ambiguous condition were simply due to the increased joint rotations and the resulting increase in movement time. Since extreme wrist and forearm rotations in the PCB are the very same biomechanical constraints that give rise to motor ambiguity, these two variables are perfectly confounded.

Consider a hypothetical control task in which the participant is required to make grasps in the ambiguous region with a pre-determined wrist posture, thus eliminating the decision-making element of the task. Even here, the motor ambiguity hypothesis would predict longer RT in the ambiguous region. There are two reasons for this prediction. First, the motor ambiguity hypothesis considers the stimulus in terms of its affordances, and it is these affordances that are competing for further processing (Cisek 2007). Instructing a participant to use a particular posture in advance will not eradicate the affordances of the stimulus. Second, as we have observed in Experiment 3, when participants perform reaches in the PCB, the visuomotor system seems to somewhat impervious to explicit information about what to do in the upcoming trial. This would

render useless any prior instruction about which posture to use.

But does this mean that it is impossible to tease apart the effects of ambiguity and joint rotation? Not at the single trial level it seems; but perhaps they could be unconfounded if one were to examine performance across a number of trials. In Experiment 3, for example, RT increased with repeated ambiguous trials. Given that, on average, joint rotation was constant in the ambiguous region, one would expect RT also to remain constant if RT is a function of the amount of required wrist rotation. The same goes for trials in the unambiguous region; in Experiment 3, there was a processing cost for trials in the unambiguous region if they came immediately after a trial in the ambiguous region. Crucially, this was the case even when participants were in the alternating condition, which gave them time for preparing a response for the upcoming unambiguous orientation. This preparation time would presumably eradicate any costs associated with switching between levels of joint rotation (Monsell 2003; Hunt and Klein 2002). The fact that explicit foreknowledge (i.e., the alternating condition) did lead to the eradication of switching costs when participants switched between two unambiguous orientations (Experiment 2) also suggests that something other than joint rotation is at work in the ambiguous region. Finally, given the fact that MT in this task is known to be a simple function of joint rotation, one would predict that MT and RT should be highly correlated if RT is also a function of joint rotation. But RT and MT were not significantly correlated.

We believe the most straightforward interpretation of our results is that RT differences in the ambiguous region are predominantly due to a decision process. As discussed earlier, our task bears a strong resemblance to signal detection tasks that have been used to study perceptual decision making (Ratcliff et al. 1999). Past work on perceptual ambiguity has shown that increased similarity between perceptual alternatives (Mcsorley and Mccloy 2009; Mazurek et al. 2003) or an increase in the number of perceptual alternatives (Kiani et al. 2008) lead to longer RT. This observation can be explained by a number of models, some of which explicitly suggest a functional role of local inhibitory interactions between neural populations representing the various alternatives (Usher and McClelland 2001; Bogacz et al. 2007; Wang 2002), and others of which do not. An example of the latter is Shadlen et al. (2006), who argue that the apparently strong anti-correlation between activity in the accumulators for the two perceptual options accounts for the majority of variability in LIP firing rates (during a perceptual decision-making task), making it unnecessary to posit any direct competition between them. This non-competitive race (i.e., no important role for local inhibition) between anti-correlated accumulators is another

possible mechanism that could account for our finding that motor ambiguity results in longer RT.

Thus, one unique aspect of our study is the importing of a motor discrimination task into a theoretical framework that was designed around empirical work on perceptual discriminations, along with the observation of results that suggest that the mechanisms subserving discrimination in the former are similar to those demonstrated to be subserving discrimination in the latter. But how novel is our finding that RT increases when motor discriminations are required? Rosenbaum found that RT increased as less information about the upcoming movement was precued (Rosenbaum 1980). This could be taken to be a sort of motor discrimination effect upon RT (i.e., as fewer movement possibilities are ruled out by a precue, the number of possible movements increases, leading to longer RT). Goodman and Kelso (1980) replicated this finding and extended it to show that the precue effect was persistent but attenuated in conditions of high S-R compatibility. These studies are consistent with the finding that increasing directional uncertainty leads to longer RT (e.g., Pellizzer and Hedges 2003, 2004). However, while these past studies showed that RT increases when people have more movement options because of a lack of prior information about the stimulus, the present study showed that RT can also increase when people have multiple movement options in spite of being in possession of all possible information about the stimulus.

One of the ancillary motivations of the present experiment was to replicate past work showing that wrist posture selection in the PCB is subject to hysteresis. In the wrist posture selection task, the PCB between pronated and supinated grasping patterns is largely determined by a biomechanical cost function that biases toward postures that minimize forearm rotation (Kent et al. 2009; Cruse 1986; Cruse et al. 1990; van Bergen et al. 2007; Fischman 1998). This minimal rotation bias can be superseded by other constraints. For example, the PCB has also been found to shift in response to manipulations of visual context such as the simultaneous tilt illusion (Glover et al. 2005; Glover and Dixon 2001) and the rod-and-frame illusion (Craje et al. 2008). Other constraints take into account either the immediate future (i.e., the end-state comfort effect; see Zhang and Rosenbaum 2008; Rosenbaum et al. 1992) or the immediate past (e.g., hysteresis or sequential effects; see Kelso et al. 1994; Weigelt et al. 2009; Rosenbaum et al. 1992; Kent et al. 2009).

Despite the consistent observation of hysteresis in previous work, there was no apparent influence of hysteresis upon the selection of wrist posture in our task. One possible explanation for this null result is that the studies in which hysteresis was observed had the stimulus object oriented in the frontal plane, whereas in the present study the stimulus

was oriented in the horizontal plane. There are important differences between the types of postures that can be adopted in the two different planes. Full pronation (i.e., palm down) and supination (i.e., palm up) of the forearm is possible in the frontal plane, whereas in the horizontal plane supination of the forearm lifts the thumb away and out of reach of the object (leaving only pronation of the forearm, as well as abduction [i.e., moving away from saggital midline] and adduction [i.e., bringing closer to sagittal midline] of the wrist as possible movements). With the added degree of freedom provided by forearm supination, the 'absolute' critical boundaries (i.e., the limits of forearm rotation) for the two possible movement patterns in the frontal plane overlap considerably more than they do in the horizontal plane. Indeed, in the horizontal plane, the preferred critical boundaries are not far from the absolute critical boundaries, which means that the majority of wrist postures adopted within the preferred critical boundaries are going to be uncomfortable. Thus, it could be said that in the frontal plane there is a region that equally affords two comfortable wrist postures, while in the horizontal plane there is a region that equally prohibits (and only by extension, equally affords) the two less-comfortable wrist postures.

In conclusion, our analysis demonstrated that when the motor system encounters motor ambiguity, current and immediately subsequent behaviors suffer from an RT cost. There appears to be a gradual accumulation of this cost over the course of successive trials in the ambiguous condition. Furthermore, providing the participant with exact information about the nature of the upcoming trial-type offsets a cost of switching between different wrist postures unless the previous trial was performed in conditions of motor ambiguity. This suggests that recent experience with motor ambiguity temporarily closes off the mechanisms of sensorimotor decision making from modulatory influences associated with endogenous preparation for upcoming movements.

## References

Bernstein N (1967) The coordination and regulation of movements. Pergamon Press, Oxford

Bogacz R, Usher M, Zhang J, Mcclelland JL (2007) Extending a biologically inspired model of choice: multi-alternatives, non-linearity and value-based multidimensional choice. Philos Trans R Soc Lond B Biol Sci 362(1485):1655–1670. doi:10.1098/rstb.2007.2059

Buchanan JJ, Kelso JA, Fuchs A (1996) Coordination dynamics of trajectory formation. Biol Cybern 74(1):41–54

Cisek P (2007) Cortical mechanisms of action selection: the affordance competition hypothesis. Philos Trans R Soc Lond B Biol Sci 362(1485):1585

Craje C, van der Kamp J, Steenbergen B (2008) The effect of the "rod-and-frame" illusion on grip planning in a sequential object manipulation task. Exp Brain Res 185(1):53–62. doi:10.1007/s00221-007-1130-x

Cruse H (1986) Constraints for joint angle control of the human arm. Biol Cybern 54(2):125–132

Cruse H, Wischmeyer E, Brüwer M, Brockfeld P, Dress A (1990) On the cost functions for the control of the human arm movement. Biol Cybern 62(6):519–528

Desmurget M, Prablanc C, Arzi M, Rossetti Y, Paulignan Y, Urquizar C (1996) Integrated control of hand transport and orientation during prehension movements. Exp Brain Res 110(2):265–278

Dijkerman HC, McIntosh RD, Schindler I, Nijboer TCW, Milner AD (2009) Choosing between alternative wrist postures: action planning needs perception. Neuropsychologia 47(6):1476–1482

Emeric EE, Brown JW, Boucher L, Carpenter RHS, Hanes DP, Harris R, Logan GD, Mashru RN, Paré M, Pouget P, Stuphorn V, Taylor TL, Schall JD (2007) Influence of history on saccade countermanding performance in humans and macaque monkeys. Vision Res 47(1):35–49. doi:10.1016/j.visres.2006.08.032

Fischman MG (1998) Constraints on grip-selection: minimizing awkwardness. Percept Mot Skills 86(1):328–330

Fitts PM, Seeger CM (1953) Sr compatibility: spatial characteristic of stimulus and response codes. J Exp Psychol 46:199–210

Frak V, Paulignan Y, Jeannerod M (2001) Orientation of the opposition axis in mentally simulated grasping. Exp Brain Res 136(1):120–127

Gentilucci M, Daprati E, Gangitano M, Saetti MC, Toni I (1996) On orienting the hand to reach and grasp an object. Neuroreport 7(2):589–592

Glover S, Dixon P (2001) Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. J Exp Psychol Human 27(3):560–572

Glover S, Dixon P, Castiello U, Rushworth MF (2005) Effects of an orientation illusion on motor performance and motor imagery. Exp Brain Res 166(1):17–22. doi:10.1007/s00221-005-2328-4

Gold JI, Shadlen MN (2007) The neural basis of decision making. Annu Rev Neurosci 30:535–574. doi:10.1146/annurev.neuro.29.051605.113038

Goodman D, Kelso JA (1980) Are movements prepared in parts? Not under compatible (naturalized) conditions. J Exp Psychol Gen 109(4):475–495

Hick WE (1952) On the rate of gain of information. Q J Exp Psychol 4(1):11–26. doi:10.1080/17470215208416600

Hunt A, Klein R (2002) Eliminating the cost of task set reconfiguration. Mem Cognit 30(4):529–539

Johnson SH (2000) Thinking ahead: the case for motor imagery in prospective judgements of prehension. Cognition 74(1):33–70. doi:S0010-0277(99)00063-3[pii]

Kelso JAS (1995) Dynamic patterns: the self-organization of brain and behavior. MIT Press

Kelso J, Buchanan J, Murata T (1994) Multifunctionality and switching in the coordination dynamics of reaching and grasping. Hum Mov Sci 13(1):63–94

Kent SW, Wilson AD, Plumb MS, Williams JH, Mon-Williams M (2009) Immediate movement history influences reach-to-grasp action selection in children and adults. J Motor Behav 41(1):10–15. doi:L54242H410380278[pii]

Kiani R, Hanks TD, Shadlen MN (2008) Bounded integration in parietal cortex underlies decisions even when viewing duration is dictated by the environment. J Neurosci 28(12):3017–3029. doi:10.1523/JNEUROSCI.4761-07.2008

Kinoshita S, Mozer MC (2006) How lexical decision is affected by recent experience: symmetric versus asymmetric frequency-blocking effects. Mem Cognit 34(3):726–742

Kirk RE (1995) Experimental design: procedures for the behavioral sciences. Psychology series, 3, illustrated edn. Brooks/Cole, Pacific Grove

Klapp ST, Erwin CI (1976) Relation between programming time and duration of the response being programmed. J Exp Psychol Human 2(4):591–598

Lacquaniti F, Soechting JF (1982) Coordination of arm and wrist motion during a reaching task. J Neurosci 2(4):399–408

Leonard JA (1959) Tactual choice reactions. Q J Exp Psychol 11(2):76–83

Longstreth LE, el-Zahhar N, Alcorn MB (1985) Exceptions to hick's law: explorations with a response duration measure. J Exp Psychol Gen 114:417–434

Mark LS, Nemeth K, Gardner D, Dainoff MJ, Paasche J, Duffy M, Grandt K (1997) Postural dynamics and the preferred critical boundary for visually guided reaching. J Exp Psychol Human 23(5):1365–1379

Mazurek M, Roitman J, Ditterich J, Shadlen M (2003) A role for neural integrators in perceptual decision making. Cereb Cortex 13(11):1257. doi:10.1093/cercor/bhg097

Mcsorley E, Mccloy R (2009) Saccadic eye movements as an index of perceptual decision-making. Exp Brain Res 198(4):513–520. doi:10.1007/s00221-009-1952-9

Monsell S (2003) Task switching. Trends Cogn Sci 7(3):134–140

Munro H, Plumb MS, Wilson AD, Williams JHG, Mon-Williams M (2007) The effect of distance on reaction time in aiming movements. Exp Brain Res 183(2):249–257. doi:10.1007/s00221-007-1040-y

Parsons LM (1987) Imagined spatial transformation of one's body. J Exp Psychol Gen 116(2):172–191

Parsons LM (1994) Temporal and kinematic properties of motor behavior reflected in mentally simulated action. J Exp Psychol Human 20(4):709–730

Pellizzer G, Hedges JH (2003) Motor planning: effect of directional uncertainty with discrete spatial cues. Exp Brain Res 150(3):276–289. doi:10.1007/s00221-003-1453-1

Pellizzer G, Hedges JH (2004) Motor planning: effect of directional uncertainty with continuous spatial cues. Exp Brain Res 154(1):121–126. doi:10.1007/s00221-003-1669-0

Rand MK, Stelmach GE (2005) Effect of orienting the finger opposition space in the control of reach-to-grasp movements. J Motor Behav 37(1):65–78

Ratcliff R, Van Zandt T, McKoon G (1999) Connectionist and diffusion models of reaction time. Psychol Rev 106(2):261–300

Roitman JD, Shadlen MN (2002) Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. J Neurosci 22(21):9475–9489

Romo R, Hernández A, Zainos A (2004) Neuronal correlates of a perceptual decision in ventral premotor cortex. Neuron 41(1):165–173

Rosenbaum DA (1980) Human movement initiation: specification of arm, direction, and extent. J Exp Psychol Gen 109(4):444–474

Rosenbaum DA, Vaughan J, Barnes HJ, Jorgensen MJ (1992) Time course of movement planning: selection of handgrips for object manipulation. J Exp Psychol Learn 18(5):1058–1073

Shadlen MN, Hanks TD, Churchland AK, Kiani R, Yang T (2006) The speed and accuracy of a simple perceptual decision: a mathematical primer. In: Bayesian brain: probabilistic approaches to neural coding. MIT Press, Cambridge

Soechting JF, Flanders M (1993) Parallel, interdependent channels for location and orientation in sensorimotor transformations for reaching and grasping. J Neurophysiol 70(3):1137–1150

Song JH, Nakayama K (2007) Automatic adjustment of visuomotor readiness. J Vis 7(5):2.1–9. doi:10.1167/7.5.2/7/5/2/[pii]

Stasik S, Mark L (2005) Comfort as a determinant of the location of critical boundaries in the act of reaching. In: Studies in perception and action VIII: thirteenth international conference on perception and action, Monterey, CA, USA, 2005. Lawrence Erlbaum, p 23

Stelmach GE, Castiello U, Jeannerod M (1994) Orienting the finger opposition space during prehension movements. J Motor Behav 26(2):178–186

Todorov E, Jordan MI (2002) Optimal feedback control as a theory of motor coordination. Nat Neurosci 5(11):1226–1235. doi:10.1038/nn963

Usher M, McClelland J (2001) The time course of perceptual choice: the leaky, competing accumulator model. Psychol Rev 108:550–592

van Bergen E, van Swieten LM, Williams JH, Mon-Williams M (2007) The effect of orientation on prehension movement time. Exp Brain Res 178(2):180–193. doi:10.1007/s00221-006-0722-1

Wang X-J (2002) Probabilistic decision making by slow reverberation in cortical circuits. Neuron 36(5):955–968

Weigelt M, Rosenbaum DA, Huelshorst S, Schack T (2009) Moving and memorizing: motor planning modulates the recency effect in serial and free recall. Acta Psychol 132(1):68–79. doi:10.1016/j.actpsy.2009.06.005

Whitwell RL, Goodale MA (2009) Updating the programming of a precision grip is a function of recent history of available feedback. Exp Brain Res

Whitwell RL, Lambert LM, Goodale MA (2008) Grasping future events: explicit knowledge of the availability of visual feedback fails to reliably influence prehension. Exp Brain Res 188(4):603–611. doi:10.1007/s00221-008-1395-8

Zhang W, Rosenbaum DA (2008) Planning for manual positioning: the end-state comfort effect for manual abduction-adduction. Exp Brain Res 184(3):383–389. doi:10.1007/s00221-007-1106-x