Grasp Orientation in Ambiguous Settings is Sensitive to Prior Object Motion

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Author Contributions

NJM, DSS and AK designed the study and programmed the behavioural paradigm. NJM collected and processed the data, performed analyses and wrote the manuscript. AK performed analyses. DSS and AK supervised, provided resources, and edited the manuscript.

Abstract

The wrist posture chosen to grasp an object is normally consistent, determined by the optimal, most efficient strategy learnt from previous experience. Yet in certain settings, despite object properties remaining constant and intention the same, the action chosen by an individual can vary with a lack of clear preference for one posture over another. This is referred to as motor ambiguity. Here, we investigate the influence of preceding dynamically changing visual information on participants' choice between two possible wrist postures when grasping an object at various orientations. We found that the decision is influenced by the participant observing rapid object rotation. Surprisingly, rather than being biased to choose the grasp that would have been appropriate for the initial position before object rotation, participants become more likely to use the alternate wrist posture. When object rotation is blocked from view, the bias effect is abolished. Furthermore, the bias strength was found to be independent of the motion magnitude, and persists even when greater decision time is allowed. We suggest that the influence of motion on ambiguous grasping could be attributed to participants overestimating the object's final position when its motion is observed, preparing them to use the grasp appropriate for the upcoming region of certainty. The overestimation may be due to miscalculations in the cerebellar internal model or the gain computation induced by the pairing of rapid motion with the uncertainty of the ambiguous context.

Significance Statement

The wrist posture chosen for a precision grasp is determined by the object's visual properties/location, and a person's comfort preferences. Situations whereby these factors are constant yet the motor response actioned is variable is known as motor ambiguity, though its neural mechanisms are unknown. Our findings suggest observation of object motion causes subjects to overestimate its final position, leading to a bias towards using a grasp opposite to that needed for the initial position. Our results provide a platform to study neural mechanisms and test motor control theories in situations

of motor ambiguity when different choices do not lead to severe enough consequences to warrant adaptation in motor behaviour, and therefore can be revealed in our experimental design.

Introduction

On any given day humans perform hundreds of movements that involve interacting with our environment. Any motor action requiring contact with an object requires consideration of its appearance, weight, location, and context in order to successfully complete the task according to need (Rosenbaum et al., 2012). From even the most basic of actions such as grasping a pencil to the more complex skills that take years to develop (e.g. learning to play the violin), each task can present with several different ways to completion. The response selection for a given task can be consistent, determined by the optimal, most efficient strategy learnt from previous experience. Yet in some cases, despite object properties remaining constant and intention the same, the action chosen is variable. This lack of clear preference in response has been coined 'motor ambiguity' (Wood and Goodale, 2011).

Take for example the familiar action of reaching out to grasp a pen placed on a table. When perpendicular to the body's midline, it comes naturally to position the thumb on the side of the pen proximal to the body, and the index finger on the distal side. As the pen rotates clockwise on the table to approach alignment with the body's midline, it continues to be natural to grasp in the same configuration as before (visually the thumb is now placed on the pen's left side), yet it is also reasonable, and more importantly comfortable, to grasp by placing the index finger on the pen's left side and thumb on the right by rotating the forearm. This principle of motor ambiguity can also be extended to hand choice and situations wherein an object can be grasped using a precision or power grip (Seegelke et al., 2016).

The neural mechanisms underlying a precision grip action are well established for determinate/certain settings. When the motor response required is clear, a rehearsed pathway spanning the parietal, premotor and primary motor cortices is actioned to yield the preferred movement. The ventral premotor cortex (PMv) plays a key role in adapting hand shape to target objects, likely via cortico-cortical connections with M1 (Cerri et al., 2003; Davare et al., 2006). These PMv-M1 interactions are

driven by an information transfer of target object properties from the anterior intraparietal area (AIP) to PMv, and when disrupted produces deficits in hand posture (Gallese et al., 1994; Davare et al., 2010; Davare et al., 2011). The AIP continues to monitor hand shaping after the preparation stage via a feedback loop with PMv, enabling 'on-line' adaption if a change in object position or properties occurs (Raos et al., 2006; Buch et al., 2010). The AIP receives inputs from areas located in the dorsal and ventral streams, providing it with object property and identity details (Davare et al., 2011).

Any choice based on visual information requires accumulation of evidence over time until a decision is reached. The power of prior visual information on influencing movement execution has been investigated since the 1990s when Craighero and colleagues reported that participants are quicker to initiate movement towards a target if they had previously been presented with a priming object congruent in orientation with the target (Craighero et al., 1996; Craighero, 1998). In addition to initiation time, exact positioning of the index finger and thumb during a precision grip can be influenced by the orientation and similarity of another object that is presented prior to the grasp (Roche et al., 2015). Still, it remains unknown whether grasp choice of an object at an ambiguous orientation can be influenced by the same object's positional history.

This study was designed to explore the hypothesis that presentation of an initial orientation prior to an upcoming ambiguous target will bias subject behaviour. How the grasping system adapts to new visual information in ambiguous settings and the impact this has on behaviour was investigated using a task with a moveable target object that affords two possible grasp configurations.

Materials and Methods

Participants

All participants bar two were right-handed and all were naïve to each experiment and its predictions. A total of 49 healthy volunteers (22-50 years old, 34 females 15 males) were recruited to take part in different experiments in this study (Experiment 1: 12 participants; Experiment 2: 10 participants;

Experiment 3: 10 participants; Experiment 4: 6 participants; Experiment 5: 11 participants). Subjects were unpaid and some took part in several experiments - in which case each experiment was separated by at least 6 days. Ethical approval was granted by the Newcastle University Ethics Committee and written informed consent was obtained from all volunteers.

Experimental Design

Task-Setup

In total, five experiments were conducted to investigate the influence of the timing of visual information on grasp selection in an ambiguous setting. The experimental paradigm required participants to perform a precision grip movement on a triangular prism block (6cm long by 2cm wide) with their right-hand upon hearing a go cue (auditory beep lasting 50 ms). The target object was designed with the intention to afford only one possible grasp: the thumb and finger at opposing ends of the prism block (Stelmach et al., 1994). The object was mounted onto a grey rectangular stage and connected to as stepper motor to enable rotation in steps of 0.9° angles – controlled by custom written Arduino scripts. Thin triangular metal plates were glued to each end of the prism block and connected to a custom made circuit that allowed detection of skin contact by a change in impedance. By placing a glove onto the index finger to impede contact with the object, hand orientation selection could be recorded in terms of thumb placement, either 'thumb-left' or 'thumb-right' (Figure 1).

Participants were seated in a chair with their forearm positioned on the arm rest (Figure 1). A circular 'home-pad' button (6 cm in diameter) was placed at the distal end of the arm rest and used as the starting location for the wrist. The target object was positioned 35 cm anterior to the centre of the home pad and 15 cm superior, with its rotation occurring in the frontal plane. This resulted in the object lying 25 cm to the right of the body's midline. As comfort and therefore choice of grasp has been shown to be sensitive to body and head posture (Wood and Goodale, 2011), a chin rest was used to mitigate any postural shifting that could introduce unwanted variability to behaviour.

To initiate a trial, participants were asked to depress the home-pad with their wrist positioned mid-pronation while lightly pinching their finger and thumb together. The length of time required to hold down the home-pad was uniformly varied from trial to trial (1000-1300 ms) to prevent participants acting on anticipation of the go cue. Upon hearing the auditory beep, participants were asked to reach out and comfortably grasp the target object between their thumb and index finger, pinching it lightly. After the precision grip, they returned to the home-pad to initiate the next trial sequence. If the home-pad was released too early (i.e. prior to the Go Cue), an error tone would sound to indicate the subject should return to the start button. The timing of the go cue as well as object visibility was varied between experiments (see *Study Design below*), nevertheless the above-mentioned instructions to participants remained constant.

Study Design – Calibration Task

To begin each experiment, a calibration task was performed to calculate an estimate of the subject's 'switch-point', defined by when there is a 50% chance of using either wrist posture to grasp the object. Due to individual differences in posture, height, and anatomical flexibility, a determinate angle for one subject could be ambiguous for another. The switch-point therefore acted as an individualised 'zero' position for which the target angles of subsequent experiments were focussed around. A total of 72 trials (randomised for each subject) across 19 unique target angles spanning 88.2° were used to estimate the switch-point (example calibration curve is shown in Figure 2a). For this task, participants wore LCD goggles (PLATO goggles; Translucent Technologies, Toronto, Canada) to occlude their vision until the object had rotated into place at the target angle. The goggles have a transition time from opaque to visible of 4 ms. Synchronous with the auditory go cue, the goggles transitioned from an opaque state to transparent to allow subjects to perform the prehension movement. In cases where participants wore visual correction glasses, the goggles were placed over the top and secured with a headband.

Study Design – Experimental Tasks

To investigate the influence of prior visual information on grasping in ambiguous conditions, the main task trial sequences were designed to first present subjects with the target object at a randomised initial angle for which they would not reach for but instead only observe. This was followed by the object rotating either 5.4°, 14.4°, or 28.8° clockwise (CW) or counter clockwise (CCW) to the target angle from said initial position (Figure 2c), taking 10-50 ms depending on the shift magnitude. A total of 23 unique target angles spanning 50.4° either side of the measured switch point (Figure 2b) were presented in a randomised order, with each subject given their own randomisation.

To reduce unnecessary sampling of the determinate region, target angles far from the switch-point (>±14.4°) were only given shift magnitudes of 5.4°. To further reduce experimental time and minimise repetition fatigue, the remaining targets were randomly given two of the three potential shift magnitudes, with optimised balance of all three magnitudes across the ambiguous range (<=±14.4°). Finally, determinate angles were sampled at half the frequency of ambiguous orientations, with greater inter-angle spacing. All experiments consisted of a total of 216 trials with the exception of Experiment 4 which had 270.

Each experiment primarily varied the timing of the go-cue relative to object rotation. A comparative timeline of each experiment's sequence is shown in Figure 3.

Experiment 1

For this experiment, the go-cue was given immediately before target angle presentation. As stated previously, trial sequence began upon home-pad depression, triggering object rotation to an initial angle. Following the hold-time waiting period, the go cue sounded and was ceased after 50 ms - its cessation synchronous with object rotation from the initial angle to the target angle. Together, 60-100 ms passed between go cue onset and presentation of the target angle.

Experiment 2

As with Experiment 1, trials within Experiment 2 began with home-pad depression and observation of object movement to an initial angle. However, after the hold-period concluded, initiation of object rotation to the target angle was followed by a 150 ms delay until the go cue sounded.

Experiment 3

Experiment 3 takes the identical format to Experiment 2, with the exception of the go cue being deferred until 500 ms post object rotation onset.

Experiment 4

Experiment 4 consisted of two trial types with the intention to investigate mid-flight adaptation. The trial sequence begins as for Experiments 1-3 until conclusion of the hold-period. Here, the go cue is given and for eighty percent of trials (n=216), object rotation to the target angle is delayed until 200 ms post home-pad release. Twenty percent of trials (n=54) were randomised catch trials wherein the initial angle was equivalent to the target angle, i.e. no secondary object rotation. The catch trials were introduced to avoid subjects waiting for the object rotation to stop before completing the reaching movement. The catch trials were excluded from analysis since no object movement happened on these trials.

Experiment 5

For Experiment 5, participants were asked to wear LCD goggles with the purpose of blocking object rotation from the visual field. Synchronous with home-pad depression, the goggles transitioned to an opaque state to ensure view of the rotation to the initial angle was blocked. After becoming transparent for 1.5 s to allow subjects to view the initial position, the goggles transitioned back to an opaque state. Upon completion of the remaining hold time, the auditory cue was delivered, object rotation initiated, and 150 ms later goggles converted to a transparent state.

Data and Statistical Analyses

Grasp choice data were gathered using the custom designed contact circuit and sampled at 5 kHz (CED Micro 1401, Cambridge Electronic Design) using Spike2 software. Data analysis and statistics were performed using custom written MATLAB scripts. Reaction time (RT) was measured as time from go cue to home pad release with the exception of Experiment 2 which used onset of LCD goggle transparency. Movement time (MT) was measured as time from release of home pad to contact with the target object.

Calibration Task

Choice of grasp was coded with reference to which edge of the target object the thumb made contact with. For the calibration experiments the probability of using a 'thumb-right' wrist posture was calculated for each target angle and a logistic regression curve was fitted to the data using the function below, where x_o is the subject's switch point and k is a scaling parameter.

$$f(x) = \frac{1}{1 + e^{-k(x - x_o)}}$$

This allowed two metrics to be calculated, the switch point and halfwidth. The angle for which there is a 50% chance of using a Thumb-right wrist posture was used as an estimation of each participant's switch point, later referred to as the 0° angle (Figure 2a). The halfwidth provided a measure of switch sharpness, calculated as the difference between the 75th and 25th percentiles. This is an indicator of subject uncertainty across the task as a whole.

Experimental Tasks

For each target angle, the average decision was calculated as the probability of using a 'thumb-right' wrist posture. The decision probability could then be further split by direction of rotation and shift magnitude.

To correct for any potential drifts of the switch point during the experimental tasks, a re-alignment of participants' data was carried out post-hoc. This involved re-calculations of the switch-point from the

pooled across all conditions experimental data and shifting the analysis window from the estimated switch point following calibration to the true switch-point. This was to ensure that for each individual, we sampled the same range of angles relative to their true centre of ambiguity.

For analysis of the contribution of the different experimental factors, a generalised linear mixed effect model (GLME) approach was adopted. GLME analysis allowed parametrisation of the strength of each fixed factor (target angle (TA), direction (Di), and shift magnitude (SM)) and its relationship with grasp choice, with a comparison across each experiment. Direction was coded as a categorical variable (CW, 0; CCW, 1) whilst target angle and shift magnitude were numerical. The shift magnitude variable was mean-centered. The model binary choice data (C) using GLME a Logit link function was applied. Approximate Laplace was used as the method for estimating model parameters. Subject specific variation (S) was accounted for by its introduction as a mixed effect into the model.

In total eight GLME alternatives with increasing complexity were designed to compare which combination of parameters achieved the best fit for the data. These include combinations of main factors and interactions between them. Formulae in Wilkinson notation for each model are given below.

Model 1: C ~ TA + (1|S);

Model 2: C ~ TA + Di + (1|S);

Model 3: C ~ TA*Di + (1|S);

Model 4: C ~ TA + SM + (1|S);

Model 5: C ~ TA*SM + (1|S);

Model 6: C ~ TA + Di + SM + (1|S);

Model 7: C ~ TA + Di + SM + Di:SM + (1|S);

Model 8: C ~ TA*Di*SM + (1|S).

For each study, the best-fit model was determined by the lowest Bayesian Information Criterion (BIC) value and once selected, T-statistic values and coefficient estimates (CE) were obtained for each factor. The threshold of T-values were set to a p-value of 0.05 for each experiment. Statistics throughout are given as mean ±SE.

Reaction and Movement Time Analysis

Previous work has shown that both RTs and MTs are longer for ambiguous grasps than determinate (Wood and Goodale, 2011). We used a GLME approach to explain our RT and MT data using absolute difference of the target angle from the ambiguity point as the single factor in the models below:

RT Model: $RT \sim |TA-X_o| + (1|S)$

MT Model: $MT \sim |TA-X_o| + (1|S)$,

where X_o is a switch point. A significant linear decrease is these models would correspond to longer RT/MT for ambiguous target angles in comparison to determinate angles. Reported effects are estimated from each model as the difference between switch point (0°) and determinate angle of 50°.

Results

Calibration

To begin each experiment, participants were asked to perform reach and precision grasp movements to a triangular prism presented at randomised target orientations. As expected, subjects transitioned from using a thumb-left grip to thumb-right as the object sampled more clockwise angles (e.g. Figure 2a). Across all calibration experiments, the switch-point for subjects ranged between -35.1° and 55.8°, with varying degrees of sharpness (halfwidth 7.79° ± 6.72°).

GLME Analysis

All 8 models were fitted to the data from each experiment. A comparison of BIC values across experiments and GLMEs are shown in Figure 4.

To investigate any possible influences that prior visual information could have on grasping in ambiguous settings, experimental tasks added an additional component of an initial angle for which subjects would not reach for but only observe, before the object rotated CW or CCW towards the target angle.

Experiment 1

Of the GLMEs that were designed, using solely target angle and direction as parameters led to the best fit of the data when cessation of the go cue was synchronised with onset of object rotation (Model 2). When a CW rotation was observed, subjects were more likely to select a thumb-right grasp than thumb-left (Direction CE=-0.73±0.11, t-stat=-4.96, $p<0.0001$; Target Angle CE=0.094±0.004, t-stat=22.9, $p<0.0001$). Including shift magnitude as a variable in addition to direction (Model 6) increased the BIC value by 7.78, indicative of a less-well fitted model, and the factor becomes an insignificant contributor to the model (Shift Magnitude CE=-0.0014±0.005, t-stat= -0.26, $p=0.79$; Direction CE=-0.73±0.11, t-stat=-6.98, $p<0.0001$; Target Angle CE=0.09±0.004, t-stat=22.9, $p<0.0001$).

In order to comparatively visualise the effect of direction on behaviour with subsequent experiments, the Model 2 was used to predict grasp choice for CW and CCW conditions for each target angle 50° either side of the switch-point. As expected, the greatest difference between CW and CCW conditions occurs around the centre of ambiguity, reducing in prominence as the target angle approaches the determinate extremes (Figure 5a).

To restate these findings, a clockwise rotation to an ambiguous target angle increased the likelihood of a thumb-right grasp, while a counter-clockwise motion increased the likelihood of thumb-left grasp. The GLME analyses showed that the magnitude of rotation is not an important contributor to this effect.

Experiment 2 and 3

Delaying the go cue until 150 ms post-rotation onset led to a similar behavioural profile to that seen in Experiment 1. Model 2 remained optimal with the lowest BIC value and although the effect size of

direction decreased, it remained significant (Direction CE=-0.64±0.13, t-stat=-4.96, p<0.0001; Target Angle CE=0.16±0.01, t-stat=21.3, p<0.0001). Extending the time elapsed from target angle presentation to hearing of the go cue from 150 ms to 500 ms further reduced the effect of direction, yet significance held with Model 2 remaining the best fit (Direction CE=-0.49±0.13, t-stat=-3.76, p<0.001; Target Angle CE=0.20±0.01, t-stat=21.6, p<0.0001). Furthermore, when using Model 2 to predict grasp choice, the halfwidth of the sigmoid plots as visualised in Figure 5 decreased from 11.7° in Experiment 1, to 6.9° and 6.1° in Experiments 2 and 3 respectively, indicative of reduced uncertainty across the task as a whole. Visually, the difference in grasp choice between CW and CCW trials becomes narrower the longer the go cue is delayed (Figure 5b-c). Or in other words, the greater the delay between target angle presentation and the Go Cue, the weaker the strength of the bias effect.

Experiment 4

Inversely, when object rotation occurred after the go cue, post home-pad release (mid-flight), subjects became more likely to continue on the trajectory of performing the grasp that they would have used for the initial angle. In this condition, the optimal GLME includes all factors and the addition of interaction term between direction and shift (Model 7: Direction CE=2.06±0.19, t-stat=11.0, p<0.0001; Target Angle CE=0.095±0.006, t-stat=14.9, p<0.0001; Shift CE=-0.09±0.01, t-stat=-6.2, p<0.0001; direction:shift CE=0.15±0.02, t-stat=7.4, p<0.0001). Note a different sign of the direction effect indicating an opposite difference in choice for CW vs CWW directions. Interaction between direction and shift is illustrated by Model 7 prediction: the larger the shift magnitude, the greater effect direction has on grasp choice (Figure 5d). To summarise, when object rotation is delayed until subjects are mid-reach, the effect of rotation as seen with Experiments 1-3 is not strong enough to override the already initiated prehension movement. They instead continue to execute the grasp that would have been appropriate for the initial angle.

Experiment 5

Contrastingly, when subjects were presented with an initial angle but visually blocked from observing its rotation to the later unveiled target angle, the optimal model to explain grasp choice included only target angle (Model 1: target angle coefficient estimate 0.152±0.01, t-stat =23.1, $p<0.0001$). Inclusion of direction raised the BIC value by 5.42, with the parameter insignificantly contributing to model (Model 2: direction coefficient estimate 0.19±0.12, t-stat=1.53, $p=0.13$). Visualisation of choice split by direction further illustrates the lack of influence of initial angle on ambiguous grasping (Figure 5e). The key overall point to note here with Experiment 5 is that blocking object rotation from view abolishes the bias effect as seen above, with the initial angle having no influence on grasp choice at the ambiguous target orientation.

Reaction and Movement Times

When completing each trial, participants were instructed to act quickly but with priority to accuracy and comfort. As such, each experiment was not designed as a RT task. Despite this, significant differences in RTs were observed both within (ambiguous versus determinate target angles) and across (go cue timing) experiments.

Averaged across all target angles, the timing of the go cue had a significant effect on RTs ($p=0.007$, dF=4, one-way ANOVA). Post hoc analyses (using the Tukey-Kramer correction) revealed that Experiment 1 had significantly longer RTs than Experiment 3 ($p=0.034$), with averages of 548.1 ms and 389.8 ms respectively (Figure 6a). The average RT for experiment 2 was 481.2 ms, falling between Experiment 1 and 3. Experiment 4 had the longest average RTs with 600.9 ms – significantly longer than Experiment 3 ($p=0.015$). The average RT of Experiment 5 was 433.7 ms. Movement times were not significantly affected by the timing of the go cue (Figure 6b) with smallest MT observed in Experiment 3 (600.7 ms).

To investigate the effect of target angle on reaction and movement times, a GLME approach was used to extrapolate estimates from the behavioural data. In agreement with previous work, reaction times

346 for target orientations closer to the centre of ambiguity were greater than those more determinate
347 (Table 1). Though this trend was seen with all experiments, it was only significant when the go cue
348 was given at or after target angle onset; a greater RT difference between 0° (switch point) and 50°
349 (determinate) was observed the greater the interval between target onset and go cue became
350 (Experiment 1 difference 31 ms, p=0.006; Experiment 2 difference 75 ms p<0.001; Experiment 3
351 difference 97 ms, p<0.001). When the go cue is given pre-rotation or rotation is blocked from view,
352 there is no significant effect of target angle on reaction time (Experiment 4 difference 35 ms, p=0.119;
353 Experiment 5 difference 11 ms, p=0.540).

354 Furthermore, MT was greatest for trials closer to 0°, the duration shortening as orientations
355 approached the extremes of 50°. Though again this trend was seen with all experiments, target angle
356 (TA) had a significant effect on MT for all experiments except Experiment 2 and 5 (see Table 1 for all
357 differences and their significance).

358

Experiment	*Reaction Times*		*Movement Times*	
	Difference (ms)	P-value	Difference (ms)	P-value
1	31	**0.006**	49	**0.001**
2	75	**<0.001**	21	0.055
3	97	**<0.001**	18	**0.008**
4	35	0.119	58	**<0.001**
5	11	0.540	13	0.105

359 *Table 1. Statistics from generalised linear mixed effect model for reaction and movement times for*
360 *Experiments 1-5. Using the GLME as a prediction tool to extrapolate from the behavioural data, the*
361 *difference in timing between the target angle at the centre of ambiguity (0°) and the most extreme*
362 *(50°) is calculated by dividing the coefficient estimate by 50. P-values are given for the singular variable*
363 *of target angle.*

364 # Discussion

365 In this study subjects were placed into ambiguous settings with an object that afforded one of two
366 precision grasps (thumb-left or thumb-right) in order to investigate the influence of visuomotor
367 priming on motor ambiguity. Though previous studies (Borghi et al., 2007; Vainio et al., 2007; Seegelke
368 et al., 2016) have shown that priming can influence the execution of reach-to-grasp movements when
369 primes are congruent with the target, the results of this study demonstrate that the mere presentation
370 of an initial, priming orientation of the object (at either a determinate or ambiguous orientation) was
371 not sufficient to influence choice of grasp when the object was then shown at an ambiguous
372 orientation (Experiment 5). Yet, when rotation of the object from the initial angle to the target position
373 was visible, a significant effect of directional bias on grasp choice was found.

374 The nature of this bias depended heavily on when the go signal was given relative to the rotation of
375 the object. When the end of the auditory cue was synchronised with rotation onset, the ambiguous
376 grasp performed was more likely to be the opposite choice of what would have been used for the
377 initial angle (Experiment 1). For example, a clockwise rotation from an observed thumb-left position
378 to an ambiguous angle increased the likelihood of a thumb-right grasp, and vice-versa. Upon
379 establishment that rotation directionality influenced choice of grasp, two further experiments were
380 designed to delay the go cue until post target angle presentation. A relatively short delay of 150 ms
381 from rotation onset to sounding of the go cue still produced the bias effect, although it reduced in
382 strength (Experiment 2). A longer delay of 500 ms still produced a significant bias effect, though again
383 was much reduced in strength (Experiment 3). Interestingly for all experiments in which this bias was
384 observed, the distance by which the object rotated had no significant influence on the strength of the
385 bias effect.

386 Furthermore, subjects were also asked to complete trials when the go cue was given early (object was
387 still set to the initial orientation), with rotation occurring mid-flight as subjects began their reach
388 towards the object (Experiment 4). Here the bias was congruent with the initial angle, i.e. the grasp

389 that would be used for the prime is then subsequently used for the target orientation. The bias effect
390 observed here could likely be explained in terms of cost efficiency. It has been shown that kinematic
391 differentiation between grasp choices of an ambiguous target can be achieved after only 10% of the
392 movement has occurred (Dijkerman et al., 2009). By the timing of rotation, ~30% of the movement
393 has been completed and so as long as the target angle is still expected to be comfortable with the
394 current wrist posture, then the cost-benefit of switching is often deemed insufficient to warrant an
395 overhaul. In support of this is the evidence that the greater the magnitude of rotation, the stronger
396 the bias effect. Given that the smaller shifts often moved the object from one ambiguous position to
397 another, it is likely that the reduced bias strength does not indicate increased switching mid-flight but
398 rather that they were already on course to perform a grasp that was congruent with what the final
399 position became.

400 What seems to be less clear is why the inverse bias effect as seen with Experiments 1, 3 and 5 is
401 occurring. One reason could be that subjects are overestimating the final target position of the object
402 as they observe its rapid rotation, pushing subjects to plan a grasp that would be appropriate for an
403 orientation that is further towards being determinate than what the actual target position becomes.

404 Predicting the future location of a moving object is a familiar task, yet some consistent biases are
405 known to the prediction literature. It could be considered a good strategy for example, that if an
406 occluded object is approaching an observer, to overestimate its speed in order to be cautious and
407 avoid potential collision (Schiff and Oldak, 1990). Contrastingly, when asked to intercept an occluded
408 object moving parallel to the observer, its speed is often underestimated, causing people to intercept
409 its path too late (e.g. (Peterken et al., 1991; Sokolov and Pavlova, 2003; Battaglini and Ghiani, 2021)).
410 Despite our study being more methodologically aligned with parallel motion, the results complement
411 more with approaching motion. Of course, the major comparative difference between above studies
412 and this study is the presence of occlusion. Without occlusion, one has a reasonable expectation of
413 greater prediction accuracy (Menceloglu and Song, 2023), yet it appears in this instance that

414 inaccuracy can be achieved in the absence of occlusion as long as the motion is quick and towards
415 ambiguity.

416 Though the task itself does not ask of subjects to predict the object's final position, it appears that
417 synchronising the go cue close to rotation introduces enough added uncertainty that the planning of
418 the movement might recruit spatial prediction circuitry to compensate. Indeed, the earlier the go cue
419 is given relative to object rotation, the slower participants are at reacting to any given target angle.
420 Furthermore, this added uncertainty is also seemingly reflected in the increased difference in reaction
421 time between ambiguous and determinate orientations, in comparison to when rotation is blocked
422 from view. Despite not enforcing subjects to react as quick as possible, the reaction time still reflects
423 the time needed for the motor circuitry to choose between grasps (Rosenbaum et al., 1992; Wood
424 and Goodale, 2011). The increased difference therefore begs the question, how and where does this
425 additional time accumulate.

426 It has been well documented that in temporal-spatial perceptual prediction tasks increased cerebellar
427 activity is associated with a shift in cortical activation patterns (O'Reilly et al., 2008). Both aIP and PMv,
428 areas vital for preparation of object-directed grasping, also become engaged in spatial prediction tasks
429 (Schubotz and von Cramon, 2001; Assmus et al., 2003), with the suggestion that the nature of the
430 cerebellar perceptual prediction may bias the recruitment of motor responses (O'Reilly et al., 2008).
431 The consistent overestimation observed could be attributed to a consequence of cerebellum
432 involvement in the decision making and preparation processes, or alternatively further upstream as a
433 sensory input miscommunication. The lack of dependence on the magnitude of the object rotation
434 may provide evidence against the latter, as one might expect the bias effect to scale with the sensory
435 input for a given error.

436 The internal forward-model theorem of the cerebellum describes a proposed mechanism to cope with
437 sensory prediction in uncertainty, and relies upon two processes: prediction and prediction error
438 detection (Wolpert et al., 1998; Tanaka et al., 2020). An important function of this model is its role in

439 optimal feedback control, computing gain matrices for Kalman filtering and feedback control (Todorov
440 and Jordan, 2002). The Kalman filter is a strategy to estimate the current state from integration of
441 prediction from the internal forward model and sensory afferents (Tanaka et al., 2020). The optimal
442 estimated state is then what propels the feedback controller to generate appropriate motor
443 commands (Todorov and Jordan, 2002). Computation of the Kalman gain requests the accuracy of the
444 internal model, however dysregulation in the cerebellar internal model or the gain computation can
445 lead to preparation of suboptimal motor commands (Filip et al., 2013; Bodranghien et al., 2016). In
446 our case, the errors in orientation prediction caused by observation of the rotating object do not lead
447 to severe enough consequences to warrant adaptation, and so the prediction error continues to
448 persist through the Kalman filter to yield the bias effect in each experiment.

449 One caveat of this overestimation theory is the persistence of the bias effect even after sufficient time
450 has passed to allow feedback on the accurate final position of the object. An alternate (but not
451 mutually exclusive) theory for how the grasping network deals with ambiguity could be that if indeed
452 two neural populations are competing for each wrist posture, perhaps the observation of the object
453 moving away from the preferred position of one population inhibits its activity. Further experiments
454 aimed at disrupting cerebellar or PMv processing might help delineate the neural mechanisms behind
455 this bias.

456 In conclusion, observation of object rotation towards an ambiguous orientation causes subjects to
457 become biased in their grasp choice, with a preference for selecting the grasp congruous with the
458 upcoming determinate region had the object continued its rotation path. Potentially due to an
459 overestimation effect caused by the uncertainty induced by the speed of rotation, the bias persists
460 even after time for feedback on the correct position has been allowed for. This, in conjunction with
461 evidence that the overestimation does not depend upon the magnitude of rotation, could be
462 explained by cerebellar recruitment and subsequent failure of the internal forward model, and/or
463 cortical inhibitory circuits.

Figure Legends

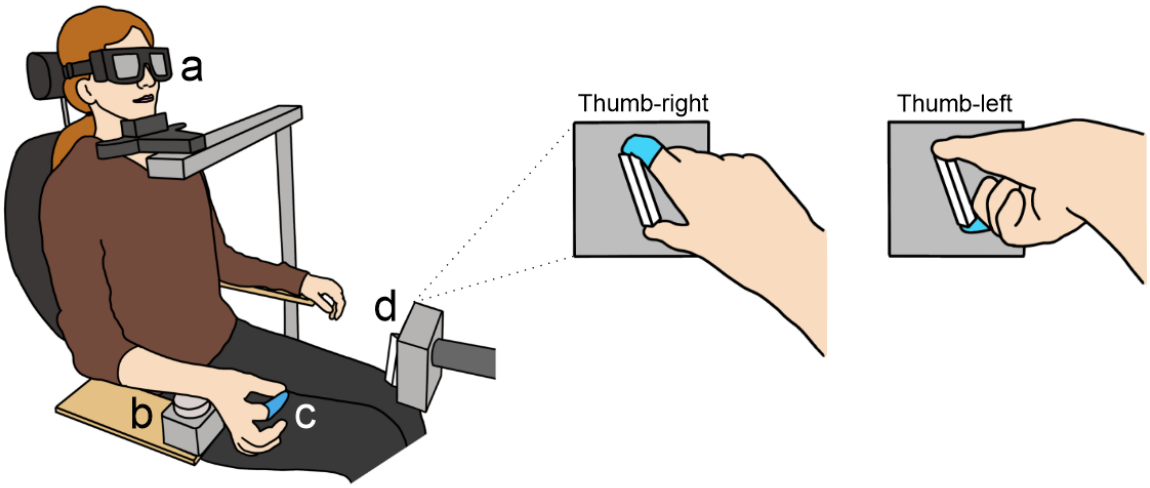

Figure 1. Illustration of experimental task set-up. *Participant is seated with LCD goggles (a) covering their visual field and head placed on a chin rest. Their right-wrist is used to depress the home-pad button (b) to initiate the trial sequence. A latex glove on the index finger (c) impedes touch with the contact circuit on the target object (d) to allow detection of wrist posture (thumb-right or thumb-left) on a trial-by-trial basis.*

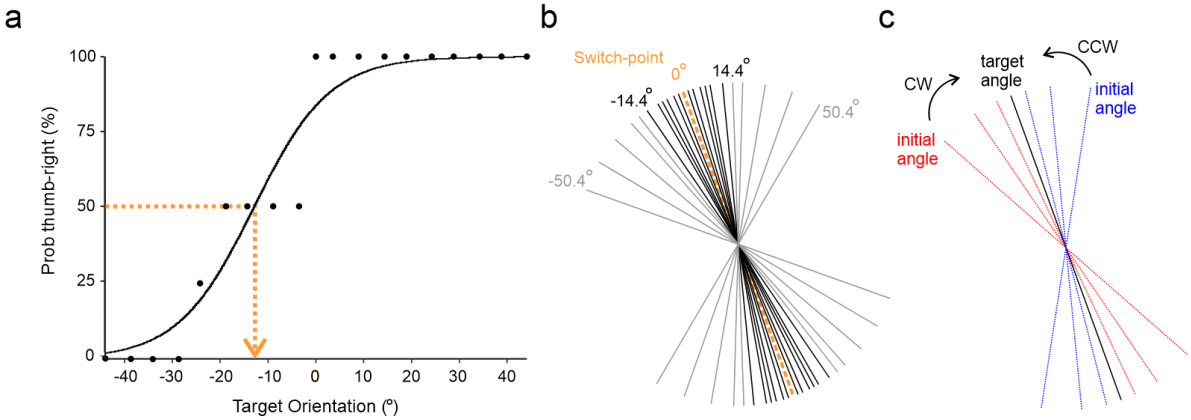

Figure 2. Study design of calibration and experimental tasks. *a) Calculation of the midpoint was done by marking the 50th percentile (orange dotted line) on a logistic fit of the average probability of using a Thumb-right grasp posture following Calibration task. Black dots show average probability of choosing a Thumb-right posture for each target angle sampled. b) Trial design of Experimental tasks showing sampling of target angles, with '0°' representing the subject's switch-point. c) Trial design of Experimental tasks illustrating visual perturbation of object rotation clockwise (red lines, CW) or counter-clockwise (blue lines, CCW) from initial position towards target angle by either 5.4°, 14.4° or 28.8°.*

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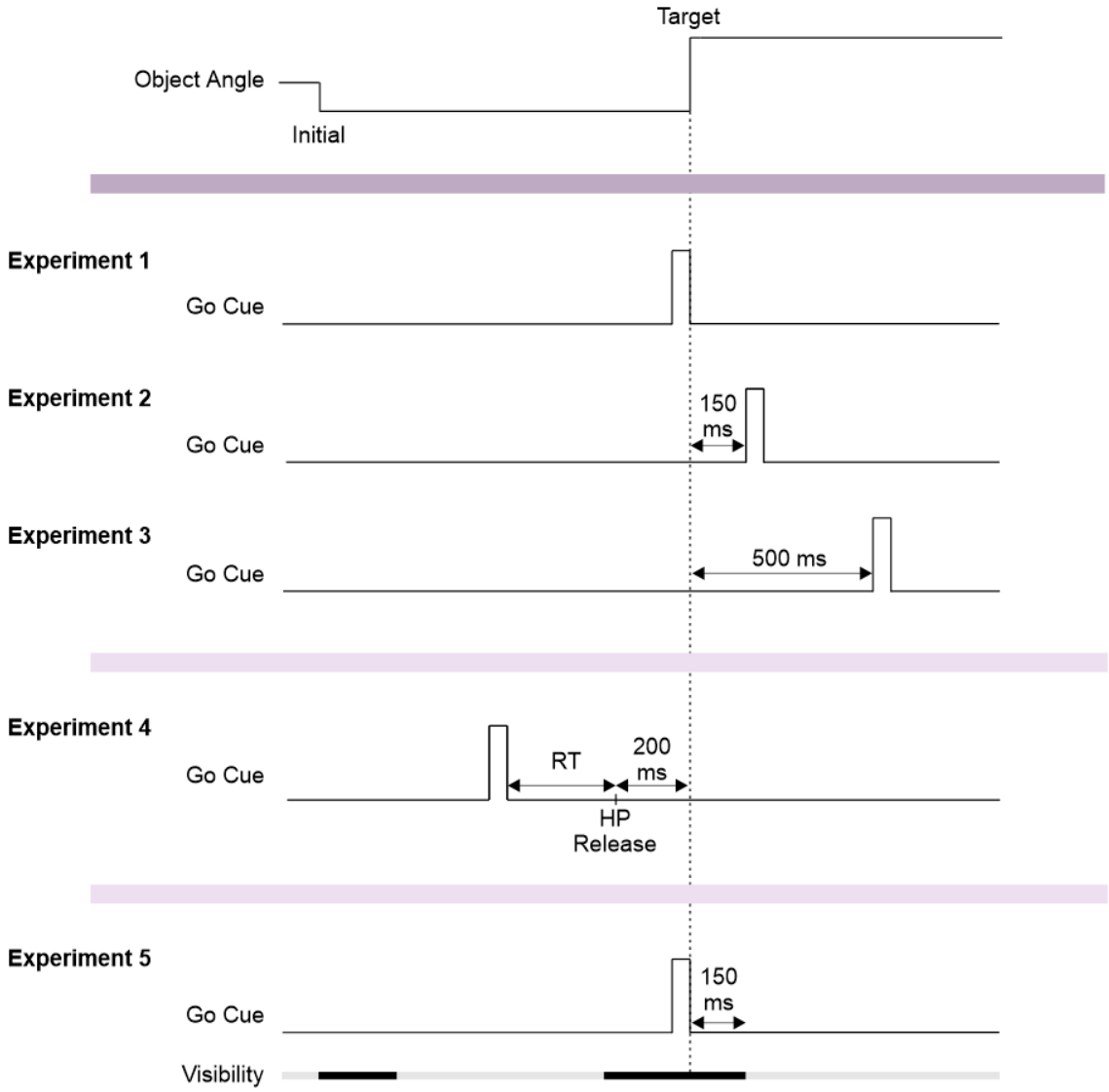
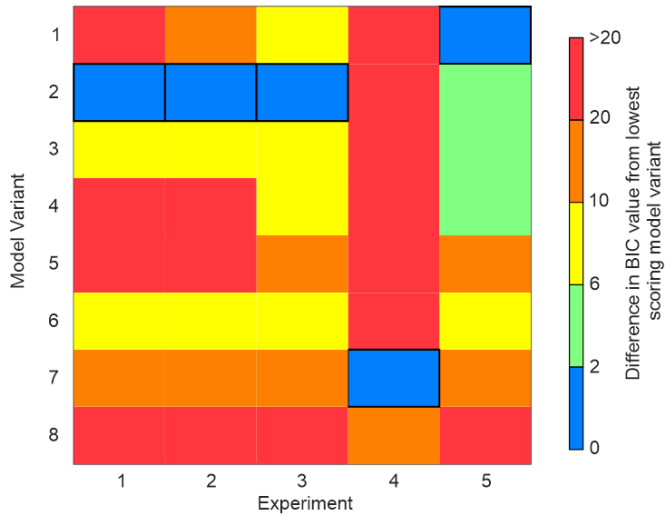


483

484 ***Figure 3. Comparative experimental timeline of onset of go cue with object rotation from initial***
485 ***position to target orientation.*** *Duration of go cue was 50 ms, with variable onset depending on*
486 *experimental condition. Rotation of object took 10-50 ms, dependent upon whether an extreme or*
487 *minor shift was performed. For Experiment 5 periods of object visibility and obscurity are illustrated by*
488 *light and dark bars respectively. RT, reaction time; HP, home-pad.*



489

490 ***Figure 4. Comparison of BIC values across each GLME variant for Experiments 1-5.*** *Difference in BIC*

491 *value relative to the lowest scoring model variant (shown in blue with black outline) was calculated to*

492 *illustrate quality of fitting to the grasp choice data; a greater difference reflects a lesser fitted GLME*

493 *variant.*

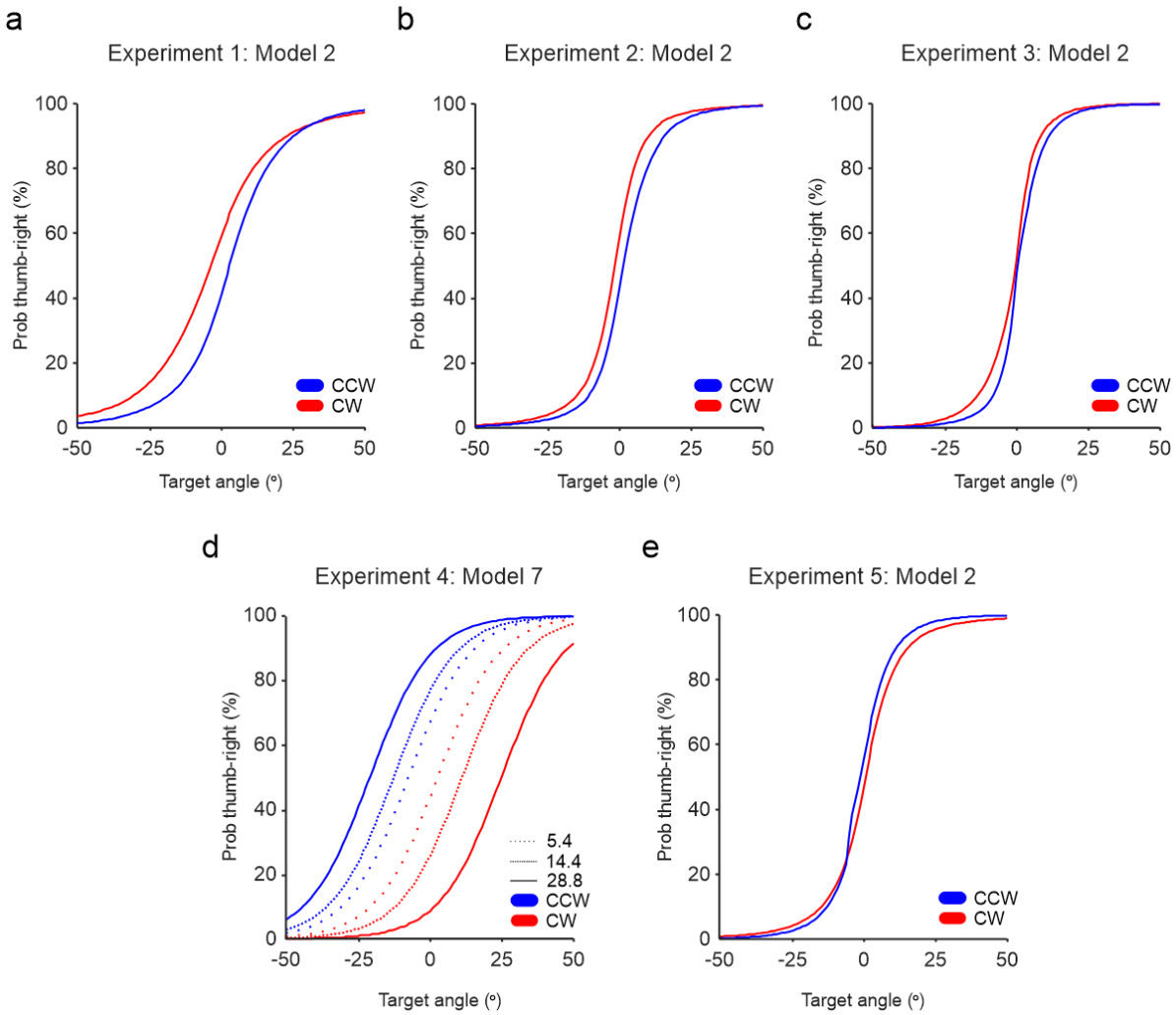


Figure 5. Generalised linear mixed-effect model visualisation of the effect size of direction across experiments. *For each of Experiments 1-3, the best-fitted model (Model 2) is used to predict choice when split by directional rotation for target angles 50° either side of the centre of ambiguity. Experiment 4 is further split by shift magnitude (Model 7). For Experiment 5, although be it less well fitted than solely using target angle, Model 2 is shown in order to illustrate the lack of effect of direction on choice. Model 2: C ~ TA + Di + (1|S); Model 7: C ~ TA + Di*SM + (1|S); CW, clockwise; CCW, counter-clockwise.*

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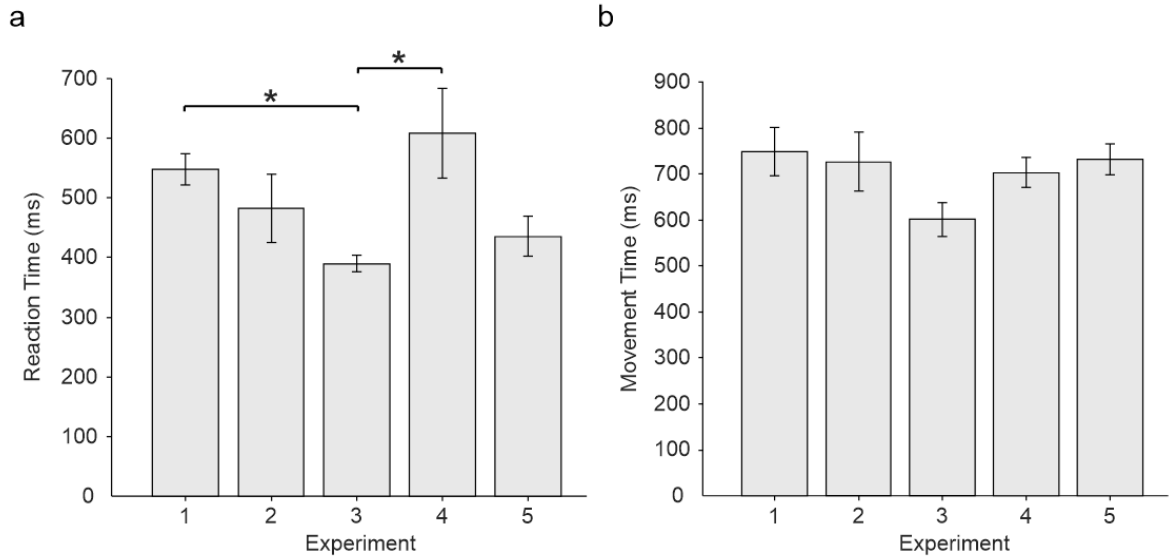

505

506 ***Figure 6. Reaction and movement times****. Average reaction (a) and movement (b) times across all*

507 *target angles and participants for each experimental condition (Exp.1 n=12; Exp.2 n=10; Exp.3 n=10;*

508 *Exp.4 n=6; Exp.5 n=11). The error bars represent ±1 standard error of the mean. * P<0.05.*

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