Grasp Orientation in Ambiguous Settings is Sensitive to Prior Object Motion

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Number of:

Pages - 35

Figures - 6

Tables - 1

Multimedia - 0

3D models - 0

Words in:

Abstract - 200

Main text - 4478

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. By presenting an initial orientation prior to the grasping of an ambiguous orientation, we found that subjects become biased to select a grasp for the ambiguous target that would be most congruent with the initial, determinate orientation. However, when object motion is observed between the initial and target positions, the bias is reversed, i.e. subjects choose the alternate wrist posture. Furthermore, the bias strength was found to be independent of the motion magnitude, and persists even when greater decision time is allowed. We provide evidence that this bias effect is not a perceptual phenomenon, and suggest it is potentially a behavioural manifestation of inhibitory circuits that delay decisions in conditions of motor ambiguity.

Keywords

Motor planning, Motor ambiguity, Grasping, Inhibition, Action selection.

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 [1]. 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 as 'motor ambiguity' [2].

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 [3].

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 [4,5]. In the context of motor ambiguity, the width of the previously presented object (i.e. graspability) can influence an individual's grip aperture when moving

to reach for an ambiguously sized object [6]. These findings exemplify that the execution of a movement toward an always identical object can be a varying consequence of prior context. Furthermore, the orientation and similarity of another object presented prior to the grasp can lead to minor adjustments in exact positioning of the index finger and thumb during a precision grip [7]. For more gross decisions such as choice of grasp posture, it has been shown that the presentation of two potential reach targets, whether simultaneous or sequenced, leads to the motor plan formed for each target to interact and co-optimise [8,9]. When one of the potential targets, if ambiguous, is then cued to grasp, this co-optimisation ultimately results in subjects becoming biased to grasp the ambiguous target in a way that matches the non-cued determinate target. Yet, how motor planning adapts to dynamically changing rather than the addition of visual information and the consequences this has for gross decisions such as grasp posture in situations of motor ambiguity, is unknown.

To explore whether grasp selection can be influenced by prior, dynamically changing visual information, we designed a target object that depending on orientation, placed subjects into decision settings where grasp selection was clear and consistent (determinate), or uncertain and variable (ambiguous). Given previous studies, we predicted that the visual presentation of a determinate orientation prior to the grasping of an ambiguous orientation will bias subjects to select a grasp for the ambiguous target that would be most congruent with the initial, determinate orientation. We also explored how an individual's perception of prior visual information may provide insights into the mechanisms through which it may influence grasp behaviour.

Materials and Methods

Ethical approval was granted by the Newcastle University Ethics Committee and written informed consent was obtained from all volunteers.

Grasping Study

Participants

All participants bar two were right-handed and all were naïve to each experiment and its predictions. A total of 21 healthy volunteers (22-50 years old, 14 females 7 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: 10 participants). Some took part in several experiments - in which case each experiment was separated by at least 6 days.

Grasping Study - Task Setup

In total, four experiments were conducted to investigate the influence of prior visual information on grasp selection in ambiguous settings. The experimental paradigm required participants to perform a precision grip movement on a triangular prism block (6 cm long by 2 cm wide, see Fig. 1) with their right-hand upon hearing a go cue (auditory beep 500 Hz, 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 [10]. The object was mounted onto a grey rectangular stage and connected to a stepper motor to enable rotation in steps of 0.9° angles – - the stepper motor was driven by an Arduino UNO R3 and motor shield R3, and 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 'Grasp 1' whereby the thumb was placed on the left or top end of the object or 'Grasp 2' whereby the index finger was used instead (Figure 1a). Previously studies have referred to these two grasp postures as 'thumb-left'/'supination' or 'thumb-right'/'pronation' respectively (e.g. Stelmach et al., 1994; Wood and Goodale, 2011), however given both of these nomenclatures lose validity at certain positions we opted for Grasp 1/ Grasp 2.

Participants were seated in a chair with their forearm positioned on the arm rest (Figure 1a). 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 [2], 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 quickly 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 (200 ms, 200 Hz) 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.

Grasping Study – Calibration Task Design

Before 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, the switch-point was variable between subjects 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 (TA) of subsequent experiments were centred 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 1b). 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.

Grasping Study – Experimental Task Design

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 (IA) for which they would not reach, 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 1d), 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 1c) 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 a balanced distribution 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.

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 2a.

Grasping Experiment 1: No delay

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

Grasping Experiment 2: 150 ms delay

As with Experiment 1, trials within Experiment 2 began with home-pad depression and observation of object movement to an IA. However, after the hold-period concluded, initiation of object rotation to the TA occurred 150 ms prior to the onset of the go cue.

Grasping Experiment 3: 500 ms delay

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.

Grasping Experiment 4: Rotation blocked from view

For Experiment 4, 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 IA was blocked. After becoming transparent for 1.5 s to allow subjects to view the IA, the goggles transitioned back to an opaque state. Upon completion of the remaining hold time, object rotation was initiated and 150 ms later the goggles converted to a transparent state, simultaneous with the auditory cue.

Visual Study

A second study was designed to investigate the perceptual consequences of observing a shift in object orientation, thereby exploring the mechanisms by which prior visual information may affect grasp choice.

Participants

All participants were right-handed and naïve to each experiment and its predictions. In total, 27 healthy volunteers (20-54 years old, 20 females 7 males) were recruited for this study (Experiments 1 - 6: 11 participants; Experiments 7 - 10: 6 participants) with some taking part in several experiments, however there was no overlap in participation between this visual study and the previous grasping study. All had normal or corrected to normal vision.

Visual Study - Task Set-Up

In this study, participants were seated with the identical set-up as described in *Grasping Task Set-Up*. As with the grasping task, participants initiated the trial sequence by holding down the home-pad. However, after observing object rotation from an IA to a TA, participants were asked not to execute a grasp as before, but instead only continue to observe. Upon revelation of the TA, a set delay was allowed before visual input of the object was blocked by goggle opaqueness. During this period, the object underwent a secondary movement, concluding at a 'test' angle (TE) located either CW/CCW ('catch' trials), or unchanged from the TA orientation. To prevent participants from using auditory cues to distinguish between trial types, the object rotated on all trials before concluding at the final TE position. After a delay, vision was restored and participants were asked to report (by reaching to press keys on a keyboard placed in front of them) whether the object appeared to have shifted orientation between the TA and TE positions. If the TE appeared CCW relative to the TA, subject were asked to press '1'. If the TE appeared unchanged from the TA, '2' was used. Finally, if it appeared CW, '3' was pressed. Subjects were given unlimited time to observe the TE and report their decision. An overview of the trial sequence for visual experiments is illustrated in Figure 2b.

Visual Study – Task Design

As with the grasping study, subjects began with the calibration task to find an estimate of their centre of ambiguity. Following this, the main visual task was designed to investigate whether observing rapid

object motion from an 'initial' position to 'target' leads to changes in how the target position is perceived by an individual.

Four variables were adjusted across ten experiments: time given to observe the TAs before visual blocking; duration of visual blocking; magnitude of rotation from TA-TE on catch trials; frequency of catch trials.

Visual Experiments 1 - 3

The first three experiments varied the time given to observe the TA before blocking (Experiment 1: 100 ms; Experiment 2: 300 ms; Experiment 3: 500 ms) whilst keeping constant the duration of visual blocking (500 ms), TA-TE catch trial shift magnitude (5°), and frequency of catch trials (10%).

Visual Experiments 4 - 6

The next experiments kept constant the time given to observe the TA (500 ms), however varied the duration of visual blocking (Experiment 4: 310 ms; Experiment 5: 1000 ms; Experiment 6: 2000 ms). TA-TE catch trial shift magnitude and frequency of catch trials remained as for Experiments 1 - 3.

Visual Experiments 7 - 8

Two further experiments kept the same variable values as Experiments 3 and 4, however the TA-TE shift magnitude was increased to 10°.

Visual Experiments 9 - 10

Finally, the frequency of catch trials was increased to 25%. The variable values remained as for Experiments 3 and 4.

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. All data analyses and statistics were performed using custom written MATLAB scripts. For the grasping task, reaction time (RT) was

measured as time from go cue to home pad release. 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 'Grasp 2' 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 either wrist posture was used as an estimation of each participant's switch point (=x_o), later referred to as the 0° angle (Figure 1b). The halfwidth provided a measure of switch sharpness, calculated as the difference between target angles for the 75% and 25% choice probabilities (=$2ln(3)/k$). This was used as an indicator of subject uncertainty across the task as a whole.

Grasping Experimental Tasks

For each target angle, direction, and shift magnitude the average decision was calculated as the probability of using a 'Grasp 2' wrist posture. The decision probability could then be further split by direction of rotation and shift magnitude.

For analysis of the contribution of the different experimental factors, a generalised linear mixed effect model (GLME) approach was adopted. GLME analysis allowed estimation of the contribution of each fixed factor (final target angle (TA), direction (Di), and shift magnitude (SM)) to grasp choice (C), 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. A GLME with binomial distribution and logit link function was used. Approximate Laplace

248 was used as the method for estimating model parameters. Subject specific variation (S) was accounted
249 for by its introduction as a random effect into the model.

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

254 Model 1: C ~ TA + (1|S);
255 Model 2: C ~ TA + Di + (1|S);
256 Model 3: C ~ TA*Di + (1|S);
257 Model 4: C ~ TA + SM + (1|S);
258 Model 5: C ~ TA*SM + (1|S);
259 Model 6: C ~ TA + Di + SM + (1|S);
260 Model 7: C ~ TA + Di*SM + (1|S);
261 Model 8: C ~ TA*Di*SM + (1|S).
262

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

267 *Grasping Task: Reaction and Movement Time Analysis*

268 Previous work has shown that both RTs and MTs are longer for ambiguous grasps than determinate [2].
269 We used a GLME approach to explain our RT and MT data using the absolute difference of the target
270 angle from the ambiguity point as the single factor in the models below:

271 RT Model: ln RT ~ $|TA-X_o|$ + (1|S)
272 MT Model: ln MT ~ $|TA-X_o|$ + (1|S),

273 where X_o is a switch point estimated by fitting a sigmoid function for each subject separately. A
274 significant linear decrease in these models would correspond to longer RT/MT for ambiguous target
275 angles in comparison to determinate angles. Reported effects are estimated from each model as the
276 difference between the centre of ambiguity, 0°, and ± 40° from this switch-point, and then reversed
277 transformed from log values. Trials for which RT was longer than 1.5 s or shorter than 150 ms were
278 excluded from analysis; MTs however had no explicit high/low cut-off. For both RT and MT analysis
279 any remaining trials outside the mean ± 3 SD were also excluded - this was then repeated recursively
280 until no more trials could be excluded. On average across all 4 experiments, 2.6% of the trials were
281 discarded for reaction time analysis and 1.3% for movement time analysis.

282 *Visual Experimental Tasks*

283 Perceptual data were obtained from subjects' key presses of '1' (TE appeared CCW to TA), '2'
284 (appeared unchanged), or '3' (TE appeared CW to TA). These decisions are denoted throughout as
285 'Left', 'Unchanged', and 'Right', as to distinguish object motion direction from subject perception.

286 Trials for which the TEs were indeed shifted CW or CCW from the TAs acted as catch trials, with the
287 remainder trials (i.e. TE = TA) denoted 'unchanged'.

288 For unchanged trials, the results were first split by directionality of object rotation from IA to TA,
289 dividing the data into CW and CCW trials. Given the frequency of trials for each TA varied according to
290 level of ambiguity, matching the grasping task, the subject decisions (i.e. Left, Unchanged, Right) per
291 TE were expressed as a percentage. The percentage of each decision was then averaged across all TEs.
292 To investigate the effect of rotation directionality on object position perception, paired t-tests were
293 used to compare CW and CCW conditions for each decision.

Results

Grasping Task: 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 Grasp 1 to Grasp 2 as the object sampled more clockwise angles (e.g. Figure 1b). Across all unique subjects, the switch-point for the calibration experiments ranged between -58.1° and 32.8°, relative to the vertical axis, with varying degrees of sharpness (halfwidth 15.58 ± 13.44°).

Grasping Task: GLME Analysis

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 but only observe, before the object rotated CW or CCW towards the target angle. Example raw data for each experimental variation is shown in Figure 3a-d.

All 8 models were fitted to the data from each experiment. A comparison of BIC values across models within each experiment is shown in Figure 4.

Experiment 1

When the end of the auditory go cue was synchronised with onset of object rotation the best model with the smallest number of variables was Model 2, including only target angle and direction of rotation. When a CW rotation was observed, subjects were more likely to select Grasp 2 than Grasp 1 (Direction CE = -0.732 ± 0.105, t-stat = -6.96, $p < 0.0001$; Target Angle CE = 0.096 ± 0.005, t-stat = 20.97, $p < 0.0001$). Probability of Grasp 2 at the switch-point estimated from Model 2 was 0.14 higher than the probability of Grasp 1. Including shift magnitude as a variable in addition to direction (Model 6) increased the BIC value by 6.7, and the shift factor was an insignificant contributor to the model (Shift Magnitude CE = -0.001 ± 0.005, t-stat = -0.23, $p = 0.82$; Direction CE = -0.732 ± 0.105, t-stat = -6.96, $p < 0.0001$; Target Angle CE = 0.096 ± 0.005, t-stat = 20.97, $p < 0.0001$).

To restate these findings, a clockwise rotation to an ambiguous target angle increased the probability of Grasp 2 (a grasp non-congruent with the initial position) by 14% at the switch-point in comparison to Grasp 1 (a grasp congruent with the initial rotation), while a counter-clockwise motion increased the likelihood of Grasp 1. The GLME analyses showed that the magnitude of rotation is not an important contributor to this effect, i.e. a transition from either a determinate or ambiguous initial angle towards an ambiguous target angle yielded a bias effect of similar strength.

In order to comparatively visualise the effect of direction on behaviour with subsequent experiments, 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 3e).

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 (Experiment 3) further reduced the effect of direction, yet significance held with Model 2 remaining the best fit (Direction CE= -0.48 ± 0.13, t-stat = -3.74, $p < 0.001$; Target Angle CE = 0.20 ± 0.01, t-stat = 21.2, $p < 0.0001$). Furthermore, when using Model 2 to predict grasp choice, the halfwidth of the sigmoid plots as visualised in Figures 3a-c, e-g decreased from 25.10 ± 3.72° in Experiment 1, to 14.0 ± 3.10° and 10.69 ± 1.92° in Experiments 2 and 3 respectively, indicative of significantly reduced uncertainty across the task as a whole (one-way ANOVA, df = 3, F = 4.58, $p = 0.0078$). Post-hoc comparisons revealed that the halfwidth was just significantly different between Experiment 1 and Experiment 2 (unpaired t-test, $p = 0.049$), and also significantly decreased between Experiment 1 and Experiment 3 (unpaired t-test, $p = 0.0064$). Visually,

the difference in grasp choice between CW and CCW trials becomes narrower the longer the go cue is delayed (Figure 3a-c, e-g). *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

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 still included only target angle and direction (Direction CE= 0.43 ± 0.12, t-stat = -3.71, $p < 0.001$; Target Angle CE = 0.13 ± 0.01, t-stat = 20.7, $p < 0.0001$). Yet interestingly, the effect of direction was inversed (Figure 3d, h). For example, the presentation of the object at an initial position that would require Grasp 1 increased the likelihood of subjects then later adopting Grasp 1 for the ambiguous target angle. Visualisation of choice split by direction further illustrates the influence of initial angle on ambiguous grasping, with the halfwidth estimate falling comparatively between Experiments 1 and 2 at 17.17 ± 2.37° (Figure 3h). The key point to note with Experiment 4 is that blocking object rotation from view still elicits the bias effect, yet it is the inverse to that previously described, i.e. subjects become more likely to adopt the grasp for the ambiguous target angle that would be congruent with the initial angle.

Grasping Task: 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 ($p = 0.032$, dF = 3, F = 3.27, one-way ANOVA). Post hoc analyses (using the Tukey-Kramer correction) revealed that Experiment 1 had significantly longer RTs than Experiment 3 ($p = 0.023$), with averages of 541.6 ± 27.0 ms and 393.0 ± 14.2 ms respectively (Figure 5a). The average RT for experiment 2 was 468.3 ± 50.3 ms, falling between Experiment 1 and 3. The average RT of Experiment 4 was 507.0 ± 42.4 ms.

368 Movement times were not significantly affected by the timing of the go cue (p = 0.128, dF = 3, one-
369 way ANOVA) with smallest MT observed in Experiment 3 (596.2 ± 36.8 ms) and greatest in Experiment
370 4 (738.8 ± 32.6 ms) (Figure 5b).

371 To investigate the effect of target angle on reaction and movement times, a GLME approach was used.
372 In agreement with previous work, reaction times for target orientations closer to the centre of
373 ambiguity were greater than those more determinate (log transformed raw values are shown in blue
374 in Figure 6). The GLME-estimated decrease in RTs from the switch point (0°) to 40° was 30.9 ms for
375 Experiment 1, 70.5 ms for Experiment 2, 83.7 ms for Experiment 3, and 50.0 ms for Experiment 4
376 (estimated values for each distance from the switch point are shown in red in Figure 6). We noticed
377 that the rate of RT change within ambiguous orientations range (± 15° from switch-point, emboldened
378 in Figure 6) is greater than for determinate orientations, especially for Experiment 2 and 3. The RT
379 decrease in the ambiguous range was estimated for each individual subject using GLM and compared
380 using one-way ANOVA (Supplementary Figure 1). The mean rates of change coefficient estimates were
381 lowest for Experiment 1 with -0.0006 ± 0.0009, followed by Experiment 4 with -0.0010 ± 0.0022,
382 Experiment 2 with -0.0066 ± 0.0031, and finally Experiment 3 with -0.0154 ± 0.0062. A significant effect
383 of experimental condition on the rate change was found (p = 0.016, F=3.877, dF = 3, one-way ANOVA).
384 Post-hoc analyses (using the Tukey-Kramer correction) showed that both Experiment 1 and 4 had a
385 significantly smaller decrease in RTs with distance from switch-point than Experiment 3 (p = 0.020,
386 and p = 0.034, respectively). To put into context, the greater the uncertainty induced by the
387 experimental condition, as shown by halfwidth measure, the slower the reaction times both across
388 experiments and smaller the influence of ambiguity on reaction time within experiments.

389 Furthermore, MT was greatest for trials closer to 0°, the duration shortening as orientations
390 approached the extremes of 40°. Though again this trend was seen with all experiments, GLME
391 analysis revealed that target angle had a significant effect on MT for Experiments 1 (coefficient
392 estimate -0.0010 ± 0.0004, t-stat = -2.65, p < 0.01) and 2 (coefficient estimate -0.0010 ± 0.0004, t-stat

393 = -2.63, $p < 0.01$), but not Experiment 3 (coefficient estimate -0.0002 ± 0.0003, t-stat = -0.49, $p = 0.62$)
394 or Experiment 4 (coefficient estimate -0.0007 ± 0.0004, t-stat = -1.67, $p = 0.096$).

395 ## Visual Task

396 Given the findings that the directionality of object rotation can influence grasp choice, we explored
397 whether this may be attributed to how the target position is perceived post-rotation. In this secondary
398 study, subjects were asked to observe IA-TA object rotation as before, except post-rotation, visual
399 input was briefly blocked before subjects were re-shown the object at a test angle (TE) and asked to
400 report whether it appeared further CW ('right'), CCW ('left'), or 'unchanged' from the TA position.

401 Four factors were varied across ten experiments: the time given to observe the TA position prior to
402 visual blocking (T1; Experiments 1-3), the duration of visual blocking between presentation of TA and
403 TE (T2; Experiments 4-6), the magnitude of rotation from TA to TE (M; Experiments 7-8), and the
404 frequency of catch trials wherein there is rotation from TA to TE (C; Experiments 9-10). Average
405 choices on non-catch trials from Experiment 1 are shown in Supplementary Figure 2. For non-catch
406 trials (i.e. TA = TE), in no instance was there a significant difference between the error rate of reporting
407 'left' or 'right' when the IA-TA rotation direction was CW, nor when it was CCW (see Table 1). This
408 suggested that the perception of the TA position is not influenced by directionality of object rotation
409 from an initial position. *Thus, the effect of rotation directionality on grasp choice is likely not due to a*
410 *perceptual bias.*

411 # Discussion

412 In this study subjects were placed into ambiguous settings with an object that afforded one of two
413 precision grasps (Grasp 1 or Grasp 2) in order to investigate the influence of visuomotor priming on
414 motor ambiguity. In agreement with previous studies [3,11,12] that have shown that priming can influence
415 aspects of the execution of reach-to-grasp movements when primes are congruent with the target,
416 the results of this study demonstrate that the presentation of an initial, priming orientation of the

object (at either a determinate or ambiguous orientation) was sufficient to influence choice of grasp when the object was then shown at an ambiguous orientation (Grasping Experiment 4). Yet, when rotation of the object from the initial angle to the target position was visible, a significant but inverse effect of directional bias on grasp choice was found (Grasping Experiments 1-3).

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

In addition to the inverse bias effect, another consequence of observing object motion is greater uncertainty in grasp choice. This was revealed by a shallower transition between grasp choices the earlier the go cue was given, a consequence of increased variability suggestive of more inefficient planning [13]. Interestingly, when rotation was blocked from view, the transition steepness comparatively lied between giving the go cue synchronous with object motion and delaying it by 150 ms. This suggested that although the mere presentation of an initial angle does generate uncertainty and with it the bias effect, object motion induces greater uncertainty and with it an inversed bias effect.

441 Expectedly, participants were slower to react to any given target angle the earlier the go-cue was given
442 when rotation was visible. Yet curiously, blocking rotation from view did result in quicker reaction
443 times compared to when the go-cue was given synchronous with visible rotation. Although this was
444 not a significant difference, it does align with the findings that visible rotation, with a synchronous go-
445 cue, induces greater uncertainty than the mere presentation of the initial angle. Despite not enforcing
446 subjects to react as quickly as possible, the reaction time still reflects the time needed for the cortical
447 circuitry to choose between grasps [2,14]. This increased uncertainty is also highlighted in the smaller
448 difference in reaction time between ambiguous and determinate orientations, in comparison to when
449 greater time is granted for planning.

450 The mechanisms by which object motion induces these signs of increased uncertainty, and how this
451 may be linked to the inverse bias effect is unclear. Given that for Experiment 1 the go cue and object
452 rotation onset were triggered synchronously, initiating movement planning prior to knowing the
453 target orientation could explain the greater uncertainty and lead participants to incorrectly predict
454 the final target orientation. Predicting the future location of a moving object is a familiar task, yet
455 some consistent biases have been reported in are known to the literature. It could be considered a
456 good strategy for example, that if an occluded object is approaching an observer, to overestimate its
457 speed in order to be cautious and avoid potential collision [15]. Contrastingly, when asked to intercept
458 an occluded object moving parallel to the observer, its speed is often underestimated, causing people
459 to intercept its path too late (e.g. [16-18]). An overestimation of the final target position would push
460 subjects towards planning a grasp different from the grasp that would have been used for the actual
461 target position, and therefore could be a mechanism for the inverse bias effect. In Experiments 2 and
462 3 (whereby the go cue is given after rotation is finished), prediction of the final object orientation is
463 unnecessary and could be planned anew when the go cue is given, yet this does not seem to be true.
464 The inverse bias effect, although smaller, persists, therefore suggesting that the plan to grasp is not in
465 fact updated at the go cue, but rather stays similar to the one created during the rotation of the object.

466 An alternative suggestion for why grasp selection in ambiguous settings is sensitive to target rotation
467 could be that rapid object rotation leads to momentary changes in how the target angle is visually
468 perceived. If the target orientation is perceived to have rotated further than is true, the bias effect
469 could then be attributed to a perceptual error that degrades with greater time given to observe the
470 target position prior to grasping. To investigate whether the object motion has consequences for
471 perception of the target orientation, a second study was performed without the grasping action. Here,
472 participants observed the same object motion but had to report object orientation with a keypress
473 rather than planning to grasp the object. Object position was manipulated behind opaque goggles and
474 participants were given time to report whether the object appeared at the same position as before. If
475 a perceptual error is present, we hypothesised that, on trials when the final object position was not
476 changed during visual blocking, participants' perception of object position would be affected by
477 rotation direction from the initial angle to target. Yet, the proportion of error decisions of 'left'
478 compared to 'right' was not influenced by rotation direction. *This suggests the inverse bias effect*
479 *observed in the grasping task cannot be attributed to perceptual phenomenon and instead is linked to*
480 *motor planning.*

481 It has been shown that in situations affording more than one possible action, the brain prepares
482 multiple competing movements before selecting one [19,20]. Indeed, when presented with multiple
483 reach targets and forced to act before knowing the final location, the initial movement vector reflects
484 an average of the competing motor plans [21,22]. In tasks wherein an ambiguous and determinate target
485 are shown simultaneously before one is cued, the wrist posture adopted for the ambiguous trials is
486 more likely to be compatible with the posture required for the determinate target rather than the
487 alternate posture choice [8]. This is likely explained by the convergence of two parallel motor plans (one
488 for each potential target) to form one singular plan, resulting in lower reaction and movement times,
489 thus improving overall performance. It has also been demonstrated that sequential rather than
490 simultaneous presentation of potential targets can lead to proactive influence, i.e. the movement
491 preparation associated with the first target can influence the motor plan for a secondary target [9]. In

492 Gallivan *et al.,* 2016, (Experiment 2) the presentation of the first target was later accompanied by the
493 presentation of a second target, before participants were cued to grasp one of the two potential
494 targets. This led to subjects becoming biased to adopt a grasp for the cued ambiguous target that was
495 congruent with a determinate angle shown prior to (proactive co-optimisation) or after (retroactive
496 co-optimisation) the ambiguous target. The bias effect observed with our Experiment 4 is consistent
497 with this co-optimisation, whereby the choosing of Grasp 2 is more likely if the object was rotated
498 from an initial position greater in congruency with Grasp 2, and likewise for Grasp 1. It is curious,
499 however, that for trials that began and ended ambiguous, this bias effect was still observed. Though
500 Gallivan and colleagues showed that in their study a similar trial type yielded no bias, a key
501 experimental difference is that whilst they showed the exact same ambiguous orientation, ours
502 changed by 5.4°.

503 The inverse bias effect, the result of Experiments 1-3, could also be explained by co-optimisation if
504 we hypothesise that observable rotation of the object from a starting position towards the final
505 ambiguous position triggers a motor plan for an overestimated final position. Given our study design
506 of having varying object starting positions, the classification of both the bias and inverse bias effect
507 into proactive or retroactive influence is trial-by-trial dependent upon whether the starting position
508 was ambiguous or more determinate. Still, these analogies between our and previous experiments
509 should not be over-interpreted due to substantial differences in experimental designs. Firstly, our task
510 was not designed as a strict reaction time task, subjects were not informed about their reaction and/or
511 movement time, and though they were encouraged to be as quick as possible, precision placement
512 was emphasized. Secondly, our task requires greater precision - the index finger and thumb had to be
513 positioned at opposite sides of the object at a given object orientation, rather than within a range of
514 orientations (15° as in Gallivan et al 2016). Thirdly, in our task, only one object orientation was present
515 at any time and for Experiments 1-3, subjects observed a change in object position from the initial to
516 the target one.

517 If indeed two neural populations within the grasping network are competing for each wrist posture
518 (i.e. each planned simultaneously) in situations of motor ambiguity, perhaps the observation of the
519 object moving away from the preferred position of one population first inhibits its activity, before
520 facilitating activity corresponding to the alternate grasp. The antagonism of potential actions is known
521 to be subject to bias from a variety of both cortical and subcortical inputs, with the competition playing
522 out across a reciprocally interconnected fronto-parietal system [23-25]. Evidence favouring a given choice
523 causes activity to increase for its neural population, while information against a choice instead causes
524 suppression of its neural population [20]. An increase in available information would under normal
525 circumstances reduce reaction times [26,27], however, in our study reaction times slowed after observing
526 object motion by 34.6 ms compared to when blocked. Though this difference was not significant, this
527 could be in part because our task is not reaction time task design (average reaction times, e.g.
528 Experiment 1, 541.6 ms are longer than e.g. in Gallivan et al 2016). Furthermore, the quality of
529 evidence influences changes in reaction times, and so adding observation of the object rotation may
530 not enhance processing but rather complicate a decision by forcing further processing across the
531 action selection network [28,29]. By processing, we mean here disruption of the initial plan to grasp the
532 object congruently with the initial orientation, in favour of planning a grasp congruent with predicted
533 end object position – a consequence of observing object motion.

534 In conclusion, whilst static visuomotor priming has been shown to facilitate the convergence of action
535 plans into one singular intent to influence aspects of motor execution, the mechanisms of grasp
536 selection in ambiguous settings can also be susceptible to influence if object motion of the target is
537 observed prior to grasp execution. This effect is unlikely due to be a perceptual phenomenon, but is
538 potentially a consequence of cortical inhibitory circuits involving competing neural populations.
539 Further experiments aimed at disrupting M1, PMv or AIP processing might help delineate the neural
540 mechanisms behind this inverse bias. Understanding these neural mechanisms, and in particular initial
541 inhibition, underlying this motor bias during grasping could have implications for neurodegenerative

diseases that exhibit motor planning and execution deficits, for example Parkinson's Disease and Dystonia.

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Acknowledgements

This work was supported by grants BB/P006027/1 (AK), BB/Y000625/1 (AK), Newcastle Neuroscience Fund (NJM). The funders had no role in study design, data collection or interpretation, nor in the decision to submit the work for publication. The authors thank Mr Norman Charlton for mechanical engineering of the experimental setup, and Prof. Stuart Baker for designing the contact circuit and initial Sequencer scripts. For the collection of pilot data, the authors would like to thank Ms Annabelle

Clark and Ms Amn Ashhad. We would also like to thank Dr Steven Jerjian for critical feedback on earlier versions of the manuscript and Prof. James Kilner for suggestions to study design.

Competing Interests

The authors declare no conflicts of interest.

Author Contributions

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

Data Availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Figure Legends

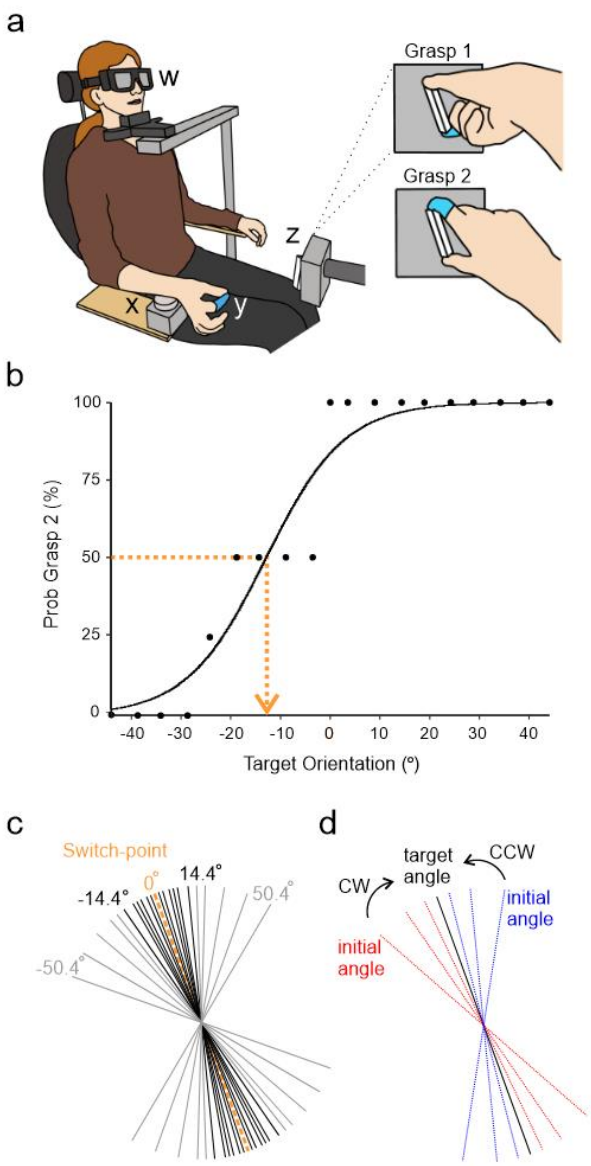


Figure 1. Illustration of experimental task set-up and study design. *a) Participant is seated with LCD goggles (w) covering their visual field and head placed on a chin rest. Their right-wrist is used to depress the home-pad button (x) to initiate the trial sequence. A latex glove on the index finger (y) impedes touch with the contact circuit on the target object (z) to allow detection of wrist posture (Grasp 1 or Grasp 2) on a trial-by-trial basis. b) 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 Grasp 2 posture following Calibration task. Black dots show average probability of choosing a Grasp 2 posture for each target*

angle sampled. c) Trial design of Experimental tasks showing sampling of target angles, with '0°' representing the subject's switch-point. d) 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°.

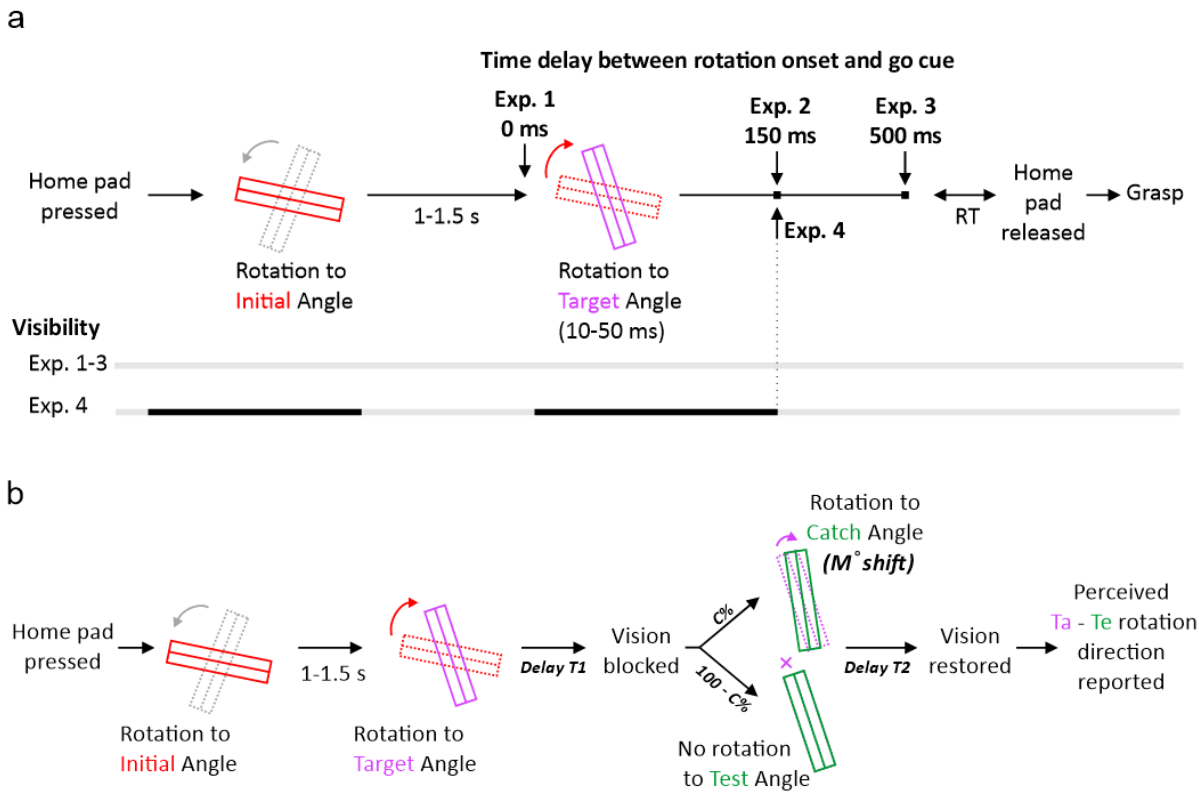
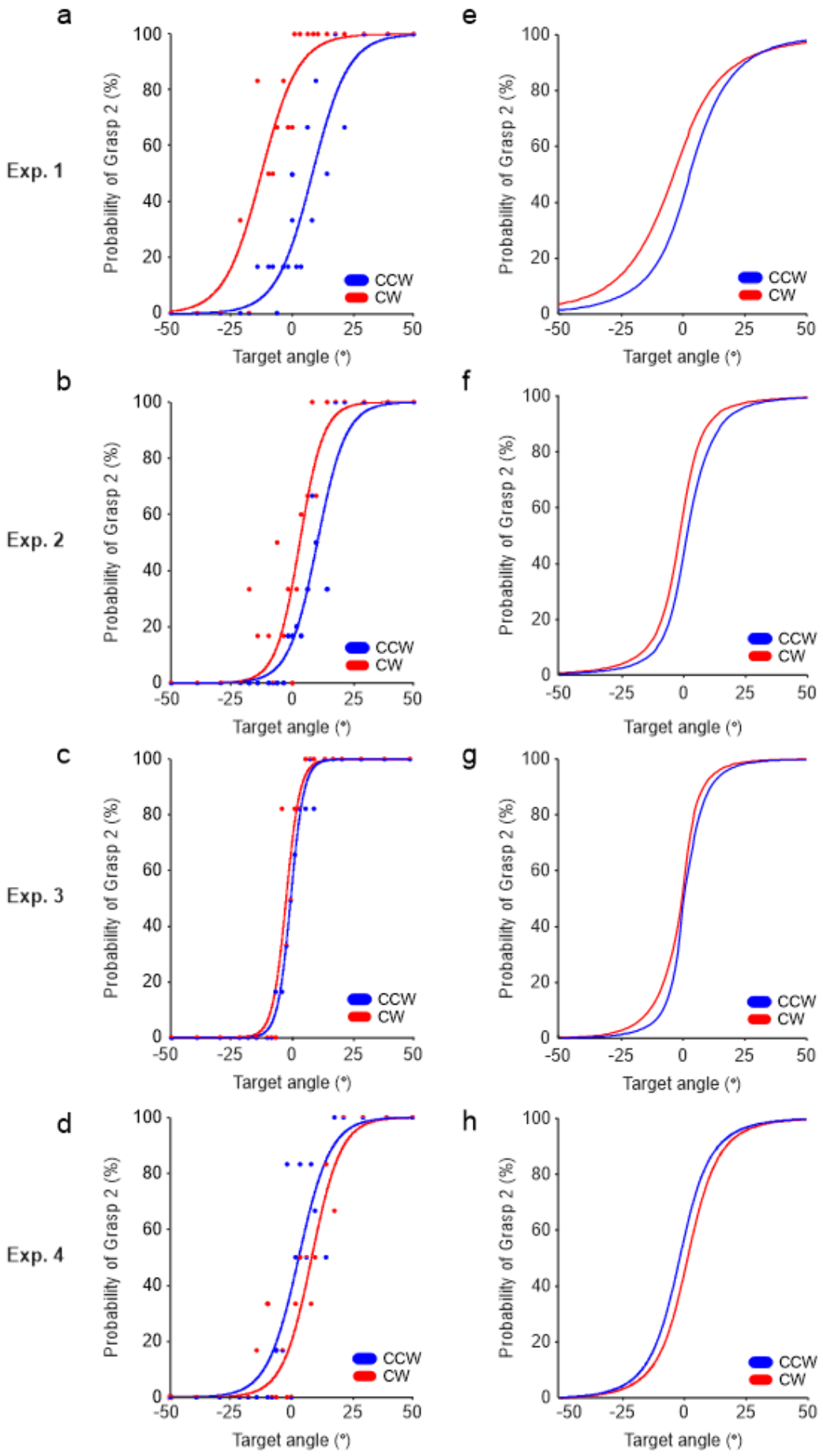


Figure 2. Comparative experimental timeline for all grasping and visual experiments. *a) For all grasping experiments, the duration of go cue was 50 ms, with variable onset relative to object rotation onset depending on experimental condition (Exp. 1 – 0 ms, simultaneous with object rotation onset, Exp. 2, 4 – 150 ms and Exp. 3 – 500 ms after rotation onset). Rotation of object took 10-50 ms, dependent upon whether an extreme or minor shift was performed. For Experiment 4 periods of object visibility and obscurity are illustrated by light and dark bars respectively. b) For visual experiments, four parameters were varied: T1, time given to observe the target angle; T2, duration of visual blocking before test angle presentation; M, magnitude of shift from target to test angles on catch trials; C, frequency of catch trials as a percentage of total trials; Ta, target angle; Te, test angle.*


a
b
c
d
e
f
g
h
Exp. 1
Exp. 2
Exp. 3
Exp. 4
Probability of Grasp 2 (%)
Target angle (°)
CCW
CW
0
20
40
60
80
100
-50
-25
0
25
50

666

Figure 3. Example raw data from a single subject and generalised linear mixed-effect model visualisation of the effect size of direction for each experiment. *a-d) Example raw and un-shifted data from a single subject. For each target orientation, trials were first split by the direction of rotation from the initial starting angle towards the target angle, with the average probability of choosing Grasp 2 then calculated for each direction (coloured dots). Sigmoid curves were then fitted to the data. e-h) GLME visualisation from all subjects. For all experiments, the best model (Model 2) is used to predict choice separately for each rotation direction for target angles 50° either side of the centre of ambiguity. Model 2: C ~ TA + Di + (1|S); C, choice; TA, target angle; Di, direction; S, subject; CW, clockwise; CCW, counter-clockwise.*

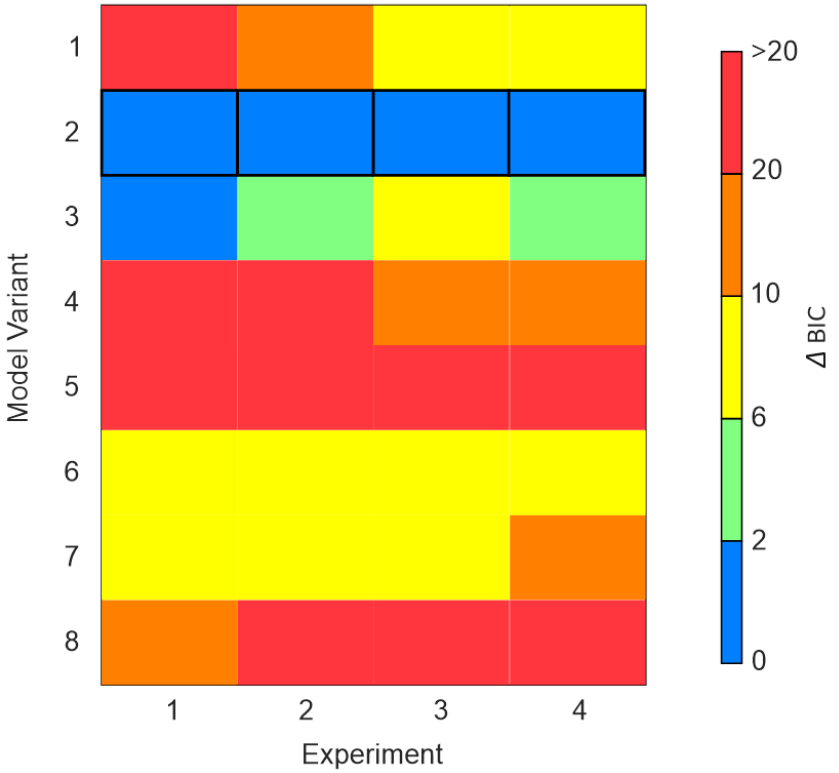


Figure 4. Comparison of BIC values across each GLME variant for Experiments 1-4. *Difference in BIC value (Δ BIC) relative to the best model variant (shown in blue with black outline). Δ BIC within the 2-6 range (green squares) indicate positive evidence in favour of the best model, 6–10 (yellow squares) indicate strong evidence and a difference greater than 10 (orange and red squares) indicates very strong evidence* [30].

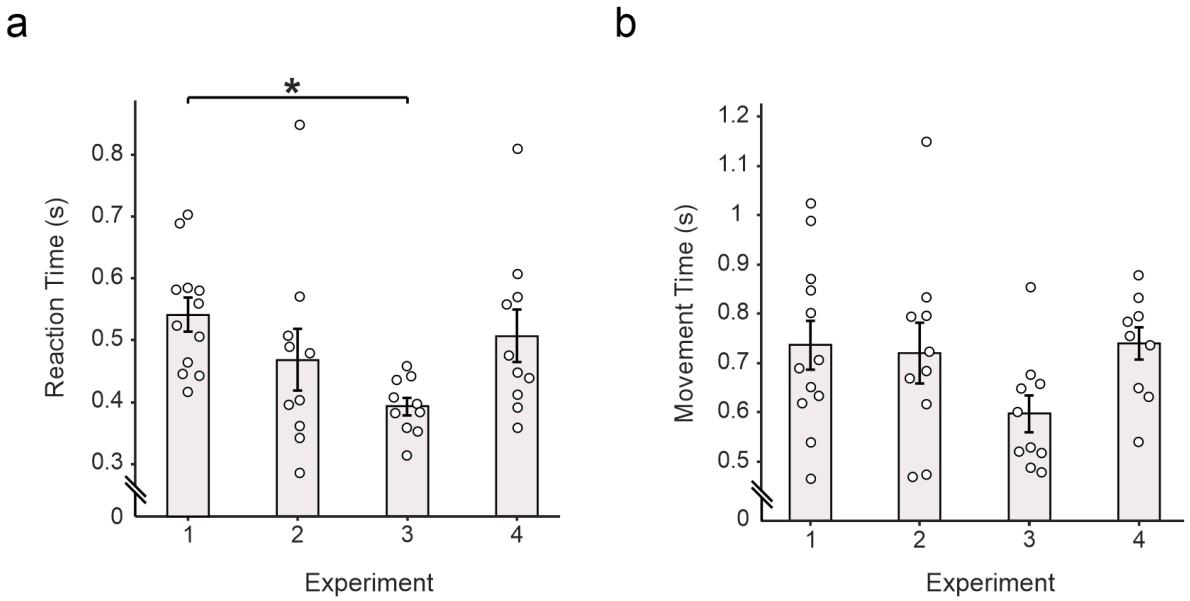
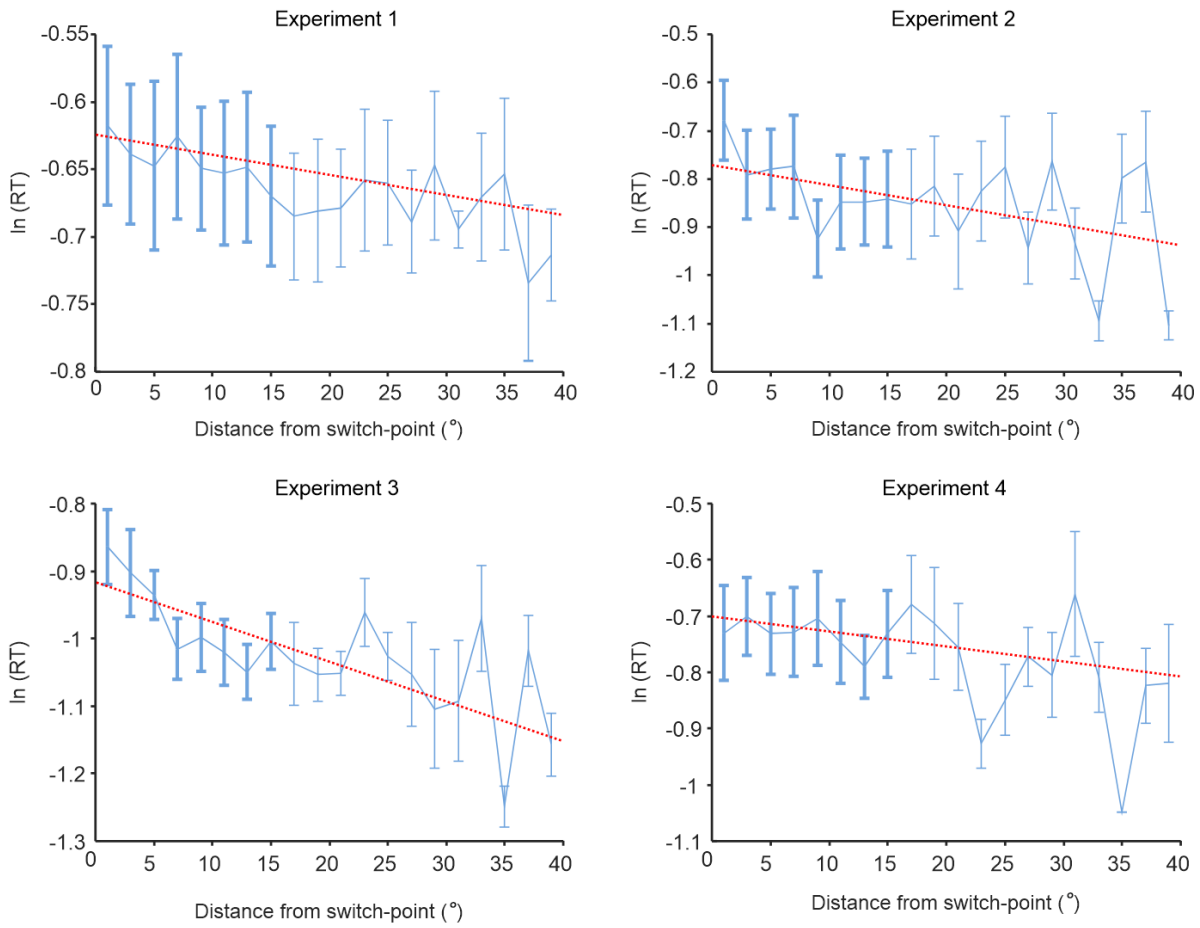


Figure 5. Reaction and movement times across Grasping Experiments 1-4*. Average reaction (a) and movement (b) times across all target angles and participants for each experimental condition (Exp.1 n = 12; Exp.2 n = 10; Exp.3 n = 10; Exp.4 n = 10). The error bars represent ± 1 standard error of the mean. * P < 0.05.*



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693 ***Figure 6. Reaction times within Grasping Experiments 1-4***. *Reaction times for each target angle were*

694 *measured from time of go cue to release of home-pad and averaged as distance from the switch point*

695 *and across subjects. Log transformed values of the averages are shown in blue (ambiguous angles are*

696 *emboldened). To illustrate the effect of distance from the switch point on reaction time, GLME analysis*

697 *was carried out for each experiment; estimated values for each distance are shown by the red lines.*

698 *GLME model: ln RT ~ |TA-X_o|<40° + (1|S); TA, target angle; S, subject. Exp.1 n = 12; Exp.2 n = 10; Exp.3*

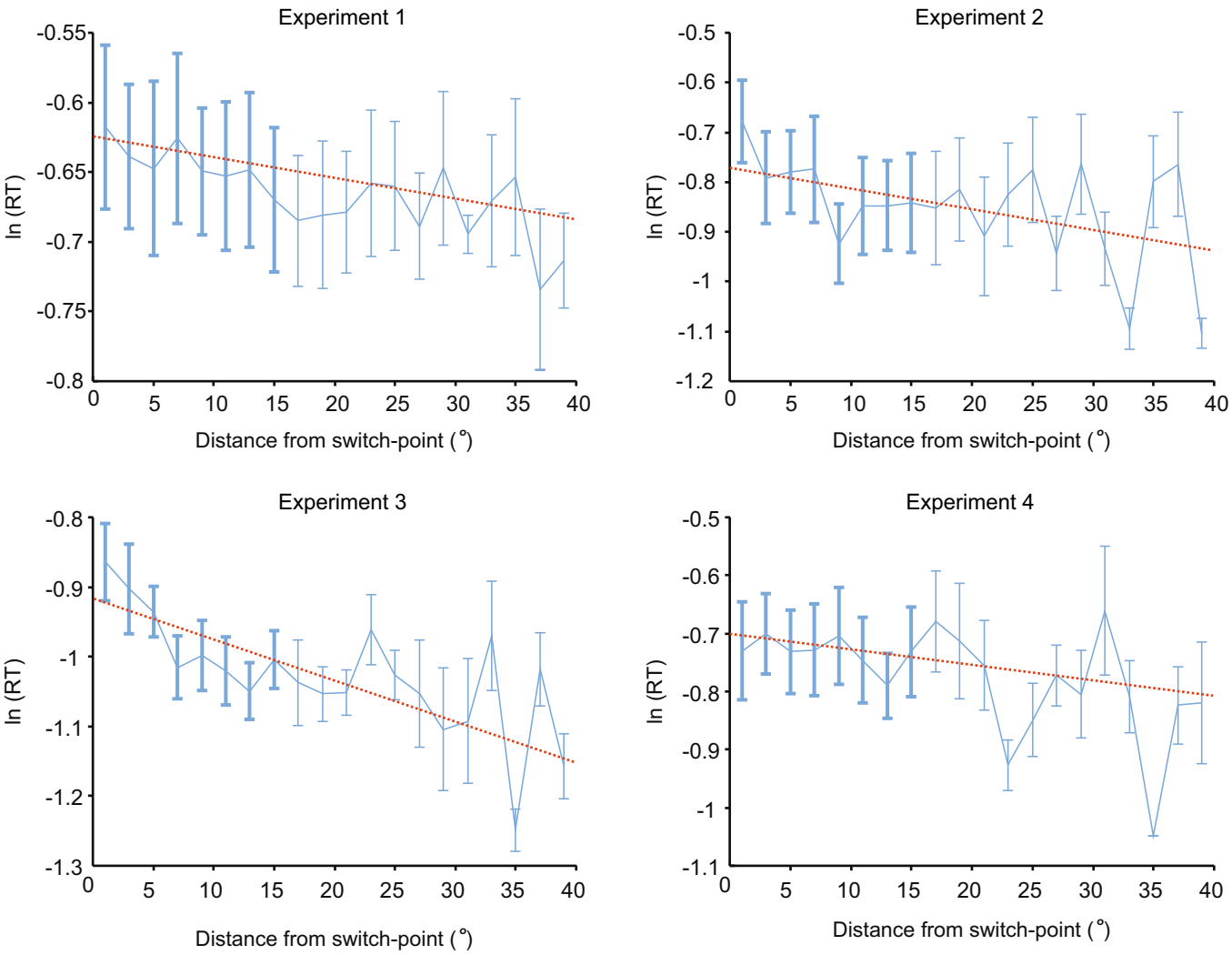
699 *n = 10; Exp.4 n = 10. The error bars represent ±1 standard error of the mean.*

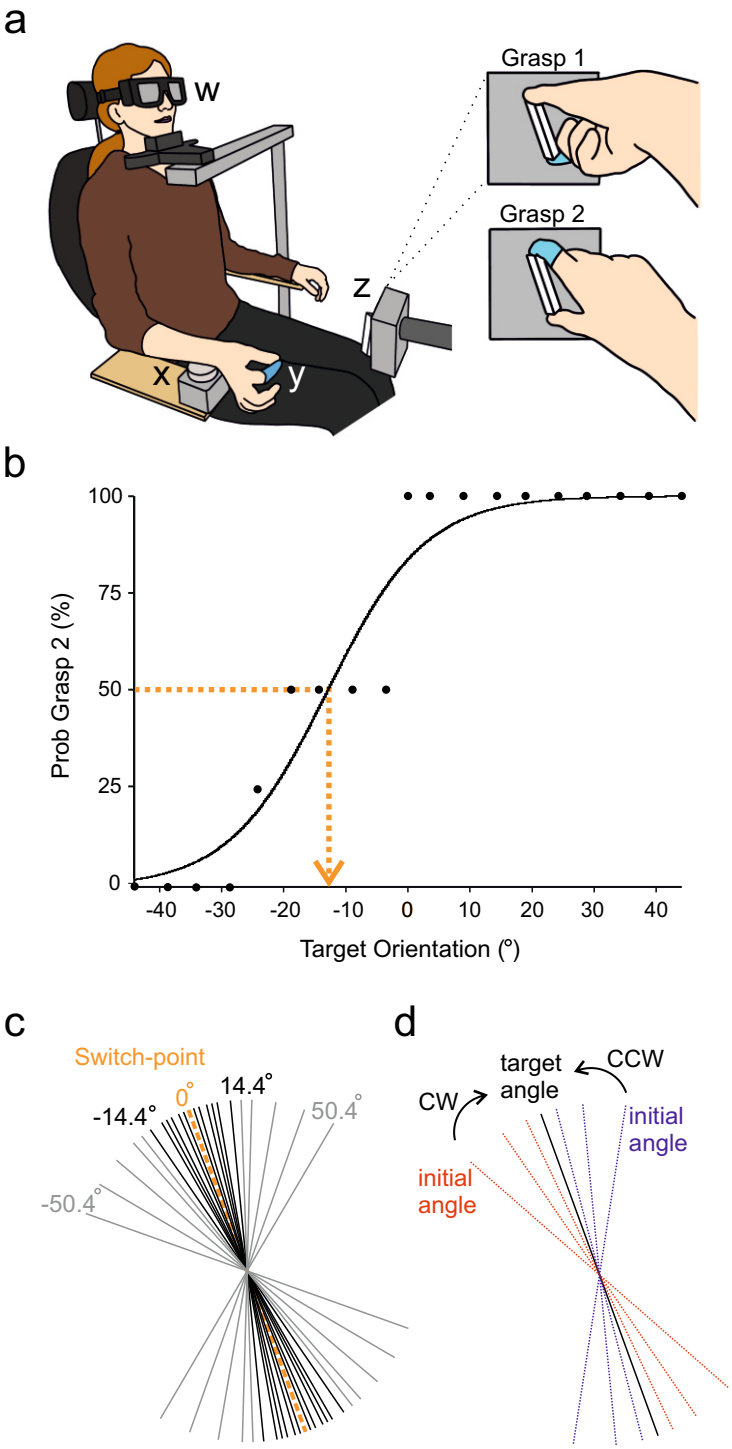
700

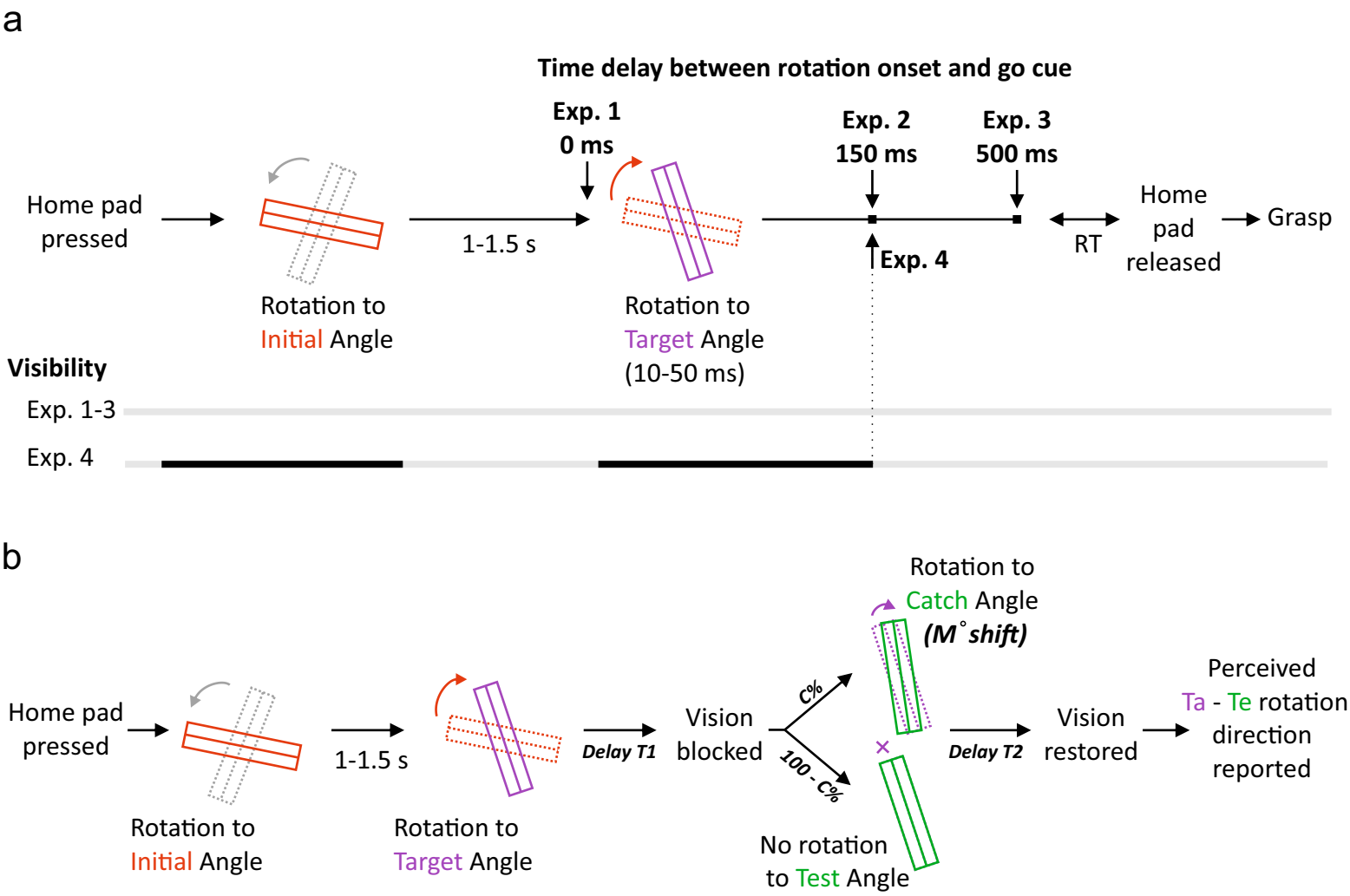
701

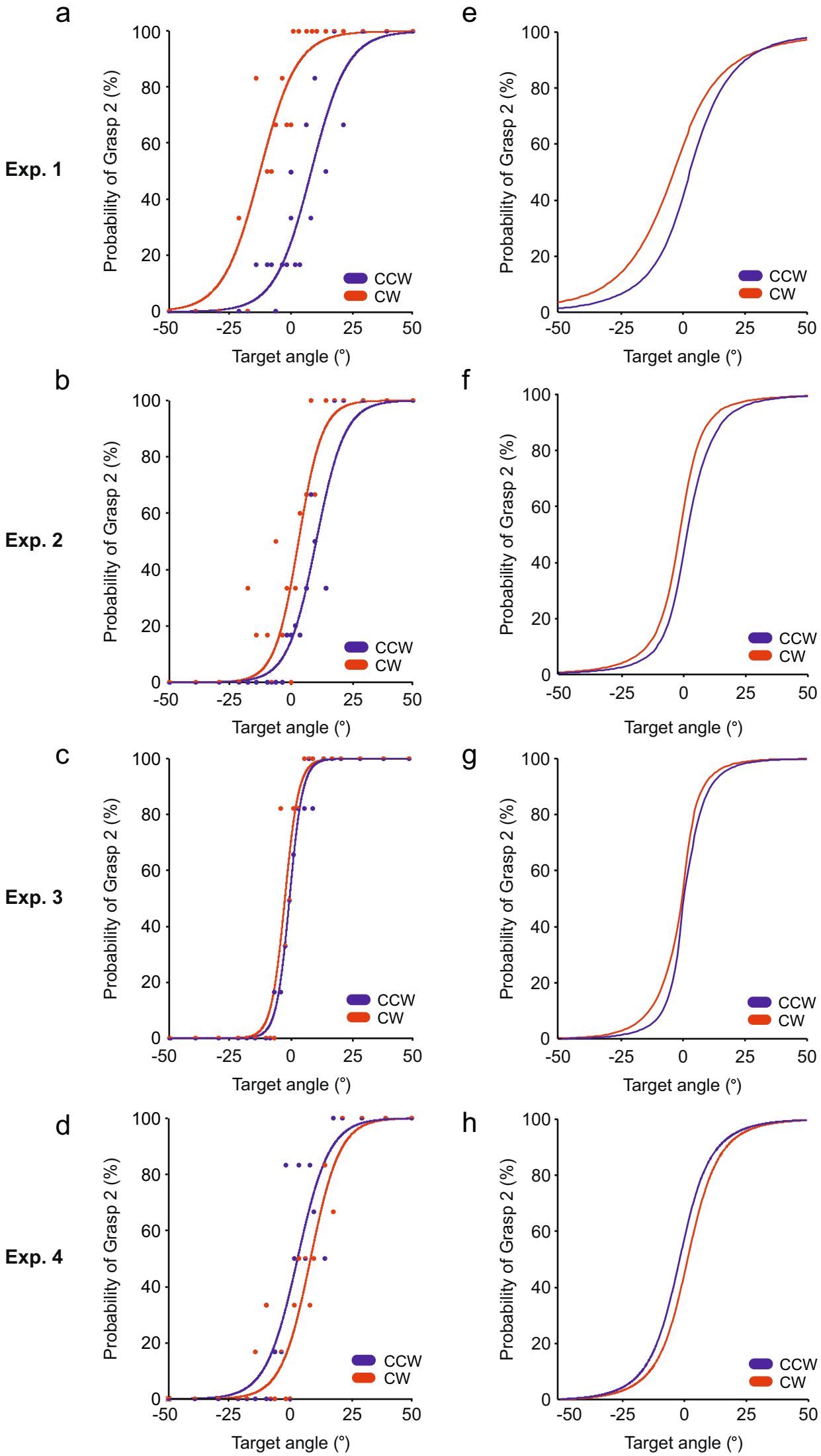
Visual Exp.	*n*	*T1, ms*	*T2, ms*	*M, °*	*C, %*	*left, CW, %*	*left, CCW, %*	*p*	*right, CW, %*	*right, CCW, %*	*p*
1	11	100	500	5	10	15.8	17.9	0.296	22.1	16.7	0.253
2	11	300	500	5	10	23.5	13.9	0.224	15.3	20.7	0.349
3	11	500	500	5	10	17.2	20.2	0.462	24.6	23.6	0.790
4	11	500	310	5	10	17.9	22.8	0.360	27.4	20.7	0.216
5	11	500	1000	5	10	13.8	16.9	0.368	20.3	11.4	0.089
6	11	500	2000	5	10	20.3	16.0	0.303	15.7	23.8	0.095
7	6	500	500	10	10	11.6	2.6	0.077	8.7	20.5	0.202
8	6	500	310	10	10	17.4	3.8	0.176	8.0	19.3	0.245
9	6	500	500	5	25	8.2	7.3	0.867	10.4	10.5	0.992
10	6	500	310	5	25	5.5	6.0	0.887	4.7	10.0	0.510

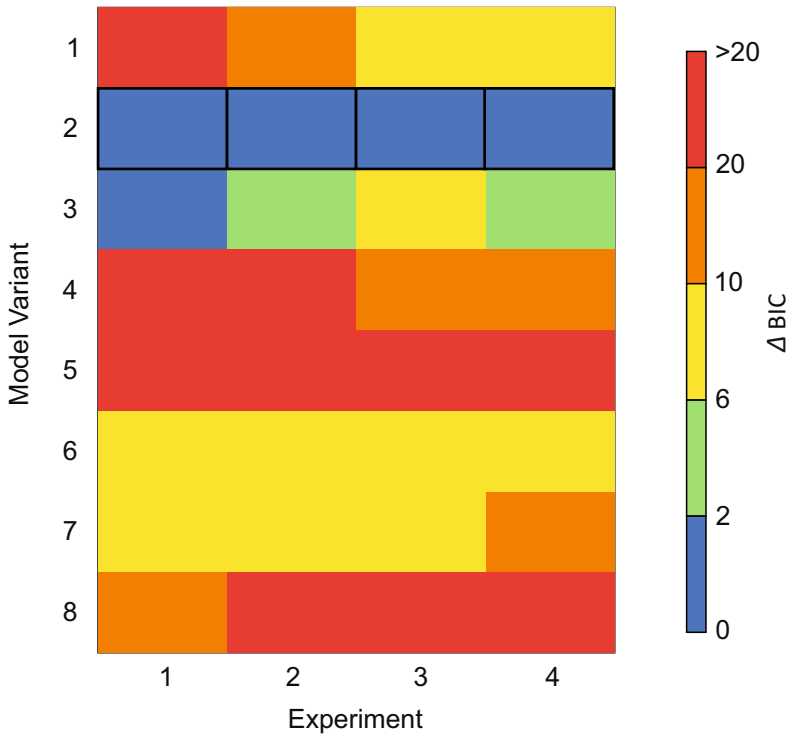
Table 1. Task parameters and results from each visual experiment. *Statistics are presented from paired t-tests. T1, time given to observe the target angle. T2, duration of visual blocking before test angle presentation. M, magnitude of shift from target to test angles on catch trials. C, frequency of catch trials as a percentage of total trials. Left/right CW (CCW) percentage of left/right choices for CW (CCW) rotations.*

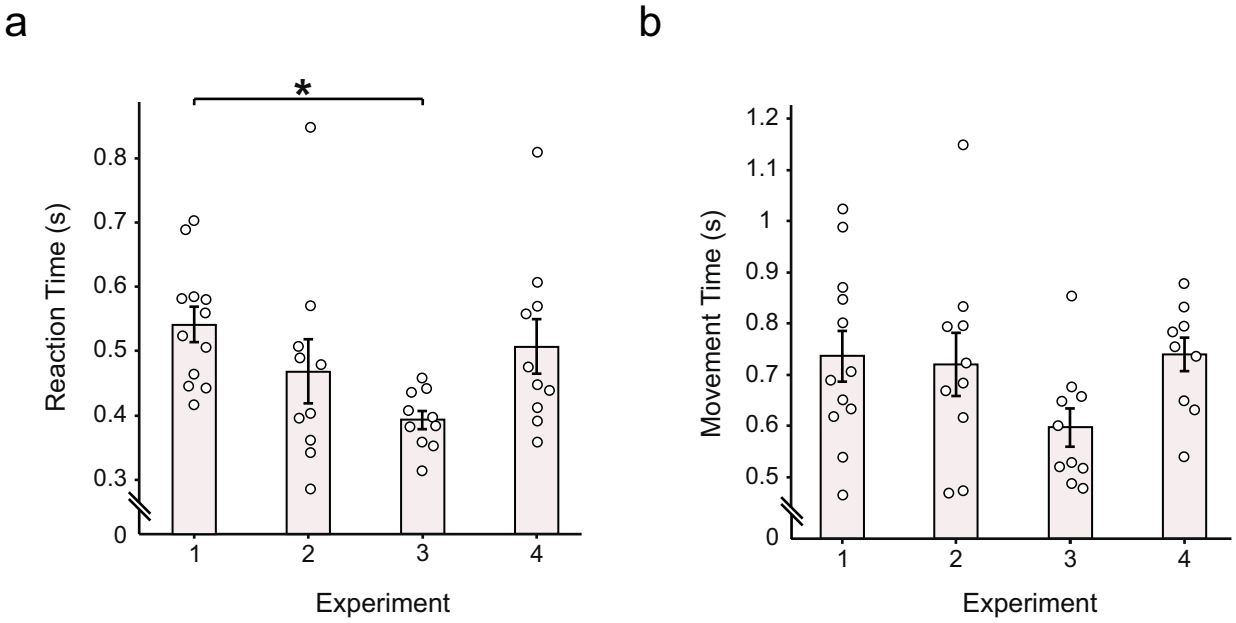

Experiment 1
-0.55
-0.6
-0.65
-0.7
-0.75
-0.8
ln (RT)
0
5
10
15
20
25
30
35
40
Distance from switch-point (°)
Experiment 2
-0.5
-0.6
-0.7
-0.8
-0.9
-1
-1.1
-1.2
ln (RT)
Distance from switch-point (°)
Experiment 3
-0.8
-0.9
-1
-1.1
-1.2
-1.3
ln (RT)
Distance from switch-point (°)
Experiment 4
-0.5
-0.6
-0.7
-0.8
-0.9
-1
-1.1
ln (RT)
Distance from switch-point (°)


a
w
z
x
y
Grasp 1
Grasp 2
b
Prob Grasp 2 (%)
100
75
50
25
0
-40
-30
-20
-10
0
10
20
30
40
Target Orientation (°)
c
Switch-point
0°
14.4°
-14.4°
50.4°
-50.4°
d
target angle
CCW
CW
initial angle
initial angle


a
Time delay between rotation onset and go cue
Exp. 1
0 ms
Exp. 2
150 ms
Exp. 3
500 ms
Home pad pressed
1-1.5 s
Exp. 4
RT
Home pad released
Grasp
Rotation to Initial Angle
Rotation to Target Angle (10-50 ms)
Visibility
Exp. 1-3
Exp. 4
b
Rotation to Catch Angle (M˚ shift)
Home pad pressed
1-1.5 s
Delay T1
Vision blocked
C%
100 - C%
Delay T2
Vision restored
Perceived Ta - Te rotation direction reported
Rotation to Initial Angle
Rotation to Target Angle
No rotation to Test Angle


a
b
c
d
e
f
g
h
Exp. 1
Exp. 2
Exp. 3
Exp. 4
Probability of Grasp 2 (%)
Target angle (°)
CCW
CW
0
20
40
60
80
100
-50
-25
0
25
50


Model Variant
1
2
3
4
5
6
7
8
1
2
3
4
Experiment
>20
20
10
6
2
0
Δ BIC


a
*
Reaction Time (s)
0.8
0.7
0.6
0.5
0.4
0.3
0
1
2
3
4
Experiment
b
Movement Time (s)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0
1
2
3
4
Experiment