From static to dynamic: how object rotation influences grasp decisions in ambiguous settings

Sensitivity of Ambiguous Grasping to Object Motion

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

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Ethical approval for all experiments was granted by the Newcastle University Ethics Committee and written informed consent was obtained from all volunteers. This study was performed in accordance with the guidelines established in the Declaration of Helsinki, except that the study was not preregistered in a database.

Abstract

The hand grasp of 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 grasp chosen by an individual can vary with a lack of clear preference for a particular grasp configuration. This is referred to as motor ambiguity. Here, we compare the influence of preceding static versus dynamic visual information on participants' choice between two possible hand configurations when grasping an object at various orientations. We confirm previous findings that presentation of an object in an initial static orientation prior to the grasping in ambiguous orientation causes subjects to select a grasp that would be most congruent with the initial, determinate orientation. However, we unexpectedly found that when object rotation is observed between the initial and target positions, the bias is inversed, i.e. subjects choose the alternate grasp configurations. Furthermore, the inverse 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 (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. The term coined to refer to a lack of clear preference in response choice is 'motor ambiguity' (Wood and Goodale, 2011).

Take for example the familiar action of reaching out to grasp a pen placed on a table perpendicular to the body's midplane. When grasping with the right hand, it comes naturally to position the right 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 midplane, it continues to be natural to grasp in the same configuration as before (visually the right thumb is now placed on the pen's left side), yet it is also reasonable, and more importantly comfortable, to grasp by placing the right index finger on the pen's left side and right 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).

A movement towards an always identical object can vary in execution depending on the context presented before movement initiation. This phenomenon 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, 1998, Craighero et al., 1996). In the context of motor ambiguity, the width of

the previously presented object can influence an individual's grip aperture when moving to reach for an ambiguously sized object (Garrido-Vásquez et al., 2021). Likewise, the grip orientation used to grasp a circular object can be influenced by the orientation of a previously seen elliptical object (Hesse et al., 2008). This has been described by some as 'proactive influence', i.e. the movement preparation associated with the first object can influence the motor plan for a secondary target (Gallivan et al., 2016). In these examples, the preceding information can be described as static and unchanging, briefly shown for a moment as a technique to prime/influence the motor planning network prior to grasp execution. Yet, it is common in real-life situations for the information available prior to grasping to behave dynamically, i.e., it can change over time, for example preparing to catch a falling object before a gust of wind changes its trajectory. In this study we aimed to explore how the motor planning network is influenced as prior information transforms from static to dynamic, and the consequences this has for behaviour in ambiguous settings.

We first sought to confirm the findings of Hesse et al., 2008, and Gallivan et al., 2016, with the prediction that an object orientation shown prior to grasping influences the grasp orientation chosen by the individual. To achieve this, we designed a grasping task with a target object that, depending on orientation, placed subjects into decision settings where grasp selection was either clear and consistent (determinate), or uncertain and variable (ambiguous). This grasping target was presented after subjects were first exposed to the same object positioned at either a determinate or ambiguous orientation, allowing us to induce the proactive influence effect. Consistent with previous literature, we confirmed that the visual presentation of a static determinate initial orientation prior to the grasping of an ambiguous target orientation biases subjects to select a grasp for the ambiguous target that would be most congruent with the initial, determinate orientation.

In a subsequent exploratory experiment, we revealed object rotation between the first 'priming' orientation, which is observed, and the second 'target' orientation, with three alternative predictions.

Prediction 1: Persistence of proactive influence in spite of object motion, i.e. the grasp that would be used for the priming orientation is subsequently used for the target orientation

Prediction 2: Object motion abolishes proactive influence, leading to no influence of the priming orientation on the grasp used at the target orientation.

Prediction 3: Object motion inverses proactive influence, i.e. the opposite grasp to that which would be used for the priming orientation is used at the target orientation.

After finding evidence in support of Prediction 3, we further hypothesised that this inverse effect would diminish with how much time subjects were given to observe the target orientation post-rotation before grasping, and investigated the possible underlying mechanisms by exploring subjects' visual perception of the task. Our findings provide insights into the interaction between mechanisms of influencing motor planning and its consequences for grasping in motor ambiguity settings.

Materials and Methods

Ethical approval for all experiments was granted by the Newcastle University Ethics Committee and written informed consent was obtained from all volunteers. This study was performed in accordance with the guidelines established in the Declaration of Helsinki, except that the study was not preregistered in a database.

Grasping Studies

Participants

All participants except for two were right-handed and all were naïve to each experiment and its predictions. A total of 20 healthy volunteers (22-50 years old, 13 females 7 males) were recruited to take part in different experiments in this study (Static Exp.: 12 participants; Dynamic Exp. 1: 10

participants; Dynamic Exp. 2: 10 participants; Dynamic Exp. 3: 10 participants). Some participants took part in several experiments - in which case each experiment was separated by at least 6 days.

Grasping Studies - Task Setup

In total, four experiments (Static Exp. and Dynamic Exp. 1-3) 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 regular triangular prism block (6 cm long, 2 cm base side, see Fig. 1) with their right-hand. 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 with the rotation axis pointing towards the subject. 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. 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 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 electrical contact with the object, grasp configuration selection could be recorded in terms of thumb placement, either 'Grasp 1' whereby the thumb was in contact with metal plate 1 or 'Grasp 2' whereby the thumb was in contact with metal plate 2 (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

157 become uncertain at certain object/wrist orientations, we opted for operational definitions: Grasp 1

158 and Grasp 2, as defined above.

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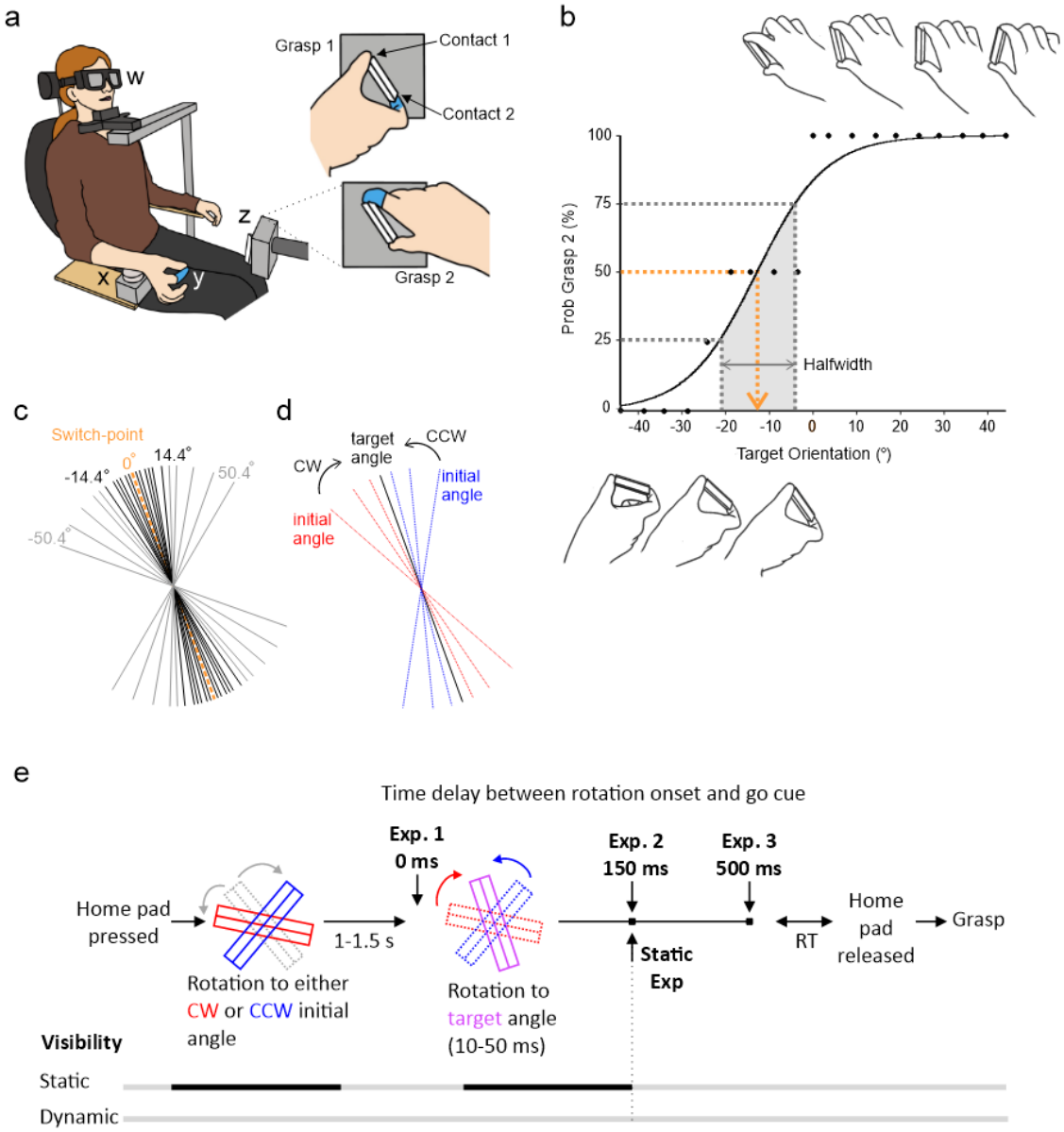

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161 ***Figure 1. Illustration of experimental task set-up and study design.*** *a) Participant is seated with LCD*

162 *goggles (w) covering their visual field and head placed on a chin rest. Their right-wrist is used to press*

163 *down the home-pad button (x), initiating the trial sequence. A latex glove on the index finger (y)*

164 *impedes electrical connection with the contact circuit on the target object (z). Therefore, only contact*

between the thumb and the object is detected, allowing automatic differentiation of a single grasp between two possible grasps (Grasp 1 or Grasp 2) on a trial-by-trial basis. b) Black dots show probability of choosing a Grasp 2 posture for each target angle sampled. Illustrations of object position at example target angles are shown above and below the graph. Estimation of the midpoint was done by taking the 50th percentile (orange dotted line) on a logistic fit of the probability of using a Grasp 2 posture in the Calibration task. Estimation of transition sharpness between the two grasp choices (an indicator of grasp uncertainty), is measured as the range of angles for which the probability of Grasp 2 lies between 25% and 75% (grey dotted lines). This value is referred to as the 'Halfwidth'. c) Trial design of Experimental tasks showing sampling of target angles, with '0°' representing the subject's switch-point. In total 23 angles, symmetric around 0°, spanning -50.4° to +50.4° range with denser sampling of ambiguous (close to switch point) were used (list of all target angles -50.4, -39.6, -29.7, -21.6, -18.0, -14.4, -9.9, -8.1, -6.3, -3.6, -1.8, 0.0, 1.8, 3.6, 6.3, 8.1, 9.9, 14.4, 18.0, 21.6, 29.7, 39.6, 50.4). d) Trial design of Experimental tasks illustrating 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°. e) Comparative experimental timeline. For all grasping experiments, the duration of go cue was 50 ms, with variable onset relative to object rotation onset depending on experimental condition (Dynamic Exp. 1 – 0 ms, simultaneous with object rotation onset, Dynamic Exp. 2, 4 – 150 ms and Dynamic Exp. 3 – 500 ms after rotation onset). Rotation of object took 10-50 ms, dependent upon shift magnitude. For the Static Experiment periods of object visibility and obscurity are illustrated by light and dark bars respectively.

To initiate a trial, participants were asked to push down on 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 go cue (auditory beep 500 Hz, lasting 50 ms), 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 Studies – Calibration Task Design

Before each experiment, a calibration task was performed to estimate of the subject's 'switch-point', defined by when there is a 50% chance of using either grasp. Due to individual differences in 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 of subsequent experiments were centred around. A total of 76 trials (randomised for each subject) across 19 unique target angles uniformly 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. Synchronously 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 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. The rotation was concealed from subjects in the first, Static Experiment, and visible in Dynamic Experiments 1-3.

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 varied the timing of the go-cue relative to object rotation. A comparative timeline of each experiment's sequence is shown in Figure 1e.

Static Experiment

For the Static Experiment, 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 angle, the goggles transitioned back to an opaque state. Upon completion of the remaining hold time (1 – 1.5 s), object rotation was initiated and 150 ms later the goggles converted to a transparent state, simultaneous with the auditory cue.

Dynamic Experiments 1-3

For Dynamic Exp. 1, the goggles were removed to allow subjects to view object rotation. Following the home-pad depression waiting period (hold time), the go cue sounded and was ceased after 50 ms - its cessation synchronous with the start of 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. Trials for Exp. 2 began identical to Exp. 1, however here the go cue was given 150 ms after initiation of object rotation to the target angle. This specific delay was chosen to allow time for visual processing delays (i.e. the time it takes for humans to perceive objects in their visual field (Hegdé, 2008)), allowing some, but limited, preparation before the go cue. For Exp. 3, this delay was increased from 150 ms to 500 ms. This delay was chosen to be large enough to allow subjects to fully prepare a movement in advance of the go cue, yet still brief enough for subjects to remain engaged with the task on each individual trial.

Visual Studies

Following the results of the grasping experiments, a second study was designed to investigate the perceptual consequences of observing a shift in object orientation, thereby investigating the mechanisms by which prior visual information may affect grasp choice. Here we wanted to test whether the same inverse bias we found in Dynamic Exp. 1-3 can be observed without the grasping action performed by the subjects, and thus can be attributed to perceptual, rather than motor planning, phenomena.

Participants

All participants were right-handed and naïve to each experiment and its predictions. In total, 11 healthy volunteers (20-22 years old, 7 females 4 males) were recruited for this study. There was no overlap in participation between this visual study and the previous grasping study, and 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*. An overview of the trial sequence for this visual experiment is illustrated in Figure 4a. As with the grasping task, participants initiated the trial sequence by holding down the home-pad. However, after observing object rotation from an initial angle to a target angle, participants were asked not to

execute a grasp as before, but instead only continue to observe. Upon revelation of the target angle, a set delay was allowed before vision was blocked by goggle opaqueness. During this period, the object underwent a secondary movement, concluding at a 'test' angle located either CW/CCW ('catch' trials), or unchanged from the target angle orientation. To prevent participants from using auditory cues to distinguish between trial types, the object rotated on all trials before concluding at the final test angle 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 target angle and test angle positions. If the test angle appeared CCW relative to the target angle, subject were asked to press '1'. If the test angle appeared unchanged from the target angle, '2' was used. Finally, if it appeared CW, '3' was pressed. Subjects were given unlimited time to observe the test angle and report their decision.

Visual Study – Task Design

Subjects began with a calibration task identical to the calibration task used in the Grasping studies, in order 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. The time given to observe the target angles before vision was blocked was 100 ms, chosen to allow sufficient time for perceptual processing (Hegdé, 2008), yet short enough that it is comparable to the time given to observe the target angle in the grasping experiments prior to the go cue. The duration of the visual blocking was 500 ms, chosen to ensure that any potential 'after-image' effects were absent. The magnitude of rotation from target angle to test angle on catch trials was fixed to 5°, and frequency of catch trials was set to 10%.

Data and Statistical Analysis

For analysis of the contribution of the different experimental factors in the grasping task, a generalised linear mixed effect model (GLME) approach was adopted. GLME analysis allowed

estimation of the contribution to grasp choice (C) of each experimental factor (target angle (TA), shift direction (Di), and shift magnitude (SM)) their pairwise interactions and triple interaction. Further detail is provided in Online Resource 1.

Results

Calibration Task

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 participants' calibration sessions, the switch-point ranged between -58.1° and 32.8°, relative to the vertical axis, with varying degrees of sharpness (Halfwidth = 17.09 ± 2.15°); the calculation of halfwidth is provided in Online Resource 1 and exemplified in Figure 1b.

Static Experiment

To confirm previous findings that prior information can bias grasp behaviour, the static experiment task added an additional component: an initial angle which subjects would not reach for but only observe. Here, subjects were presented with this initial angle for a brief moment before LCD goggles occluded their view of the task, at which point the object rotated either CW or CCW to the target angle. Post-rotation, the LCD goggles then became transparent, triggering subjects to grasp the object at the target angle.

A visualisation of the generalised linear mixed effect model (GLME) fitted to the data for the static experiment is shown in Figure 2a-c. As expected from the design of the experiment, target angle was found to be a highly significant factor on grasp choice (CE = 0.135 ± 0.009, t-Stat = 15.3, dF = 712, $p < 0.001$). Furthermore, there was a significant effect of shift direction on grasp choice (CE = 0.410 ± 0.119, t-Stat = 3.4, $p < 0.001$), suggesting that the orientation of initial angle influenced the planning of the grasp for the target angle, i.e., the presentation of the object at an initial position that would

likely require Grasp 1 increased the likelihood of subjects then later adopting Grasp 1 for the ambiguous target angle. To estimate the effect size, we calculated from the model prediction the difference in probability of Grasp 2 at the switch-point between CCW and CW object rotation directions. For shift magnitudes of 5.4°, it was 0.08, whereas for larger shift magnitudes of 14.4° and 28.8°, the effect was even greater at 0.11 and 0.14, respectively (indicated by black lines on Figure 2a-c). However, neither shift magnitude nor any interactions were found to be significant.

To summarise, the influence of prior object position on grasp choice at an ambiguous target is in agreement with the priming effects previously reported in the literature (Gallivan et al., 2015, Gallivan et al., 2016). Furthermore, there is weak evidence to suggest that the higher the likelihood of the initial position requiring Grasp 1, the stronger the effect of subjects then later adopting Grasp 1 for the ambiguous target angle, however this was not statistically significant.

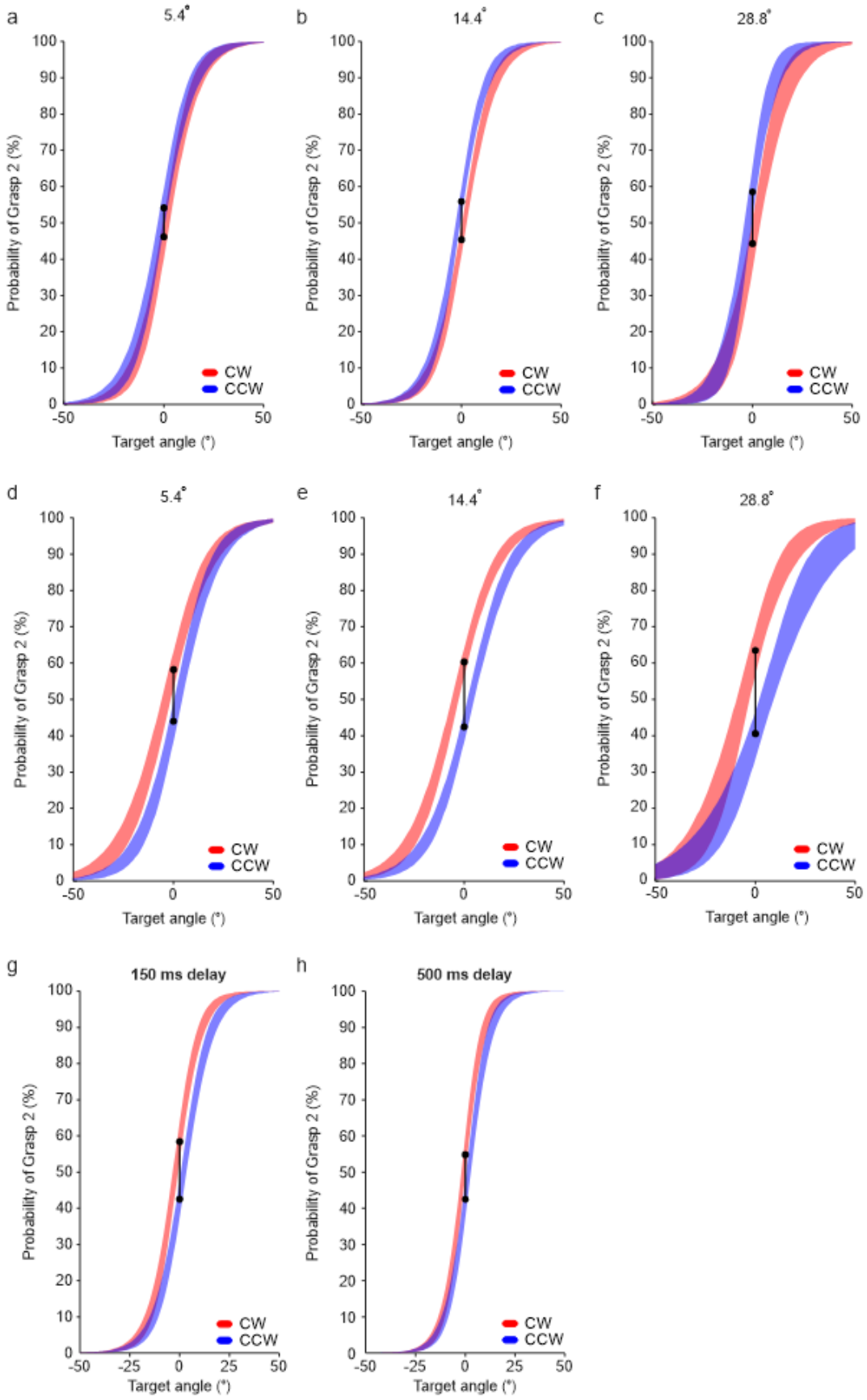
a
5.4°
b
14.4°
c
28.8°
d
5.4°
e
14.4°
f
28.8°
g
150 ms delay
h
500 ms delay
Probability of Grasp 2 (%)
Target angle (°)
CW
CCW

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Figure 2. GLME visualisation from all subjects of the Static Experiment (a-c), Dynamic Exp.1 (d-f), Dynamic Exp. 2 (g) and Dynamic Exp. 3(h). *A-F) For the Static Exp. and Dynamic Exp. 1, choice is predicted separately for each rotation direction (red and blue lines) and shift magnitude (5.4° shown in (a,d), 14.4° shown in (b,e), 28.8° shown in (c,f)) for target angles 50° either side of the centre of ambiguity. GLME model* C ~ TA + Di + SM + TA:Di + TA:SM + Di:SM + TA:Di:SM + (1|S). G-H) *For both Dynamic Exp. 2 and 3, choice is predicted separately for each rotation direction (red and blue lines) and delay (150 ms shown in (g), 500 ms shown in (h)) for target angles 50° either side of the centre of ambiguity. The SEM across all subjects is illustrated by line thickness. The difference in probability at 0° for each rotation direction is illustrated with black lines. GLME model* C ~ TA + Di + DE + TA:Di + TA:DE + Di:DE + TA:Di:DE + (1|S). *C, choice; TA, target angle; Di, direction; C, choice; TA, target angle; Di, direction; SM, shift magnitude; DE, delay duration; S, subject; CW, clockwise; CCW, counter-clockwise.*

Dynamic Experiment 1

To investigate any possible influences that prior dynamic visual information could have on grasping in ambiguous settings, the following experiment kept the same conditions as the static experiment, but without the LCD goggles, allowing subjects to watch the object rotate from the initial angle to the target angle.

A visualisation of the model fitted to the data for the dynamic experiment is shown in Figure 2d-f. As expected, the target angle was found to be a highly significant factor (CE = 0.094 ± 0.006, t-Stat = 16.8, dF = 856, $p < 0.001$). The direction of object rotation was also found to be a highly significant factor (CE = -0.703 ± 0.108, t-Stat = -6.52, $p < 0.001$), yet the effect was opposite to that observed in the Static Experiment, i.e., the presentation of the object at an initial position that would likely require Grasp 1 increased the likelihood of subjects then later adopting Grasp 2 for the ambiguous target angle. To estimate the effect size, we calculated from model prediction the difference in probability of Grasp 2 at the switch-point, estimated for both CCW and CW object rotation

directions. For shift magnitudes of 5.4°, it was -0.14, whereas for larger shift magnitudes of 14.4° and 28.8°, the effect was even greater at -0.18, and -0.23, respectively. However, neither shift magnitude nor the interaction of direction and shift magnitude were found to be significant.

To summarise these findings, a clockwise rotation to an ambiguous target angle increased the probability of Grasp 2 (a grasp non-congruent with the initial position) 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. Although this effect was slightly stronger for larger shift magnitudes, the GLME analysis revealed that rotation magnitude was not a significant contributor to this effect.

Dynamic Experiments 2 and 3

To investigate whether the timing of the go-cue relative to object rotation can influence the strength of the bias effect, this delay was varied from 0 ms in Dynamic Exp. 1, to 150 and 500 ms in Exp. 2 and 3 respectively (see Figure 1e). We predicted that the longer subjects have to observe the target angle before receiving the go cue, the bias effect would become weaker, owing to the prior information becoming more historical and thus less influential. Thus, delay was added as a factor into the GLME. As shift magnitude was not found to be a significant contributor to the bias effect in Dynamic Exp. 1, it was removed from the model for all subsequent experiments, and thus does not appear here.

The visualisation of the results of the model fitted to the data when the go cue was delayed until 150 ms and 500 ms post-rotation are shown in Figure 2g and 2h respectively. Target angle again remained highly significant (CE = 0.186 ± 0.009, t-Stat = 21.7, dF = 1432, $p < 0.001$), as expected. The direction factor also remained significant (CE = -0.574 ± 0.092, t-Stat = -6.2, $p < 0.001$), however the coefficient estimate was smaller (in absolute value) compared to Dynamic Exp. 1. There was no significant effect of go cue delay on choice, nor a significant direction-delay interaction, suggesting that the strength of the bias effect does not significantly diminish with greater planning time.

However, there was a significant interaction between target angle and delay (CE = 0.113 ± 0.049, t-Stat = 2.3, p = 0.021), indicating a steeper transition between Grasp 1 and Grasp 2, indicative of greater certainty in grasp choice. To quantify this, we estimated the change in Halfwidth from the GLME predictions. Between a delay of 150 ms and 500 ms, the Halfwidth reduced from 13.25° to 10.70° for CW and from 14.59° to 11.63° for CCW. None of the other interactions were significant.

To summarise, the greater the delay between target angle presentation and the go cue, the less ambiguity subjects show in their grasp choice. Furthermore, the strength of the bias effect persists even with greater planning time allowance.

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. Yet, one might predict that the greater the uncertainty induced by the experimental conditions, the longer the RT (Wood and Goodale, 2011). Indeed, 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 Dynamic Exp. 1 had significantly longer RTs than Dynamic Exp. 3 (p = 0.023), with averages of 541.6 ± 27.0 ms and 393.0 ± 14.2 ms respectively (Figure 3a). The average RT for Dynamic Exp. 2 was 468.3 ± 50.3 ms, falling between Exp. 1 and 3. The average RT of the Static Experiment was 507.0 ± 42.4 ms. To put into context, the greater the uncertainty induced by the experimental condition, as shown by halfwidth measure, the slower the reaction times across experiments. Movement times were not significantly affected by the timing of the go cue (p = 0.128, dF = 3, one-way ANOVA) with smallest MT observed in Experiment 3 (596.2 ± 36.8 ms) and greatest in Experiment 4 (738.8 ± 32.6 ms) (Figure 3b).

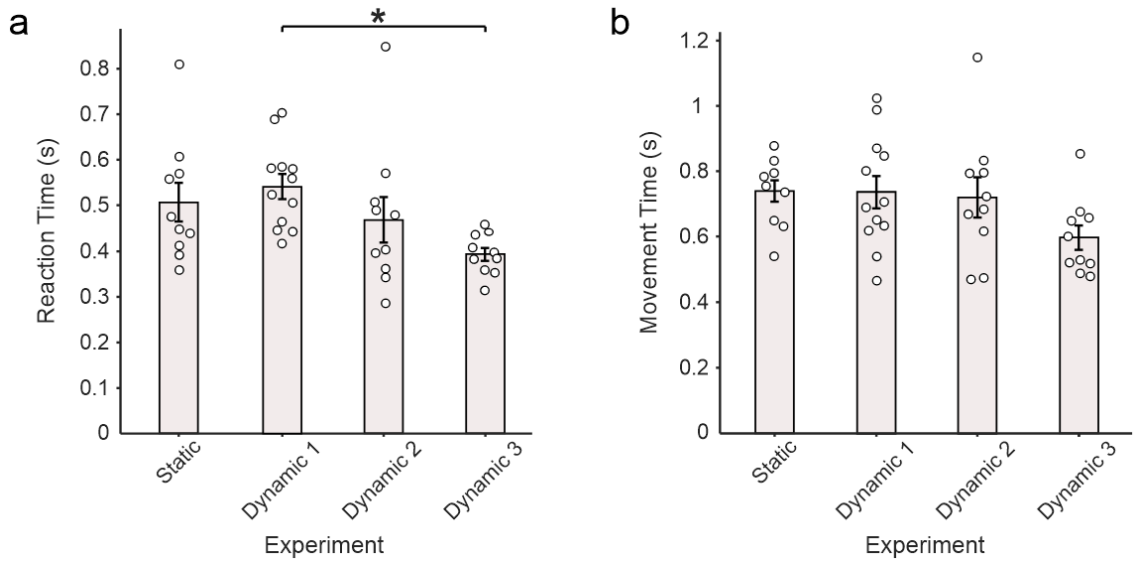

Figure 3. Reaction and movement times across the Static and Dynamic Exp. 1-3. *Average reaction (a) and movement (b) times across all target angles and participants for each experimental condition (Dynamic Exp. 1 n = 12; Dynamic Exp. 2 n = 10; Dynamic Exp. 3 n = 10; Static Exp. n = 10). The error bars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

To investigate the effect of target angle on reaction times, a LME approach was used. In agreement with previous work, reaction times for target orientations closer to the centre of ambiguity were greater than those more determinate (log transformed raw values are shown in blue in Online Resource 2).

To summarise, the greater the uncertainty induced by both the experimental condition and target angle, as shown by halfwidth measure, the slower the reaction times within and across experiments.

Visual Task

Given the finding that the directionality of object rotation can influence grasp choice, we investigated whether this could be attributed to changes in how the target position is perceived post-rotation. In this secondary study, subjects were asked to observe object rotation from initial to

target angles as before, except after target angle presentation, visual input was briefly blocked before subjects were re-shown the object at a test angle and asked to report whether it appeared further CW , CCW, or 'unchanged' from the target angle position. Here, no grasping action was required in order to allow investigation of solely perceptual phenomena. The prediction being that if the inverse bias effect was due to perceptual phenomena, then subjects would be more likely to report that the object at the test position is further 'CW' relative to the target angle when the rotation from initial to target angle was CW versus CCW, despite the object not moving between the target and test positions.

Average choices on non-catch trials are shown in Figure 4b. For non-catch trials (i.e. target angle = test angle), there was no significant difference between the error rate of reporting 'CCW' or 'CW' when the rotation direction from initial to target angle was CW, nor when it was CCW. *Thus, the effect of rotation directionality on grasp choice is likely not due to a perceptual bias.*

To confirm that participants were attending to and comparing test angle position relative to target angle, catch trials were included (Figure 4c). Here, the object, rather than remaining at the target angle following the initial angle to target angle transition as for the above, it rotated to the test angle. When this rotation was CW, subjects were on average significantly more likely to report that the test angle appeared CW relative to the target position than CCW (CW 38.01% versus CCW 6.36%, $p = 0.0056$), and significantly more likely to report CCW than CW on a CCW rotation (CW 8.26% versus CCW 45.45%, $p = 0.0054$). The error rate on catch trials was 53.72% for CW shifts and 48.18% for CCW, a reflection of a task difficulty that was necessary to induce in order to investigate perceptual phenomena on non-catch trials.

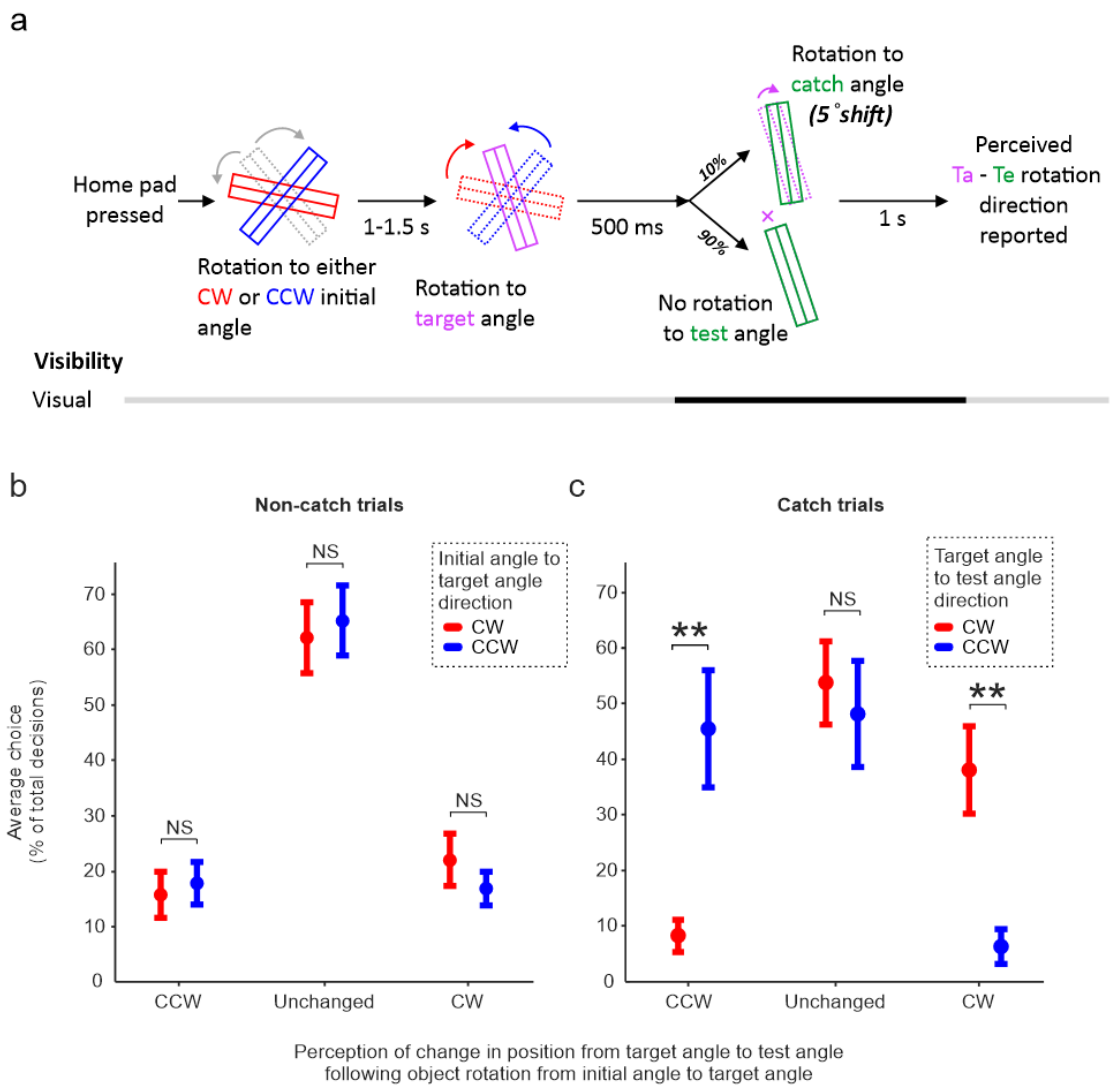

Figure 4. ***Experimental timeline and behavioural results from the Visual Experiment.*** *a) Timeline of a single trial during the visual experiment. Periods of object visibility and obscurity are illustrated by light and dark bars respectively. The time given to observe the target angle was 500 ms, whilst the duration of visual blocking before test angle presentation was 1 s. b) Following observation of object rotation (CW or CCW) from an initial angle to target angle, then subsequent presentation of the test angle, a decision of 'CCW' reflects that the subject perceived the test position to be further counter-clockwise than the target position, whilst 'CW' reflects that it appeared further clockwise. Here, averaged perceptual decisions are taken only from trials wherein the test position was unchanged*

*from the target position. c) Averaged perceptual decisions taken only from trials wherein the test position was different from the target position, following either CW or CCW rotation from the target angle to test angle. The error bars represent ±1 standard error of the mean. NS: No significant difference. ** p < 0.01.*

Discussion

In this study, subjects were placed into ambiguous settings with an object that afforded one of two precision grasps (Grasp 1 or Grasp 2) in order to compare the influence of static and dynamic visuomotor priming on motor ambiguity. In agreement with previous studies (Seegelke et al., 2016, Borghi et al., 2007, Vainio et al., 2007) that have shown that static priming can influence aspects of the execution of reach-to-grasp movements when primes are congruent with the target, we 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 (Static Experiment). More specifically, subjects are more likely to match their grasp choice for the target angle to what they would have likely used for the initial position. However, when rotation of the object from the initial angle to the target position was visible, a significant but inverse effect of rotation directional bias on grasp choice was found (Dynamic Exp. 1-3). Here, a clockwise rotation from an observed Grasp 1 position to an ambiguous angle increased the likelihood of Grasp 2, and vice-versa with a counter-clockwise rotation, referred to here as the 'inverse bias' effect.

Upon establishment that visible rotation and its directionality influenced grasp choice, two further experiments were designed to explore the persistency of the inverse bias effect with greater planning time as the prior information becomes more historical. Here, we found that a relatively short delay of 150 ms from rotation onset to sounding of the go cue still produced the inverse bias effect, reducing only slightly in strength (Dynamic Exp. 2). Surprisingly, a longer delay of 500 ms still

476 produced a significant inverse bias effect, with a similar strength as before (Dynamic Exp. 3). Thus,
477 the strength of this inverse bias depended little on when the go signal was given relative to the
478 presentation of the target angle.

479 In addition to the inverse bias effect, another consequence of observing object motion was greater
480 uncertainty in grasp choice. This was revealed by a shallower transition between the two grasp
481 choices the earlier the go cue was given, a consequence of increased variability suggestive of more
482 inefficient planning (Dijkerman et al., 2009). Interestingly, when rotation was blocked from view, the
483 transition steepness comparatively lied between giving the go cue synchronous with object motion
484 and delaying it by 150 ms. This suggested that although the mere presentation of an initial angle
485 does generate a bias effect, object motion induces greater uncertainty and with it an inversed bias
486 effect. When allowed greater planning time post object motion, uncertainty reduces and the inverse
487 bias effect slightly weakens.

488 Expectedly, participants were slower to react to any given target angle the earlier the go-cue was
489 given when rotation was visible. Yet curiously, blocking rotation from view did result in quicker
490 reaction times compared to when the go-cue was given synchronous with visible rotation (Static Exp.
491 Versus Dynamic Exp. 1). Although this was not a significant difference, it does align with the findings
492 that visible rotation, with a synchronous go-cue, induces greater uncertainty (and thus longer
493 reaction times) than the mere presentation of the initial angle. Despite not enforcing subjects to
494 react as quickly as possible (accuracy and comfort of the grasp were emphasised during task
495 instructions), the reaction time still reflects the time needed for the cortical circuitry to choose
496 between grasps (Wood and Goodale, 2011, Rosenbaum et al., 1992). This increased uncertainty is
497 also highlighted in the smaller difference in reaction time between ambiguous and determinate
498 orientations, in comparison to when greater time is granted for planning.

499 The mechanisms by which object motion induces these signs of increased uncertainty, and how they
500 may be linked to the inverse bias effect require further investigation to uncover. We suggest that

given for Dynamic Exp. 1 the go cue and object rotation onset were triggered synchronously, the initiation of movement planning prior to knowing the target orientation could explain the greater uncertainty and lead participants to incorrectly predict the final target orientation. Predicting the future location of a moving object is a familiar task, yet some consistent biases have been reported. It could be considered a good strategy for example, that if an occluded object is approaching an observer, to overestimate its speed in order to be cautious and avoid potential collision (Schiff and Oldak, 1990). Contrastingly, when asked to intercept an occluded object moving parallel to the observer, its speed is often underestimated, causing people to intercept its path too late (e.g. (Sokolov and Pavlova, 2003, Peterken et al., 1991, Battaglini and Ghiani, 2021)). An overestimation of the final target position would push subjects towards planning a grasp different from the grasp that would have been used for the actual target position, and therefore could be a mechanism for the inverse bias effect. In Dynamic Exp. 2 and 3 (wherein the go cue is given after rotation is finished), prediction of the final object orientation is arguably unnecessary and could be planned anew when the go cue is given, yet this does not seem to be true. The inverse bias effect, although smaller, persists, therefore suggesting that the plan to grasp is not updated at the go cue, but rather remains similar to the one created during object rotation.

An alternative suggestion for why grasp selection in ambiguous settings is sensitive to target rotation could be that rapid object rotation leads to momentary changes in how the target angle is visually perceived. Visual perceptual phenomena are not unfamiliar to the human mind. For example, the Fröhlich effect and representational momentum both describe visual illusions in which the location of moving objects are misperceived (Müsseler et al., 2002, Kanai et al., 2004, Fu et al., 2001). In our case, if the target orientation is perceived to have rotated further than is true, the bias effect could then be attributed to a perceptual error that degrades with greater time given to observe the target position prior to grasping. To investigate whether the object motion has consequences for perception of the target orientation, a second study was performed without the grasping action. Here, participants observed the same object motion but had to report object orientation with a

527 keypress rather than planning to grasp the object. Object position was manipulated behind opaque
528 goggles and participants were given time to report whether the object appeared at the same
529 position as before. If a perceptual error is present, we hypothesised that, on trials when the final
530 object position was not changed during visual blocking, participants' perception of object position
531 would be affected by rotation direction from the initial angle to target. Yet, the proportion of error
532 decisions of 'CCW' compared to 'CW' was not influenced by rotation direction. *This suggests the*
533 *inverse bias effect observed in the grasping task cannot be attributed to perceptual phenomenon and*
534 *instead is linked to motor planning.*

535 It has been shown that in situations affording more than one possible action, the brain prepares
536 multiple competing movements before selecting one (Stewart et al., 2013, Cisek, 2007). Indeed,
537 when presented with multiple reach targets and forced to act before knowing the final location, the
538 initial movement vector reflects an average of the competing motor plans (Stewart et al., 2014,
539 Haith et al., 2015). In tasks wherein an ambiguous and determinate target are shown simultaneously
540 before one is cued, the grasp configuration adopted for the ambiguous trials is more likely to be
541 compatible with the grasp required for the determinate target rather than the alternate posture
542 choice (Gallivan et al., 2015). This is likely explained by the convergence of two parallel motor plans
543 (one for each potential target) to form one singular plan, resulting in lower reaction and movement
544 times, thus improving overall performance. It has also been demonstrated that sequential rather
545 than simultaneous presentation of potential targets can lead to proactive influence, i.e. the
546 movement preparation associated with the first target can influence the motor plan for a secondary
547 target (Gallivan et al., 2016). In Gallivan *et al.,* 2016, (Experiment 2) the presentation of the first
548 target was later accompanied by the presentation of a second target, before participants were cued
549 to grasp one of the two potential targets. This led to subjects becoming biased to adopt a grasp for
550 the cued ambiguous target that was congruent with a determinate angle shown prior to (proactive
551 co-optimisation) or after (retroactive co-optimisation) the ambiguous target. The bias effect
552 observed with our Static Experiment is consistent with this proactive co-optimisation, whereby the

553 choosing of Grasp 2 is more likely if the object was rotated from an initial position greater in
554 congruency with Grasp 2, and likewise for Grasp 1. It is curious, however, that for all our
555 experiments, the distance by which the object rotated had no significant influence on the strength of
556 the effect, i.e. for trials that began and ended ambiguous, this bias effect was still observed. Though
557 Gallivan and colleagues showed that in their study a similar trial type yielded no bias, a key
558 experimental difference is that whilst they showed the exact same ambiguous orientation, ours
559 changed by 5.4°. Thus, one interpretation of this could be that contrast in object orientation
560 between the initial and target position, or in other words contrast between differing choice
561 certainties, is needed to induce this bias effect.

562 The inverse bias effect, the result of Dynamic Exp. 1-3, could also be explained by co-optimisation if
563 we hypothesise that observable rotation of the object from a starting position towards the final
564 ambiguous position triggers a motor plan for an overestimated final position. Still, these analogies
565 between our and previous experiments should not be over-interpreted due to substantial
566 differences in experimental designs. Firstly, our task was not designed as a strict reaction time task,
567 subjects were not informed about their reaction and/or movement time, and though they were
568 encouraged to act quickly, precision placement was emphasised. Secondly, our task requires greater
569 precision - the index finger and thumb had to be positioned at opposite sides of the object at a given
570 object orientation, rather than within a range of orientations (15° as in Gallivan et al., 2016). Thirdly,
571 in our task, only one object orientation was present at any time and for Dynamic Exp. 1-3, subjects
572 observed a change in object position from the initial to the target one.

573 If indeed two neural populations within the grasping network are competing for each grasp (i.e. each
574 are planned simultaneously) in situations of motor ambiguity, perhaps the observation of the object
575 moving away from the preferred position of one population first inhibits its activity, before
576 facilitating activity corresponding to the alternate grasp. The antagonism of potential actions is
577 known to be subject to bias from a variety of both cortical and subcortical inputs, with the

578 competition playing out across a reciprocally interconnected fronto-parietal system (Cisek and
579 Kalaska, 2005, Matelli and Luppino, 2001, Borra et al., 2017). Evidence favouring a given choice
580 causes activity to increase for its neural population, while information against a choice instead
581 causes suppression of its neural population (Cisek, 2007). An increase in available information would
582 under normal circumstances reduce reaction times (Smith and Ratcliff, 2004, Ratcliff et al., 2003),
583 however, in our study reaction times slowed after observing object motion by 34.6 ms compared to
584 when blocked. This difference was not significant, though this could be in part because our task is
585 not reaction time task design (average reaction times in Dynamic Exp. 1 (542 ms), are for example
586 longer than in Gallivan et al., 2016 (274 ms)). That being said, the quality of evidence can influence
587 changes in reaction times, and so adding observation of the object rotation may not enhance
588 processing but rather complicate a decision by forcing further processing across the action selection
589 network (Ratcliff and McKoon, 2008, Palmer et al., 2005). By processing, we mean here disruption of
590 the initial plan to grasp the object congruently with the initial orientation, in favour of planning a
591 grasp congruent with predicted end object position – a consequence of observing object motion.

592 In conclusion, whilst static visuomotor priming has been shown to facilitate the convergence of
593 action plans into one singular intent facilitating motor execution, the mechanisms of grasp selection
594 in ambiguous settings can also be influenced, and potentially disrupted, by observation of object
595 motion prior to grasp execution. This effect is unlikely due to be a perceptual phenomenon, but is
596 potentially a consequence of cortical inhibitory circuits involving competing neural populations.
597 Further experiments aimed at disrupting motor planning processes might help delineate the neural
598 mechanisms behind this inverse bias. Understanding these neural mechanisms, and in particular
599 initial inhibition underlying this motor bias could have implications for neurodegenerative diseases
600 that exhibit motor planning and execution deficits, for example Parkinson's Disease and Dystonia.

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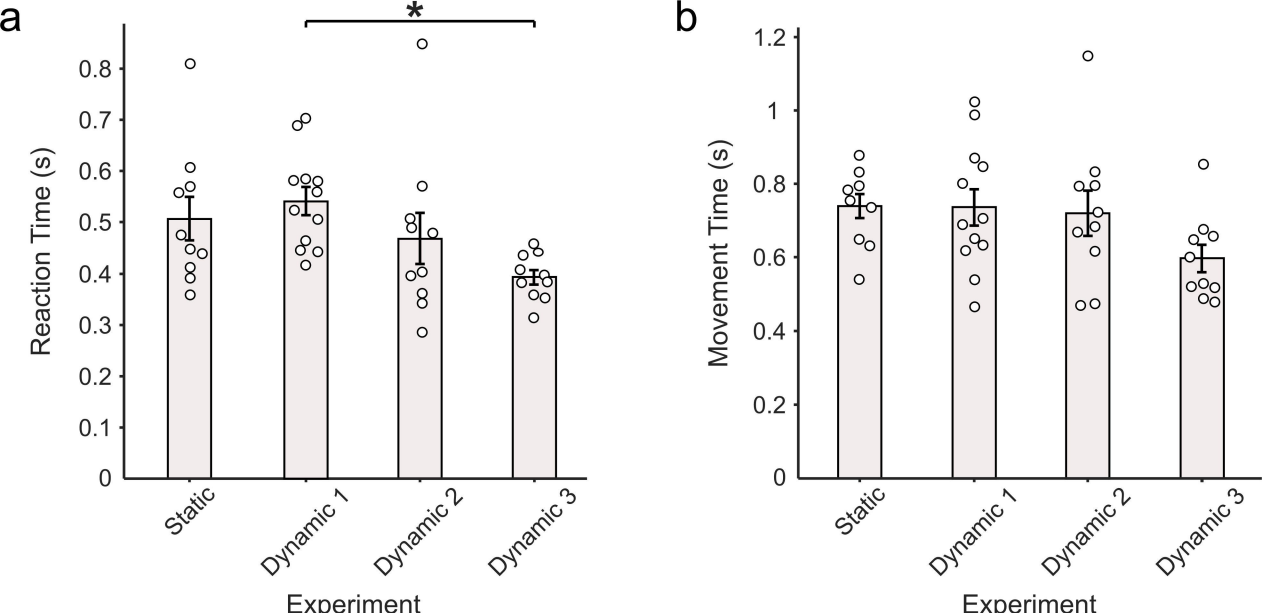
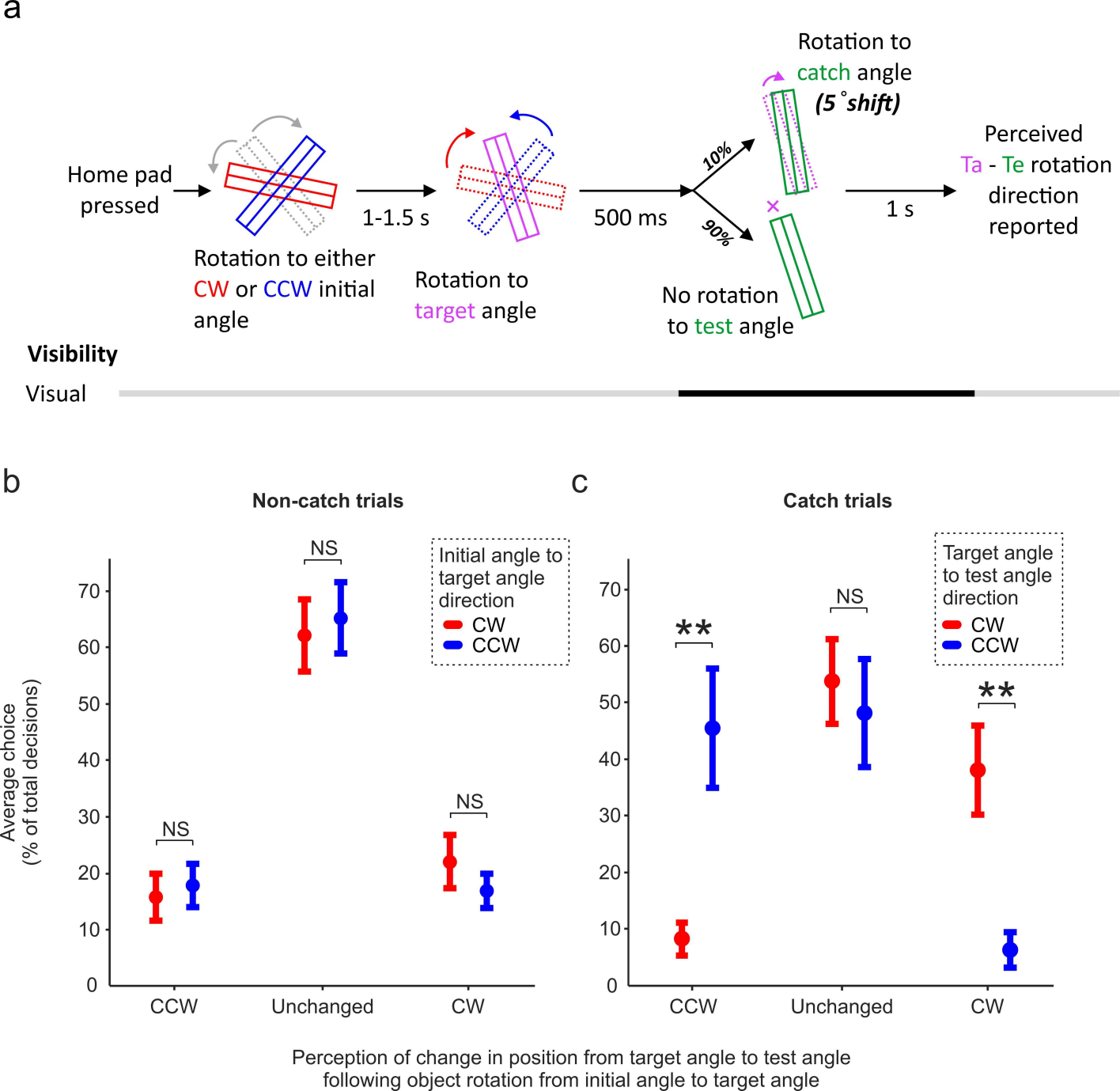
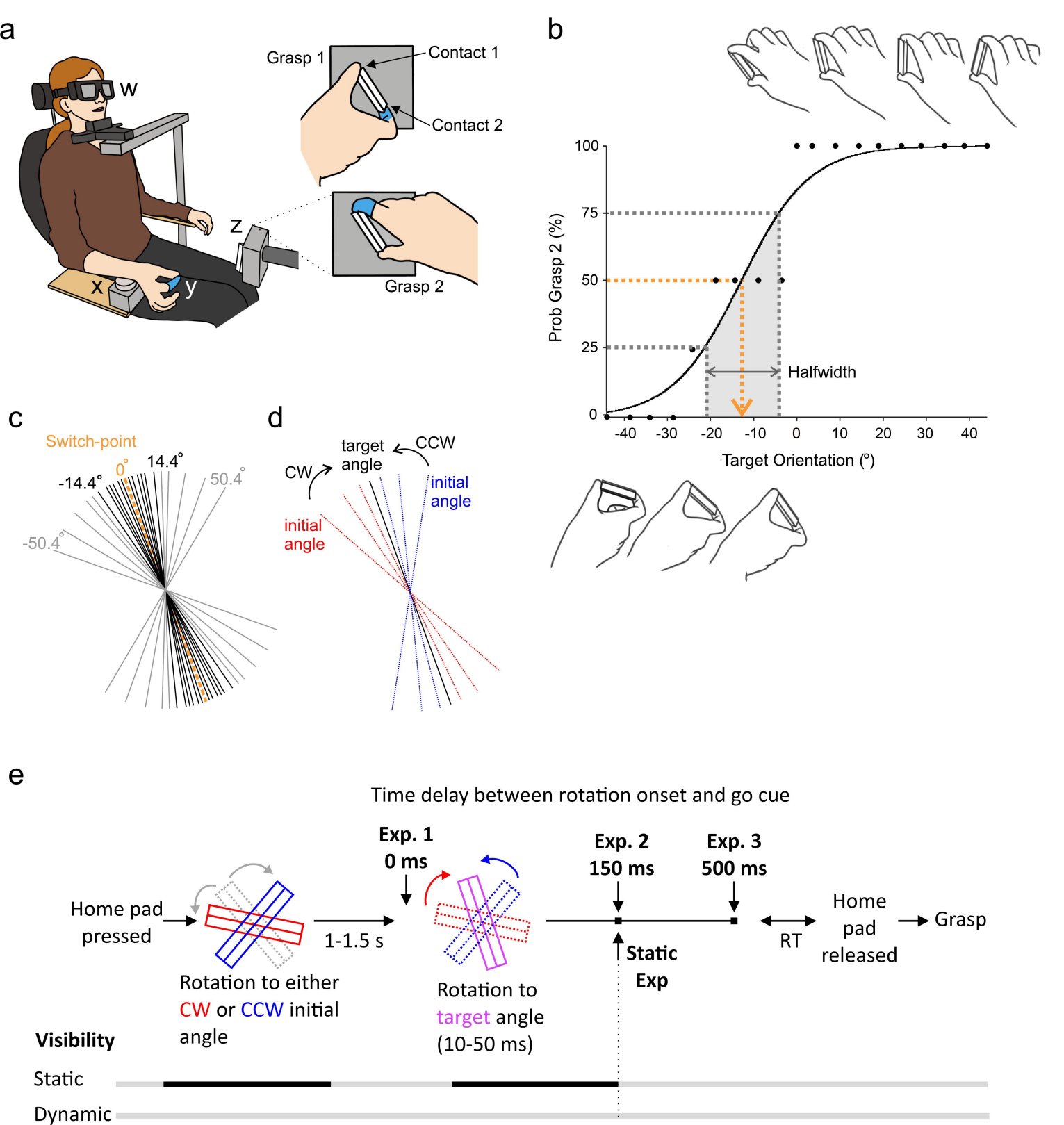
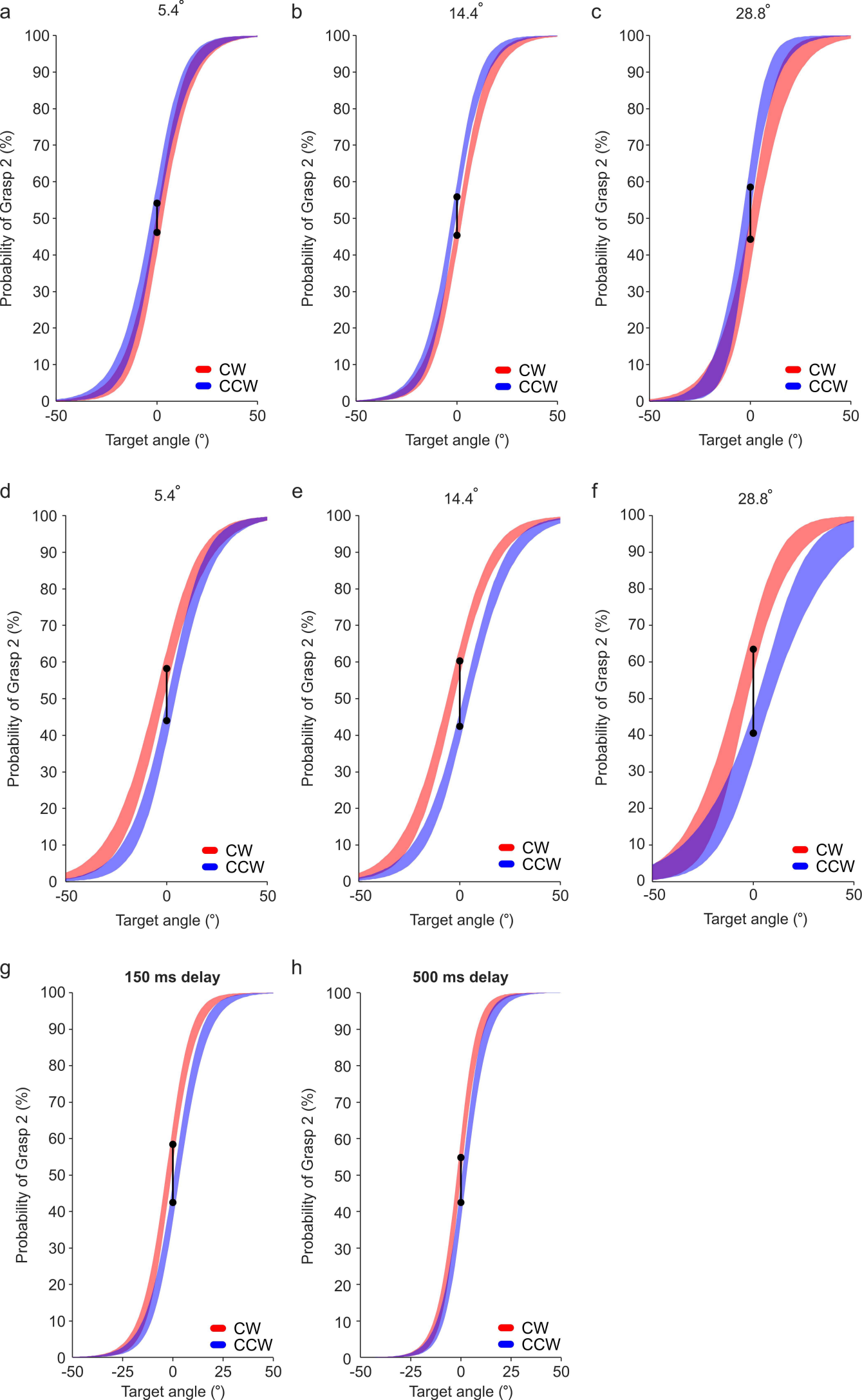

a
*
Reaction Time (s)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Static
Dynamic 1
Dynamic 2
Dynamic 3
Experiment
b
Movement Time (s)
0
0.2
0.4
0.6
0.8
1
1.2
Static
Dynamic 1
Dynamic 2
Dynamic 3
Experiment


a
Home pad pressed
Rotation to either CW or CCW initial angle
1-1.5 s
Rotation to target angle
500 ms
10%
90%
Rotation to catch angle
(5 ˚shift)
No rotation to test angle
1 s
Perceived Ta - Te rotation direction reported
Visibility
Visual
b
Non-catch trials
Initial angle to target angle direction
CW
CCW
NS
NS
NS
Average choice (% of total decisions)
0
10
20
30
40
50
60
70
CCW
Unchanged
CW
c
Catch trials
Target angle to test angle direction
CW
CCW
**
NS
**
0
10
20
30
40
50
60
70
CCW
Unchanged
CW
Perception of change in position from target angle to test angle following object rotation from initial angle to target angle


a
w
z
x
y
Grasp 1
Contact 1
Contact 2
Grasp 2
b
100
75
50
25
0
Prob Grasp 2 (%)
Halfwidth
-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
e
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
RT
Home pad released
Grasp
Static Exp
Rotation to either CW or CCW initial angle
Rotation to target angle (10-50 ms)
Visibility
Static
Dynamic


a
5.4°
b
14.4°
c
28.8°
d
5.4°
e
14.4°
f
28.8°
g
150 ms delay
h
500 ms delay
Probability of Grasp 2 (%)
Target angle (°)
CW
CCW
0
10
20
30
40
50
60
70
80
90
100
-50
-25
0
25
50